THE EFFECT OF FEMALE MATE PREFERENCE ON THE EVOLUTION OF

BATESIAN MIMICRY

Robert A. Krebs

Thesis Submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

MASTERS OF SCIENCE

in

ZOOLOGY

APPROVED:

_____

D. A. West, Chairman

_____   _____

P. B. Siegel   R. D. Fell

May 25, 1986
Blacksburg, Virginia

THE EFFECT OF FEMALE MATE PREFERENCE ON THE EVOLUTION OF BATESIAN MIMICRY

Robert A. Krebs

Abstract

Male and female <u>Papilio glaucus</u> were released in pairs in a flight cage to study courtship behavior and mate choice. The study was designed to test the hypothesis that females select the natural color pattern, an important aspect of the theory of the evolution of mimicry. Males were unpainted or were painted either yellow as a control or black to resemble a newly arisen mimetic pattern. Painted males were permitted three courtships to achieve a mating. Failure to mate was followed by the release of the other color of male to the same female.

The courtship flight was divided into four stages for analysis of sexual selection. Females directed solicitation flights more often to natural color than to black males, and these solicitation flights increased the number of inter-actions and courtships by males. Naturally colored males were rejected less frequently than the black ones in the early stages of courtship. Once the later stages were attained, there was no difference. The higher mating success and in-creased female solicitation which favored the yellow painted males over color-altered ones suggest that female-limited mimicry in <u>P. glaucus</u> is the result of selection by females for the non-mimetic pattern.

Acknowledgements

Several people deserve special recognition for there assistance to me during my research. Foremost, is my advisor, David West, not only for his instruction in genetics and butterflies, but for his patience with my writing. Without his help, the last two years would not have been such a pleasure. My committee members were also very helpful, Richard Fell for his instruction in insect behavior and Paul Siegel who I owe special thanks for his insistence that I change my experimental design to his method, one that allowed me to complete my study in one field season.

Others who were very helpful were Bill Perry who generously provided his time to teach me how to use and remain friends with a computer terminal. Mark Scriber, of the University of Wisconsin, gave me an early start by providing P. glaucus pupae and Ron Rutowski, at Arizona State helped with information on solicitation flights and encouragement to publish. Finally, I would like to thank my parents for their support, either to my morale or finances, when either was waning.

Table of Contents

Introduction

Although mimicry in the Lepidoptera was first identified
in 1862, it is still important for analysing the evolution
of complex adaptations both within and between species. The
evolution of mimicry is dependent on interactions among dis-
tasteful model species, potential predators, and mimicking
species (Vane-Wright, 1979). The numbers of mimetic species
and the different arrangements of mimetic relationships dem-
onstrate the importance of this adaptation.

Mimicry is the copying of a color pattern of one spe-
cies by another to gain protection from predation. Bates
(1862) first identified this phenomenon and proposed that the
copying species is palatable while the one being copied, the
model, is not palatable. The predators misidentify the pal-
atable species and do not attack it. Bates was able to ex-
plain the advantage of this kind of mimicry but could not
give a good general theory for its evolution.

The difficulty in developing a general theory for the
evolution of Batesian mimicry is that mimetic forms differ
among species in their number and distribution between the
sexes. In some species mimicry occurs in both sexes, and may
be either monomorphic or polymorphic. Other species show the
mimicry sex-limited to females, monomorphic or polymorphic,
sometimes including non-mimetic forms. The most complex case
is that of <u>Papilio dardanus</u>, in which males are uniformly

tailed and non-mimetic while most females are tailless and polymorphic for several mimetic forms (Ford, 1936).

The problem of how different distributions of mimetic and non-mimetic forms could evolve in different species received considerable attention during the late nineteenth century because mimicry provided a clear example of the effect of natural selection, and the early Darwinians needed proof for their theory (Remington, 1963). Wallace, Darwin, and Belt all proposed reasons for the evolution of sex-limited mimicry. Their ideas ranged from females having intrinsically more variability than males and, as the egg layers, needing greater protection, to females choosing the normal color pattern of the males when mating (Brower, 1963).

However, an understanding of genetics was needed for a general theory of the evolution of mimicry. The currently accepted theory is a two step process (Fisher, 1958). An initial mutation creates a wing pattern roughly similar to that of a non-palatable species. The new pattern will confuse some predators, providing at least some protection. Because birds can judge minor differences between species, selection will favor modifiers for a more perfect mimic (Duncan and Sheppard, 1965).

The theory can easily account for polymorphisms, as seen in Papilio dardanus, by another mutation changing the initial mimetic form to one mimicking another non-palatable species. If the fitness of the new form is higher than any other when

it appears, its frequency will increase. The polymorphism in P. dardanus evolved by a stepwise set of changes leading from the initial color pattern through many mimetic forms (Clarke and Sheppard, 1959, 1960a, 1960b).

But the simple model does not account for sex-limitation or the persistence of mimic-non-mimic polymorphisms. In the Papilionidae and Pieridae mimicry is frequently female-limited, and this limitation also occurs in other families. In addition, not all of the females in a population need be mimetic. Some populations of Papilio glaucus and P. dardanus have female-limited mimicry with a non-mimetic male-like form as well.

A general theory of mimicry must also explain why certain situations are not seen in nature. Batesian mimics are apparently never male-limited, although Vane-Wright (1984) suggests that Euthalia monina shows a male-limited polymorphism (Fleming plate 47, 1975), nor are there male mimic-non-mimic polymorphisms (Turner, 1978). In some Eurytides species there are polymorphisms in both males and females, but all of the forms are mimetic (West, 1985).

Belt (1874) first stated that females must have had a choice of mates and preferred those of the primordial color pattern. The males with the new mimetic pattern would be unable to mate. The majority of the offspring would be produced from non-mimetic males and, assuming that mimicry provides an advantage, mimetic females. Modifiers would be selected

which repress or eliminate mimicry in males and simultane-
ously enhance it in females. This gene repression is shown
by P. dardanus, which has autosomal genes for mimicry. The
male's genotype is as important as that of the female for
wing color determination of daughters, although the male
color is constant, the mimicry and taillessness being masked.

Therefore, two major questions must be answered to sup-
port Belt's hypothesis. Why should females select against
mimetic males when the latter would increase the number of
mimetic offspring, and why would the males not also select
against mimetic females?

An existing non-mimetic color pattern of a successful
species would serve a general purpose in species identifica-
tion before the mimcry first appeared in the population. This
pattern may also have other functions, as in P. glaucus,
where the black and yellow disruptive pattern is less visible
to predators (Platt et al., 1984).

In natural populations males will approach females of
other species, or any optical stimuli which appear to be
sexually positive (Magnus, 1963). Also, some closely related
species hybridize, showing that interspecific mating does
occur. The females that accept these males waste eggs, energy
and time because they produce infertile offspring. Selection
acts against these females to favor those mating with their
own species. Discrimination leads to a preference for a spe-

cific color pattern used for species identification by visual cues.

Mutations causing changes in the wing pattern of males would decrease their success in courtship because they would not "fit" the sight recognition of the females. With a mutation conferring mimicry, the males would have an increased chance of survival but would still be selected against in mating. The female, limited to the evolved response, could not "determine" that the new pattern is advantageous. Because the females contribute much to offspring production and begin oviposition after the first mating, they should accept a male with the decision to mate and end their search only if the male on hand is better than could be expected from continuing the search. When mimicry first arose, almost all of the males were non-mimetic. A female rejecting a mimetic male could expect to find a male of the normal pattern within a short time and should therefore select against the non-standard form.

The males, which can mate throughout their lives, should mate with as many females as possible to produce the most offspring. Mating with a less than optimal female costs the male at most the time and energy of producing one spermatophore, a lesser loss than for the female whose egg production is limited. Therefore, deviations from the ancestral female color pattern should not greatly inhibit courtship by males (Janetos, 1980).

Several studies show that mimetic females of <u>Papilio</u> <u>glaucus</u> are not at a disadvantage in offspring production in relation to the male-like form. Burns (1966) collected females from the wild and counted spermatophores as a measure of mating frequency. He found an average of 2.08 spermatophores in the yellow morphs and only 1.69 spermatophores in the mimetic black morphs. Platt <u>et</u> <u>al</u>. (1984), however, found no difference in mating frequency between the two morphs but did suggest a more important factor. All of the females captured in the original study and 99% of those in the later one had at least one spermatophore, with no differences between the two colors. Levin (1973) showed that one spermatophore in <u>P. glaucus</u> is sufficient for the fertilization of all of the eggs, so the number of matings, even if different, may not be important.

Two methods for the evolution of sex-limited mimicry have been proposed by Turner (1978): the sieve and the modification method. The sieve method presumes that a large number of genes within the population are able to code for changes. in wing pattern. Some of these changes could give a resemblance to another species which is not palatable to predators. Female limitation of the mimicry is due to sexual selection restricting the genes which increase in frequency to those which provide mimicry exclusively to females. Genes which change the wing pattern of the male are not selected because those males are deficient in courtship. The second

hypothesis presented by Turner is for modification of the
genes for mimicry. Again sexual selection is a factor, as the
genes for mimicry spread through the population in both
sexes. Modifiers are selected which repress the expression
of the mimicry in the male and accent its expression in the
female. The mimicry remains sex-limited to females and, as
in nature, male-limited mimicry is completely absent in
Batesian mimics (Turner, 1977, 1978).

The description of the evolution of Batesian mimicry is
presented in figure 1, p. 27 (modified from Turner, 1978),
which outlines the effect of the ratio of mimics to models
and sexual selection on the fitness of mimics and non-mimics
of both sexes. In this figure, fitness increases along the
Y axis and the mimic-to-model ratio along the X axis. The
fitness of the mimics decreases with frequency because
mimetic advantage is proportionately higher with lower
mimic-to-model ratios. The fitness of the non-mimic is con-
stant relative to the frequency of models. Additionally, the
fitness of the mimetic female is always greater than the
fitness of the mimetic male because of sexual selection
against the new male form.

Combining these factors, female mimics have a higher
fitness than female non-mimics at low mimic-to-model ratios
while the male mimic is always less fit than the non-mimic.
When the mimicry arose, the mimic-to-model ratio was low, so

the mimetic females and non-mimetic males were most fit. Given this situation, female-limited mimicry would evolve.

Note from the diagram that at higher mimic-to-model ratios, the fitness of the female mimics falls below that of the non-mimetic form. At a high population density, selection would favor male-like forms and the developement of a dimorphic female population.

Also, the theory does not deny the possibility of monomorphic Batesian mimicry. It could arise where either sexual selection is not a major factor, as in species which use pheromones for identification, or if the mimetic advantage is great enough to overcome sexual selection against mimetic males. For a detailed review of the dynamics and evolution of a mimetic population see Turner (1977, 1978, 1985).

The theory's one serious weakness is the lack of evidence for female mate choice. Silberglied (1978) showed that Colias eurytheme females preferred males which reflected ultraviolet light, and Silberglied (1977), Turner (1978), and Rutowski (1984) believe that sexual selection by females is most likely responsible for the evolution of female-limited mimicry in butterflies. There is however, no experimental evidence for mate choice based on color.

Due to this lack of evidence, Silberglied (1984) later suggested that the factor stabilizing male color is intra-sexual communication between the males. His hypothesis is

based on observations of male aggregations at mud puddles and fighting for receptive females or for territories. However, as in the sexual selection model "no one has performed an experiment to determine if color may affect the outcome of intermale combats between butterflies" (Silberglied, 1984).

Here I report experiments which suggest that females do make choices when mating and that their preference is for the naturally occurring male color pattern.

Methods and Materials

Rearing Methods

Eggs were collected from wild caught females of _Papilio glaucus_ (Virginia) and adults sent by Dr. Mark Scriber of the University of Wisconsin (Wisconsin and Illinois). The larvae were reared on fresh black cherry leaves (_Prunus serotina_) in the laboratory during the spring and summer of 1985 under a long photoperiod to prevent diapause. Approximately 300 adults were available for the field study.

Presentation Methods

The experiments were carried out in a flight cage (5x8x5 m) in Blacksburg, Virginia.

A single virgin female of the black mimetic or yellow male-like form was randomly presented with a male painted either black, to resemble a newly arisen mimic, or yellow, as a control. Three courtship flights were allowed for the male to mate. If the first male failed, he was replaced by a male of the other color. If no mating occurred after three courtship attempts by the second male, the experiment was terminated.

To control for effects due to painting, females were tested with unpainted males during the Spring of 1984 and 1985. Age of the butterflies was controlled by presenting a female with a second male of the same age if the first was

rejected and by using two females of the same age on any given day, each presented first with a different male form. Generally, females were one to two days old and males two to four. By performing even numbers of presentations each day, major weather variation was also eliminated.

Painting Methods

Males were painted with either black or yellow paint. Testors Flat Enamel 1149 Black was used to simulate the new mimetic form while the controls were painted with Testors Gloss Enamel 1112 Light Yellow. The paint was diluted to one half concentration with Testors 1156 Brush Cleaner and applied to both sides of the fore and hind wings except the area within three milimeters of the thorax and the outer dark edges. Two methods were used for applying the paint, spraying the wings with a Badger Air Brush model no. 200-3 or stroking lightly in the same direction as the overlap of the scales with a small artist's brush.

The black painted males resembled mimetic females but without the blue on the hind wings. The yellow painted males retained the black-striped yellow wing pattern. Both painted and unpainted males were photographed using a Wratten 18A filter which only passed UV light, to test for changes to the wing-pattern outside of the visible spectrum. Unpainted P. glaucus males reflect UV light from their ventral surfaces only (see Platt et al. 1984 for photographs). Painted males

lacked this reflectance. The responses of females to the two
color patterns were tested in 2 x 2 contingency tables by
chi-square using Yates's correction (Bailey, 1959).

Results and Discussion

The courtship behavior of butterflies is important when considering the evolution of sex-limited mimicry. Because the focus of this paper is on sexual selection, much of the detail of the courtship behavior has been omitted, while that which shows differences between the painted male forms has been accented for comparing mating success.

In a species such as <u>Papilio glaucus</u>, mate recognition may be based entirely on visual cues. In the wild, males fly about pursuing and courting any females they see (Brower, 1959). If the female has no opportunity to reject a male, then sexual selection cannot be a factor in the evolution of male wing-color. Where the female can make a choice, and that choice is based on an optimally stimulating color pattern, the evolution of male wing color may be highly dependent on the ability to attract mates.

Courtship in <u>P. glaucus</u> involves an exchange of behavioral responses between the sexes. The courtship flight, once begun, does not always lead to a successful mating, nor have all successful courtships involved all of the observed behaviors and responses.

The basic courtship flight appeared to begin when a female was sighted by a male. He approached her while she, in response, flew high and away with the male pursuing. After a paired flight highly variable in length, the female landed

on a high perch and the male hovered above her for a second or two and alighted laterally. The male then extended his abdomen, contacted the female's genitalia, and if accepted, moved posteriorly to the female facing the opposite direction and relaxed. They remained paired for 45 minutes to an hour. There was no post-nuptial flight as seen in the queen butterfly, Danaus gilippus berenice, probably because the tiger swallowtail mates high in the trees while the queen mates on the ground and the male carries the female to a site as high as 25m to complete the passing of the spermatophore (Brower, Brower, and Cranston, 1965).

Physical contact during the courtship of P. glaucus was rare except for the brushing of wingtips when the male pursued the female along the cage top 5m high. Occasionally, the male contacted the female's body from below. I rarely observed any contact of the male with the female's antennae, which suggests that the males do not use contact pheromones.

To analyze the importance of the courtship flight for successful mating, I divided the sequence into four stages. These stages are based primarily on the behavior of the female, which appeared to control the direction and style of flight and to provide the male with the opportunity to continue to the next step. These four stages were:

I. The female appeared or presented herself to the male which flew towards the female.

II. The female flew upward and away, followed by the male 10 to 25 cm below and behind the female.

III. The female alighted on vegetation or the cage wall, wings either partly open or more commonly, closed. The male responded by hovering over the female a second or two and attempted to land beside her.

IV. The female remained motionless and allowed the male to land and to copulate.

The recognition of these four stages is useful because male color pattern may vary in importance during courtship. The color-pattern may be used by females for species identification only early in courtship, while other factors are used later. If selection occurs only early in courtship, differential female behavior should be identifiable in courtship initiations and rejections during the paired flight but may not be discernible in the later stages of courtship.

Female mimetic and male-like forms were presented to unpainted males, yellow painted control males, and black painted males which resembled the mimetic females (see table

1.). The unpainted males mated in 16 of 30 presentations and yellow painted males in 18 of 36, showing no effect on mating due to painting. Unpainted and yellow painted males were therefore combined. The two female forms were also combined for comparing painted males because yellow males were equally successful with yellow or black females ($X^2=0.51$, $P>0.5$), as were black males ($X^2=0.1$, $P>0.7$).

If females select for the natural male color pattern, yellow males should mate more often than color-altered males independently of female color. Under the test conditions, males of the natural pattern mated in 34 of 66 presentations and black males in 13 of 36, a difference favoring the natural pattern but not significantly ($P>0.1$). However, the test conditions required a male to court a female three times before the mating was scored as completed or not. Unfortunately, this requirement forced the preference test to begin at stage II of the courtship sequence, and males which failed to perform paired flights of a measurable length were not included in the test.

The initial interaction (stage I) may be the most important for color preference in nature because it brings the male and female together from a distance. Crane (1955) and Brower et al. (1965) have shown the importance of color for courtship in the diurnal Lepidoptera. Sight is used for species identification and finding conspecifics (Silberglied, 1977). Although research on the distance vision of

Lepidoptera is minimal, Silberglied (1984) suggests that determination of specific patterns is possible only at close range, although visual range is enhanced by motion and brightness of the object. No interactions occurred in the cage from farther away than about two meters. With this limitation, the behavior of the female may be very important for increasing the number of interactions between the sexes.

The behavior of P. glaucus females which increased the number of interactions was the solicitation flight: a flight which brought her close in front of the male. Contact of wings and actual pursuit of the male were common.

Solicitation flights differed from random flights. They were generally made directly to a male in flight, although males perching in the sunlight were also solicited. The female flew across from either the top or the side of the male and passed by him within 15 cm, turned, and flew up and away. When the male did not pursue, the sequence was usually repeated.

Female solicitation flights have also been observed in Pieris protodice (Rutowski, 1980), Heliconius erato (Crane, 1955), and Danaus gilippus (Brower et al., 1965). Rutowski (pers. comm.) has suggested that the function of solicitation flights by virgin females is for "making them conspicuous to males and in nature probably involves flights out from perches where they have been hardening their wings and [were] undetected." Solicitations may help Colias females obtain

additional spermatophores while searching for oviposition sites in alfalfa fields, and solicitation flights may also prolong courtship in weakly motivated males (Rutowski et al., 1981).

Table 2 shows the differences in solicitation flights toward the two male forms. In 66 of 144 presentations, at least one solicitation flight was observed. These presentations included those in which the male courted continuously or mated quickly, making it difficult to recognize a solicitation flight. The number of observed solicitation flights may therefore be lower than that expected in nature because of the increased number of chance interactions in the limited area of the flight cage. However, those males which failed to initiate courtship became ideal subjects for observing differences in the frequency of solicitations by females to the two male color forms.

Among males that mated there was no significant difference in frequency of solicitations between the two color forms. For those males that actively courted females, the frequency of female solicitation was greater toward yellow males but differed at $.05 < P < 0.1$. Where males did not court, the frequency of solicitations toward yellow males was much higher than toward black males ($P < .001$). In addition, considering only initial interactions, solicitation flights by females were more common toward yellow than toward black males ($P < .01$).

The results show that female solicitation occurred more
frequently to the tiger-striped males than to the color-
altered black males. Rutowski (pers. comm.) suggests that
in the field these flights may occur more often to receptive
males and I have observed relatively few solicitations lead-
ing directly to copulation because of the lower receptiveness
of some males in the cage.

In addition to selection at the level of courtship ini-
tiation, the female must be able to reject males once ap-
proached. Males used in the original selection test were
actually those that had reached stage II of courtship, the
pursuit flight. Do females reject males in the remaining two
stages of courtship: (III), the female landing on vegetation
and (IV), the actual acceptance of the male?

Female rejection included postures and behaviors for
avoiding courtship and escaping from pursuit flights. Two
such postures were closing and depressing the wings to hide
from a male, and holding the abdomen against a surface when
a male landed to prevent copulation. Three rejection behav-
iors during the pursuit flight were "quick landing," a sudden
stop with wings closed and depressed; "dropping," a relaxed
free fall into brush; and a slow descending flight which
caused the male to abandon pursuit when the female hovered
less than 30 cm from the ground. Two less obvious forms of
rejection were flying through thick brush (also frequently
observed by Brower et al., (1965) in D. gilippus) and simply

not flying at all, a behavior I observed when I released fe-
males in the cage with a high density of males. Virgin fe-
males have been observed to reject males by like means in
other species (Rutowski, 1982).

Yellow males were more successful than black males in
reaching stage III after a pursuit flight (Table 3, P<.05).
Brower et al. (1965) noted that females of the queen
butterfly also rejected males by refusing to land during the
courtship flight and that mate choice may occur at this
stage.

To test for selection at the last stage of courtship,
the mating success of those males which reached stage III was
analyzed. The difference between yellow and black males is
non-significant but in the same direction as all of the other
tests, favoring males of the natural color pattern.

To estimate the importance of color pattern in
courtship, the relative fitnesses of the two male color forms
were computed based on the relative probability of initially
interacting with a conspecific (suggested by solicitation
differences) and the relative probability of mating once
courtship ensued. In both cases I have considered the fitness
of the natural form to be one and have related the fitness
of the black form to it.

The difference in stage I of courtship was derived from
the solicitations leading to the initial interactions.
Thirty-seven percent of the first interactions with yellow

males were female initiated and 63 percent male initiated. Courtship interactions begun by males are independent of male color, so the 63 percent was used as an estimate of the frequency of male-initiated interactions of black males. However, only 11 percent of the interactions with black males were female initiated. This difference between the two male forms represents interactions in nature begun by a female not seen by a male. Yellow males are solicited more than black males, providing them with more interactions and thus a greater opportunity to mate. Therefore the relative frequency of interactions for the two male forms is .63 + .37 = 1.00 for yellow males but only .63 + .11 = .74 for black males.

The probabilities of mating once courtship has begun are shown in Table 3. These values are 0.374 for yellow males and 0.245 for black. Setting the probability for yellow males at 1.00, the relative probability for black males is 1/.374 x .246 = 0.66. Taking the product of these partial fitnesses gives a relative fitness in courtship for yellow males of 1 x 1 = 1 but for black males only .74 x .66 = .49, about one half that of yellows. A difference of this magnitude would most likely prevent the establishment of a new male form in a population despite any advantage that form provided in survival.

Conclusion

Selection by females for the natural tiger-stripe pattern of male <u>Papilio glaucus</u> was observed at the level of solicitation for courtship, stage I, and by the frequency with which females landed during the paired flight, stage II. Lesser differences which also favored the yellow males were present in the later stages of courtship. However, the experimental requirement of three courtship flights of a measurable length before mating success was recorded elimated any obvious test for selection at courtship initiation, possibly the most important limitation to males deviating from the natural color pattern. Also, the behavioral interactions begun after chance meetings in the limited area of the flight cage were capable of overriding selection against the altered males, but still did not increase the mating frequency to equal that of yellow males.

Therefore, I conclude that for species which use visual cues as a major part of communication in courtship, males are dependent on an optimal color pattern to attract and induce females to mate. Males deviating from that pattern will not mate at a frequency which will maintain that genotype in the population despite the survival advantage a new form may provide. The evidence for sexual selection against a change in the male's wing pattern in <u>P. glaucus</u> supports the current

model for the evolution of sex-limited mimicry first proposed by Belt.

Literature Cited

Bailey, Norman. T. J. 1959. Statistical Methods in Biology. The English Universities Press, Ltd. London, 200 pp.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society, 23:495-566.

Belt, T. 1874. The Naturalist in Nicaragua. J. Murray, London, 402 pp.

Brower, L. P. 1959. Speciation in butterflies of the Papilio glaucus group. II. Ecological relationships and inter-specific sexual behavior. Evolution, 13:212-228.

Brower, L. P. 1963. The evolution of sex-limited mimicry in butterflies. International Congress of Zoology, 16(4):173-179.

Brower, L. P., J. V. Z. Brower, and F. P. Cranston. 1965. Courtship behavior of the queen butterfly Danaus gilippus berenice. Zoologica, 50:1-39.

Burns, John M. 1966. Preferential mating versus mimicry: Disruptive selection and sex-limited dimorphism in Papilio glaucus. Science, 153:551-553.

Clarke, C. A. and P. M. Sheppard. 1959. The breeding of Papilio dardanus Brown in England: techniques and some results. Entomologist, 92:89-95.

Clarke, C. A. and P. M. Sheppard. 1960a. The evolution of mimicry in the butterfly Papilio dardanus. Heredity, 14:163-173.

Clarke, C. A. and P. M. Sheppard. 1960b. The genetics of Papilio dardanus Brown I. Genetics, 45:439-457.

Crane, J. 1955. Imaginal behavior of a Trinidad butterfly, Heliconius erato hyadara Hewitson with special reference to the social use of color. Zoologica, 40:167-196.

Duncan, C. J. and P. M. Sheppard. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. Behaviour, 24:269-282.

Fisher, R. A. 1958. The Genetical Theory of Natural Selection. Dover, New York, 291 pp.

Fleming, W. A. 1975. Butterflies of West Malaysia and
    Singapore, vol. 1. E. W. Classey Limited, Berkshire,
    64 pp.

Ford, E. B. 1936. The genetics of _Papilio dardanus_ Brown
    (Lep.). Transactions of the Royal Entomological Society,
    London, 85:432-466.

Janetos, A. C. 1980. Strategies of female mate choice: A
    theoretical analysis. Behavioral Ecology and
    Sociobiology, 7:107-112.

Levin, M. P. 1973. Preferential mating and the maintenance
    of the sex-limited dimorphism in _Papilio glaucus_: Evi-
    dence from laboratory matings. Evolution, 27:257-264.

Magnus, D. B. E. 1963. Sex-limited mimicry II - Visual se-
    lection in the mate choice of butterflies. International
    Congress of Zoology, 16(4):179-183.

Platt, A. P., S. J. Harrison, and T. F. Williams. 1984. Ab-
    sence of differential mate selection in the North Amer-
    ican tiger swallowtail, _Papilio glaucus_, pages 245-250
    _in_ R. I. Vane-Wright and P. R. Ackery, eds. The Biology
    of Butterflies. Symposium of the Royal Entomological
    Society, London, No. 11.

Remington, C. L. 1963. Historical backgrounds of mimicry.
    International Congress of Zoology. 16(4):145-149.

Rutowski, R. L. 1980. Courtship solicitation by females of
    the checkered white butterfly, _Pieris protodice_. Behav-
    ioral Ecology and Sociobiology, 7:113-117.

Rutowski, R. L. 1982. Mate choice and Lepidopteran mating
    behavior. Florida Entomologist. 65:72-82.

Rutowski, R. L. 1984. Sexual selection and the evolution of
    butterfly mating behavior. Journal of Research on the
    Lepidoptera, 23:125-142.

Rutowski, R. L., C. E. Long, L. D. Marshall, and R. S. Vetter.
    1981. Courtship solicitation by _Colias_ females
    (Lepidoptera: Pieridae). The American Midland
    Naturalist, 105:334-340.

Silberglied, R. E. 1977. Communication in the Lepidoptera,
    pages 362-402 _in_ T. A. Sebeok, ed. How Animals Communi-
    cate. Indiana University Press, Bloomington.

Silberglied, R. E., and O. R. Taylor. 1978. Ultraviolet reflection and its role in the courtship of the sulfur byttterflies Colias eurytheme and C. philodice. (Lepidoptera: Pieridae). Behavioral Ecology and Sociobiology, 3:203-243.

Silberglied, R. E. 1984. Visual communication and sexual selection among butterflies, pages 207-223 in R. I. Vane-Wright and P. R. Ackery, eds. The Biology of Butterflies. Symposium of the Royal Entomological Society, London, No. 11.

Turner, J. R. G. 1977. Butterfly mimicry: The genetic evolution of an adaptation. Evolutionary Biology, 10:163-197.

Turner, J. R. G. 1978. Why male butterflies are non- mimetic: natural selection, group selection, modification and sieving. Biological Journal of the Linnean Society, London, 10:385-432.

Turner, J. R. G. 1985. Mimicry: The palatability spectrum and its consequences, pages 141-161 in R. I. Vane-Wright and P. R. Ackery, eds. The Biology of Butterflies. Symposium of the Royal Entomological Society, London, No. 11.

Vane-Wright, R. I. 1979. Towards a theory of the evolution of butterfly colour patterns under directional and disruptive selection. Biological Journal of the Linnean Society, London, 11:141-152.

Vane-Wright, R. I. 1984. The role of pseudosexual selection in the evolution of butterfly colour patterns, pages 251-253 in R. I. Vane-Wright and P. R. Ackery, eds. The Biology of Butterflies. Symposium of the Royal Entomological Society, London, No. 11.

West, D. A. 1985. The Batesian polymorphic butterfly Eurytides lysithous. National Geographic Society Research Reports, 21:501-506.

Figure 1. Relative fitnesses of male and female butterflies when sexual selection against a new mimetic wing-pattern is greater for males (modified from Turner, 1978).
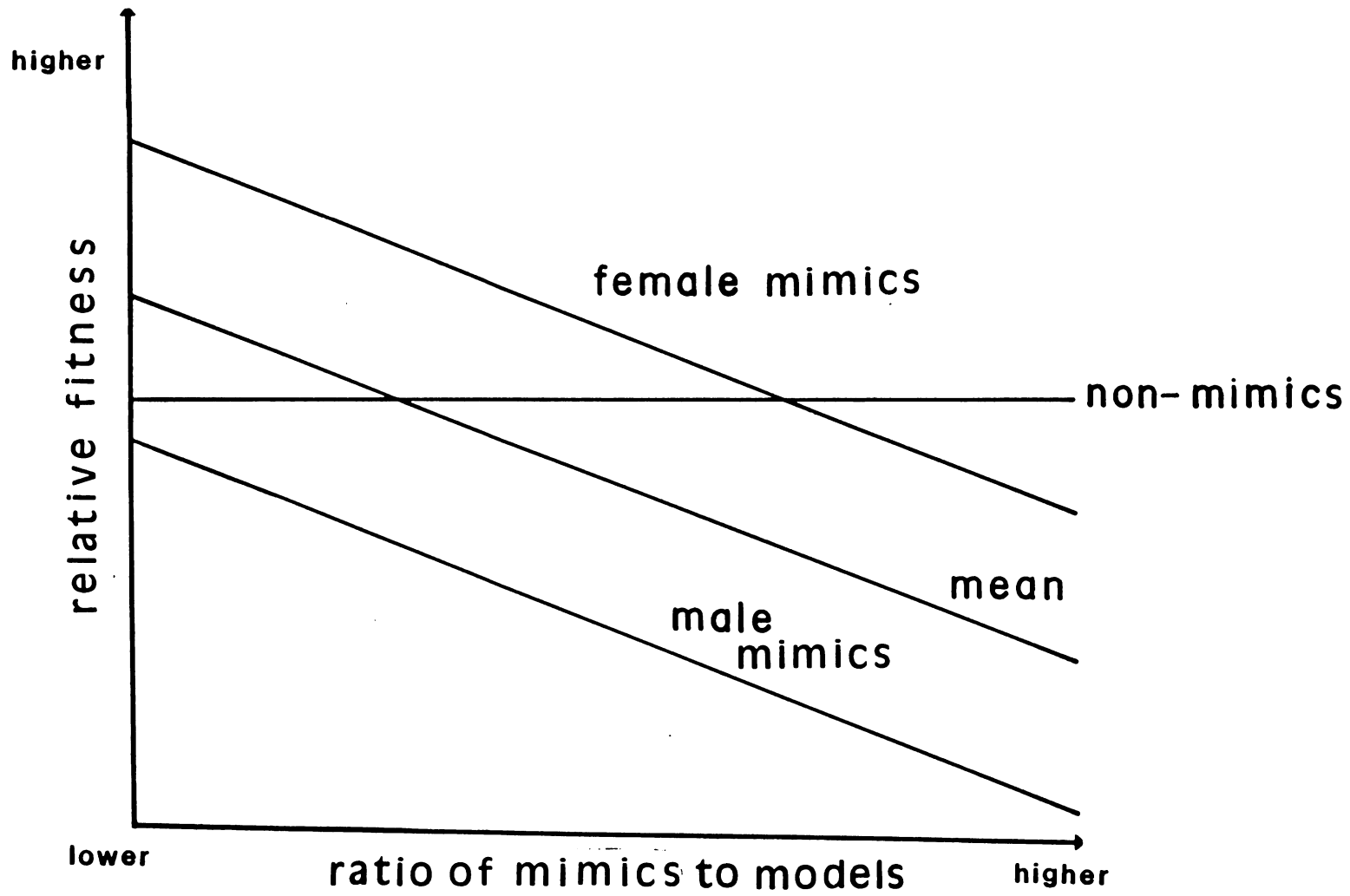
Table 1. **Mating success of male and female forms of <u>Papilio</u> <u>glaucus</u> when the males courted the females three times.**

	MALES					
	Yellow (unpainted control)		Yellow (painted control)		Black (experimental)	
	mated	not mated	mated	not mated	mated	not mated
FEMALES						
Black	10	10	11	6	5	9
Yellow	6	4	7	12	8	14
Total	16	14	18	18	13	23

Table 2. Frequencies of Solicitation Flights in P. glaucus by females toward yellow, control males and black, experimental males.

	yellow males	black males
Among all presentations	.59 (91)	.23 (53)***
Among males that courted	.49 (65)	.28 (36)¢
Among males that did not court	.85 (26)	.12 (17)***
Among males that mated	.53 (34)	.31 (13)
Among initial interactions	.37 (73)	.11 (45)**

*** $p<.001$, ** $p<.01$, ¢ $.05<p<0.1$

() denotes sample size

Table 3. Frequency of males of <u>P. glaucus</u> reaching various stages of courtship from the previous stage.

	yellow males	black males
Number released	91	53
Reaching Stage II	.71 (65)	.68 (36)
Reaching Stage III	.86 (56)	.67 (24)*
Reaching Stage IV	.61 (34)	.54 (13)
Total Frequency of Mating	.374 (34)	.245 (13)

* $P < .05$

( ) denotes number reaching that stage

The vita has been removed from
the scanned document