

Mate choice in the polymorphic African swallowtail butterfly, *Papilio dardanus*: male-like females may avoid sexual harassment

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Abstract. *Papilio dardanus*, the African swallowtail butterfly, is a species with a female-limited polymorphism for wing colour pattern. Females of the subspecies *P. dardanus tibullus* on Pemba Island, Tanzania, occur as three genetically distinct morphs; a black and white Batesian mimic (*hippocooides*), a black and yellow male-like morph (*trimeni*) and a morph that is similar to *trimeni* but with orange wing-patches (*lamborni*). Male mate choice was studied by recording the responses of wild males first to simultaneously presented pairs of pinned dead females, second, in sequential choice tests where only a single female was presented at a time, and third, during focal follows of wild females. From a distance males consistently preferred the Batesian mimic, *hippocooides*, above the andromorph, *trimeni*, and *trimeni* above the third morph *lamborni*. Preference correlated both with the frequencies of the morphs and their colour, the more common brighter morphs being preferred. It is proposed that the *hippocooides*, *trimeni* and possibly also *lamborni* morphs are maintained in a stable polymorphism by different frequency-dependent selective advantages. The morph *hippocooides* supposedly have low predation because of Batesian mimicry (frequency-dependent) but suffer costly harassment by males, whereas *trimeni* avoid this harassment through male mimicry (possibly also a frequency-dependent advantage) but are not protected from predators. The third morph, *lamborni*, which suffers the lowest levels of harassment, may gain this advantage by mimicking the orange coloration of ageing males.

The explanation of genetic polymorphism is a perennial challenge to evolutionary biologists. A particularly striking example occurs in the African swallowtail butterfly, *Papilio dardanus* Brown. In this species females are geographically variable and generally polymorphic for wing colour pattern with up to five morphs existing sympatrically, whereas males are monomorphic and share the same basic colour pattern in all areas (Ford 1936). The genetic basis of this female-limited polymorphism in *P. dardanus* is now well understood (Ford 1936; Clarke & Sheppard 1960; Clarke et al. 1985). However, little empirical work has been directed at understanding the evolutionary forces that maintain it.

The classical explanation of polymorphic Batesian mimicry suggests that where a suitable range of model species exists, polymorphism reduces the diluting effect that Batesian mimics have on each of the noxious models. This is advantageous to the

mimics because the aversive associations formed by predators between colour pattern and noxiousness will be weakened less, and individual mimics will thus gain better protection (e.g. Ford 1965). In some subspecies of *P. dardanus* (e.g. *meseres* Carpenter) all female morphs appear to be Batesian mimics, but in others a non-mimetic female morph with male-like coloration (or 'andromorph') exists which cannot be explained in this way. Two classes of hypotheses have been suggested to explain the stable maintenance of both Batesian mimics and andromorphs within a single population. The first class of explanations relies on constraints to the degree of perfection that natural selection can achieve (Dawkins 1982), in that the presence of morphs in an area may not be due to selection favouring them. For example, Ford (1965) believed that andromorphs may be maladapted homozygotes maintained solely by the superior fitness of mimetic heterozygotes. Another plausible possibility is that stable polymorphisms of andromorphs and mimics may be maintained by gene flow from areas where only one of the morphs is present.

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The second class of explanations seeks to explain the observed polymorphisms as the result of natural selection individually favouring all of the morphs. Two specific hypotheses have been proposed, both of which claim a direct advantage to andromorphs through sexual selection. (1) The pseudosexual selection hypothesis (Vane-Wright 1984; see also Clarke et al. 1991; Vane-Wright & Smith 1991) suggests that andromorphs gain a selective advantage because males initially mistake them for other males and approach them in order to engage in aggressive interactions or other activities such as communal mud puddling. The andromorphs then gain a mating advantage because males switch to sexual behaviour when close. Theoretically, females may gain from encouraging multiple matings if this increases fertilization success (Lederhouse & Scriber 1987; Watanabe 1988), enables sperm competition (Drummond 1984), or provides nutrients directly (Boggs & Gilbert 1979; Boggs 1981; Boggs & Watt 1981). Multiple matings do occur in some butterfly species (e.g. Pliske 1975; Drummond 1984), including probably *P. dardanus* (Clarke & Sheppard 1962). Burns (1966) found that *P. glaucus* andromorphs contained 20% more spermatophores than the other mimetic morph indicating that the andromorph was mated more frequently. This observation is consistent with the pseudosexual selection hypothesis but does not demonstrate any advantage to multiple matings. (2) The male avoidance hypothesis (Conrad & Pritchard 1989) suggests that when excessive copulations are disadvantageous to females andromorphs may gain by avoiding male harassment. Although forced copulation has rarely been reported in butterflies, the monarch, *Danaus plexippus*, being the only species for which this has been described (Pliske 1975; Rothschild 1978), courtship can be time consuming, physically damaging, and may increase the dangers of predation (Drummond 1984). In several butterfly species mated females show behavioural or chemical adaptations to deter males (Shapiro 1970; Gilbert 1976; Wiklund 1977; Wiklund & Forsberg 1985), and in the damselfly, *Ischnura ramburi*, a cryptic female morph appears to be in balance with a conspicuous andromorph that avoids male harassment by male mimicry but suffers higher predation risk (Robertson 1985).

In this study we aimed to test the latter two hypotheses and ascertain whether a fully adaptive explanation can plausibly account for the existence

of both mimetic and andromorph females in *P. dardanus*. The two hypotheses make opposing predictions about the preferences males should show for the different female morphs: pseudosexual selection predicts that andromorphs should be approached in preference to the mimics and male avoidance predicts the opposite. We tested these and other predictions by studying the approach behaviour of wild males to both pinned dead females and live wild females in a polymorphic population of *P. dardanus tibullus* Kirby on Pemba Island, Tanzania.

MATERIALS AND METHODS

The Study Population

We conducted experiments during July and August 1989 at a study site consisting of a series of strips of meadow bordering the Mwituu forest in the Micheweni district of northeast Pemba. Large numbers of *P. dardanus* came out of the forest canopy to feed on the flowers in the meadow in the morning, making the butterflies easy to observe and catch. Throughout the study we caught butterflies using standard hand held butterfly nets, and marked them by placing small dots on the wings with waterproof overhead projector pens (Steadler Lumocolor 318). The three female morphs encountered were: *hippocoonides*, an apparent Batesian mimic closely resembling the black and white noxious danaid *Amauris niavius dominicanus* Trimen (which was common in the same area); *trimeni*, an andromorph with black and yellow wing patterning similar to that of males, but readily distinguishable by the lack of tails on the hind wings; and *lamborni*, a rare morph similar to *trimeni* but with large orange patches in place of much, but not all, of the yellow. These three genetically distinct morphs were previously known to be present on Pemba from collections at the British Museum (Natural History), and from breeding experiments conducted on *P. dardanus* collected on Pemba reported by Clarke et al. (1985). In a preliminary mark and recapture study, local population size was estimated using Lincoln's Index (Southwood 1966) at 734 individuals (± 122.5 for 95% confidence limits), of which approximately 20% (67 out of 341) were female. Further concentrated female captures revealed morph frequencies of approximately 80% *hippocoonides*, 16% *trimeni* and 4% *lamborni* ($N = 282$).

We noticed considerable variation in the colour of the yellow portions of the wings of both males and *trimeni* females, with apparently older butterflies appearing more orange than yellow (*lamborni* were always easily distinguished from orange *trimeni* by the dark colour and discrete nature of their orange patches). This assumed relationship between colour and age is based on two observations, first that orange males had more damaged wings than yellow males, and second that the proportion of orange individuals amongst the butterflies recaptured 1 and 2 weeks after the initial capture increased (unpublished data). The colour change was probably caused by exposure to the sun since a dead yellow male and a yellow *trimeni* with one wing exposed to the sun and the other covered by aluminium foil showed a similar change to orange in the exposed wing after 2 weeks. Henceforth we refer to markedly orange males and *trimeni* females as 'faded'.

Simultaneous Choice Experiments

To investigate the response of free-ranging males to the various female colour patterns we simultaneously presented them with pairs of complete, recently dead females with their wings open as if basking. The two test stimuli were pinned 50 cm apart on the wire arms of an apparatus consisting of a stake 1 m high with a dividing partition board (20 × 30 cm) placed between the arms designed to ensure that whilst approaching males could initially see both stimuli, they were forced to choose between approaching one or the other when close-to.

In 10 separate comparisons we investigated male behaviour towards the following pairs of butterflies: (1) *hippocooides* versus *trimeni*; (2) *hippocooides* versus *lamborni*; (3) *trimeni* versus *lamborni*; (4) *trimeni* versus faded *trimeni*; (5) *lamborni* versus faded *trimeni*; (6) *hippocooides* versus males; (7) *trimeni* versus males; (8) *lamborni* versus males; (9) males versus faded males; (10) *hippocooides* versus *A. niavius* (the model; males and females are visually identical and the sexes of the specimens used were unknown). We conducted the experiments on sunny days between approximately 1200 and 1700 hours when most courtship occurred (personal observations). We used binoculars at a distance of 10 m from the apparatus. An approach was defined as occurring when a male came within approximately 30 cm of a pinned butterfly. For each male approach three behavioural variables were

recorded: (1) which subject he approached first; (2) total time spent within 30 cm of each subject; and (3) whether he attempted to copulate with the subject by curling his abdomen to attain genital contact (Krebs 1988 reported this behaviour in *P. glaucus*). Subsequent males approaching the apparatus whilst the first was still present were not recorded, because these may have been attracted by the first male rather than by the pinned specimens.

We succeeded in catching and individually marking about 32% (194 out of 614) of all males recorded during these and the following experiments immediately after they had ended their interaction with the apparatus. Since no marked male was recaptured during an experiment in which he was marked, we were confident that most approaches were made by independent males. In addition, the apparatus was moved to a new location along the forest boundary after approximately every 10 male approaches (the number of approaches ranged from 28 to 78 in different comparisons: see Table I). At each site the stand was periodically turned through 180° to avoid positional bias. In each comparison the pairs of pinned butterflies used were matched for scale wear and wing damage in an attempt to control for age and other confounding factors that may influence male preference. The pair used was changed every five approaches in order to reduce any preferences due to the characteristics of a particular pair of individuals. However, we used only four pairs of butterflies in total for each comparison in order to minimize the number of butterflies killed.

Sequential Choice Experiment

Simultaneous choice tests are a sensitive method for measuring male preference, but have limitations (e.g. Silberglied 1984; Martin & Bateson 1986). We attempted to investigate male responses in the comparison most relevant to testing the pseudo-sexual selection and male avoidance hypotheses (*hippocooides* versus *trimeni*) with a sequential choice procedure. This was designed to eliminate possible interaction effects between simultaneously presented test subjects. Using the same apparatus, *hippocooides* and *trimeni* females were presented singly and alternately for 10-min periods. Five different subject pairs were used. Presentation and recording procedures were otherwise similar to those of the simultaneous choice experiments.

Focal Follows on Wild Females

We followed wild *hippocooides* and *trimeni* females in an attempt to test the generality of male responses under more natural conditions. Individual females were watched for as long as possible, usually until they disappeared into the forest canopy. The rule for choosing a focal female was to follow the first female an observer encountered after losing the previous butterfly, with a preference being given to the rarer, *trimeni*, morph in order to balance the numbers of the two morphs followed. It is possible, but unlikely given the large population size and extent of the study site, that not all of the focal females were different butterflies; however, for the purposes of the analysis they were regarded as independent. All male approaches to within 30 cm of the focal female were recorded. Follows lasting less than 5 min were abandoned as being unrepresentative. Eleven *hippocooides* and nine *trimeni* females were followed for more than 5 min. We subtracted the time when the focal female was settled with her wings folded and her colour pattern unexposed from the total length of each follow, then calculated male approach rates for each butterfly.

RESULTS

Simultaneous Mate Choice Experiments

First approaches

In all except one of the comparisons between female morphs males showed preferences significantly different from random (by binomial tests; Table I). Comparisons 1, 2 and 6 show that males approached *hippocooides* (the Batesian mimic) in preference to *trimeni* (the andromorph), *lamborni* or males. Comparisons 7 and 8 show that males were poor at distinguishing between females of the morphs *trimeni* and *lamborni* and males. In general, males were more likely to approach conspecifics with white patterns (i.e. *hippocooides*) than conspecifics with yellow patterns (i.e. *trimeni* and males), and least likely to approach conspecifics with orange patterns (i.e. *lamborni*, faded *trimeni* and faded males). This hierarchy of male approach preferences is summarized in Fig. 1. Males were significantly more likely to approach the *hippocooides* morph than its model, *A. niavius*, although the model was approached first by 14 of 46 males.

Attempted copulations

In all comparisons involving a female both female morphs presented received some attempted copulations (Table I). In all except for one female–female comparison, once a male had approached, neither morph was more likely to elicit attempted copulation than the other. This exception is comparison 5 in which faded *trimeni* females received just significantly more attempted copulations than *lamborni* females. None of the presented males or the model species received any copulation attempts.

Interaction times

We analysed interaction times in two ways (see Table I). First, we compared interaction times with each of the test subjects for the males that visited both test subjects. Second, we compared interaction times for males that visited only one test subject. In most cases these two analyses gave similar results. Males who interacted with both subjects spent significantly longer interacting with the yellow *trimeni* morph than with faded *trimeni* or with *lamborni*. Otherwise, in the female–female comparisons there was no significant difference in the time the males spent interacting with the two morphs. In contrast, males generally interacted for significantly longer with the females in male–female comparisons (except in comparison 8 where *lamborni* elicited very little interaction). In the male–male comparison 9, males interacted for significantly longer with the younger yellow males than with the older faded males in the second analysis, but showed no difference in the paired analysis. Males interacted more with the mimic, *hippocooides*, than with its model in both analyses.

Sequential Mate Choice Experiment

As in the simultaneous comparison males were significantly more likely to approach a *hippocooides* than a *trimeni* female, but showed no significant difference in the length of time they spent interacting with the two morphs (Table II).

Focal Follows on Wild Females

We followed active *hippocooides* females for 257.6 min giving a mean observation period of 23.41 min per female ($SD = 15.67$ min), and active *trimeni* females for 279.0 min giving a mean of 31 min per female ($SD = 22.22$ min). *Hippocooides*

Table 1. Results and analysis of the simultaneous presentation mate choice experiments

No.	Comparison Morphs	No. of first approaches		No. of first approaches that resulted in a copulation attempt		Interaction times (s) (both specimens visited)			Interaction times (s) (only one specimen visited)		
		<i>N</i>	<i>P</i> *	<i>N</i>	<i>P</i> †	\bar{X}	<i>N</i>	<i>P</i> ‡	\bar{X}	<i>N</i>	<i>P</i> §
1	<i>hippocooides</i> versus <i>trimeni</i>	54		21		11.31			12.44	41	
		65	<0.001	3	NS	6.35	18	NS	7.83	6	NS
2	<i>hippocooides</i> versus <i>lamborni</i>	42		2		2.75			3.62	38	
		49	<0.001	1	NS	1.58	6	NS	6.20	5	NS
3	<i>trimeni</i> versus <i>lamborni</i>	40		12		12.23			5.67	26	
		56	<0.01	4	NS	4.82	17	<0.01	8.50	13	NS
4	<i>trimeni</i> versus faded <i>trimeni</i>	33		16		14.75			5.07	23	
		41	<0.001	1	NS	1.00	9	<0.05	5.31	9	NS
5	<i>lamborni</i> versus faded <i>trimeni</i>	16		4		6.81			3.68	11	
		28	NS	8	<0.05	8.50	8	NS	9.13	9	NS
6	<i>hippocooides</i> versus male (yellow)	41		18		14.21			13.67	35	
		52	<0.001	0	<0.05	0.85	7	<0.05	0.95	10	<0.01
7	<i>trimeni</i> versus male (yellow)	48		13		9.00			9.39	39	
		78	NS	0	<0.01	0.72	12	<0.05	0.76	27	<0.001
8	<i>lamborni</i> versus male (yellow)	26		2		1.67			4.54	22	
		69	NS	0	NS	1.00	10	NS	1.16	37	<0.05
9	Male (yellow) versus faded male	56		0		0.75			0.83	53	
		71	<0.001	0	NS	0.50	4	NS	0.50	14	<0.05
10	<i>hippocooides</i> versus <i>Amauris niavius</i>	32		7		13.25			11.87	22	
		46	<0.05	0	NS	0.64	14	<0.05	0.50	10	<0.01

**P*-values calculated from the binomial theorem.

†*P*-values calculated using the *G*-statistic with the William's continuity correction (*df* = 1). When any of the observed values in the contingency table were zero, one was added to all the observed values in the table before calculating this statistic.

‡*P*-values calculated using Mann-Whitney *U*-tests.

§*P*-values calculated using Wilcoxon paired-sample tests.

were approached at a significantly higher rate by males (20.54 ± 11.84 males/h; $\bar{X} \pm SD$), than *trimeni* (8.82 ± 7.87 males/h; Mann-Whitney *U*-test; $U = 82.5$, $N_1 = 12$, $N_2 = 9$, $P < 0.05$, two-tailed).

DISCUSSION

To our knowledge this is both the first study of mate choice in *P. dardanus* and the first study of mate

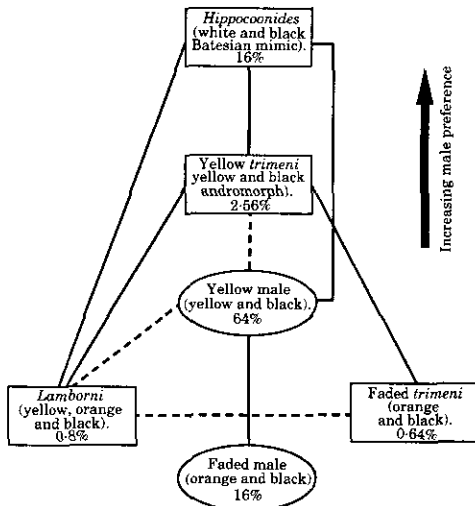


Figure 1. The transitive hierarchy of preferences in male approach behaviour obtained from the simultaneous presentation experiments. Each line represents one of the comparisons made. The dashed lines indicate comparisons where no significant preference was detected. The lengths of the lines are not to scale. Females are indicated by rectangles and males by ellipses. The percentages show the relative frequency of the different morphs present in the feeding meadow during the morning.

choice in a polymorphic species with more than two female morphs. This is timely because mate choice has recently been cited as a possible selective force in the maintenance of stable genetic polymorphisms (Vane-Wright 1984; Robertson 1985; Vane-Wright & Smith 1991). Using simultaneous choice, sequential choice and focal follows, our experiments revealed that the andromorph, *trimeni*, was approached consistently less frequently than the Batesian mimic, *hippocoonides*. In the simultaneous choice experiments the third morph, *lamborni*, was approached least frequently, and *trimeni* females that had faded from yellow to dull orange (probably with exposure to the sun) were also less attractive. This preference hierarchy (Fig. 1) is correlated both with relative morph abundance, commoner female morphs being preferred, and with our subjective assessment of morph conspicuousness, with the brighter white morph being preferred over the darker, yellow or orange ones.

Silberglied (1984) has criticized simultaneous choice experiments such as ours on three grounds. The first is that these tests are unrealistic because wild males are unlikely to encounter more than one female at a time and will therefore respond at a maximum level to anything resembling a female.

We addressed this problem by repeating the comparison between *hippocoonides* and *trimeni* both with a sequential choice test, and by following wild females. All three methods gave similar results, suggesting that our simultaneous tests do mirror natural mate choice. The second criticism is that the approach behaviour of males may be misinterpreted as sexually motivated when in reality it is for aggression or some other purpose. However, in our experiments, which were performed during periods of peak sexual activity (males were seen to switch from feeding in the morning to chasing females, or anything that resembled them such as falling leaves or other butterfly species, in the afternoon), approaching males often courted the pinned female, and attempted copulation with her. The third criticism is that choice tests with dead specimens provide little information about the role of colour patterns in stages of courtship beyond first approach. This may be true to some extent; however, in our experiments males often spent several seconds courting the female specimens and sometimes attempted copulation with them, suggesting that they did not realize immediately that the females were dead.

The approach preferences we obtained are probably due to males failing to recognize *trimeni* and *lamborni* morphs as potential mates from a distance, rather than an indication of the value that males attach to matings with different female morphs. Analysis of the data on copulation attempts and interaction times showed that, in general, males exhibited no preferences for the female morphs once they had approached, suggesting that the males do not show preferences for particular female morphs once they realize that what they have approached is a female. There are several possible reasons why males might fail to recognize *trimeni* and *lamborni* morphs as female. The morphs might be confused with other males, they might be less conspicuous and not noticed, or they might be relatively unfamiliar because of their lower frequency. Evidence suggesting male mimicry, at least in *trimeni*, is the fact that the *trimeni* colour pattern has converged very closely on that of males, even to the extent of the almost complete loss in many individuals of the black bars on the forewings characteristic of the other female morphs but not found in males. This argument assumes that the andromorph, *trimeni*, is secondarily evolved in *P. dardanus*, which is the view of Vane-Wright (1978; Vane-Wright & Smith 1991), rather than

Table II. Results and analysis of the sequential presentation mate choice experiment

No.	Comparison Morphs	No. of first approaches		No. of first approaches that resulted in a copulation attempt		Interaction times (s)		
		N	P*	N	P*	\bar{X}	N	P*
11	<i>hippocooides</i> versus <i>trimeni</i>	45	<0.001	12	NS	12.44	41	NS
		14		5		7.83	6	

*P-values calculated as for Table I.

being the primitive female form as suggested by Clark et al. (1991). The significance of *lamborni*'s orange pattern is less clear, but it is possible that it mimics the faded coloration of ageing males. Further experiments will be required to separate the roles of male mimicry, conspicuousness and rarity in male approach behaviour.

Our results that males approach the Batesian mimic, *hippocooides*, in preference to the andromorph, *trimeni*, run counter to the predictions of Vane-Wright's (1984) pseudosexual selection hypothesis, but are consistent with the male avoidance hypothesis. Several observations support the idea that females may be attempting to reduce the amount of male harassment they receive rather than maximizing their number of matings. During the afternoon when males were most sexually active and patrolled the forest boundary, females were often observed settled in the undergrowth with their wings folded making them cryptic to us, and apparently even to males flying close by. When chased by males, females were often observed to glide rapidly downwards or fly into trees or undergrowth, actions that tended to result in the female losing her pursuer (similar behaviour patterns in *Leptidea sinapis* were described by Wiklund 1977). In a study of scale wear we also found that the andromorph, *trimeni*, had wings that were less worn than those of the Batesian mimic, *hippocooides* (unpublished data), suggesting either that the andromorphs are less damaged owing to their lower levels of male courtship, or that they are younger owing to the higher predation they probably suffer, both of which are compatible with our hypothesis. Although we cannot be sure that females would generally benefit by avoiding excessive courtship (i.e. that they rarely or never go unmated, and that

multiple matings do not lead to improved fitness), it seems likely for the following reasons. It is clear from observations of the relative abundance and activity of males in this population that receptive females would not remain unmated for long. Furthermore, females of two congeneric species, *P. glaucus* and *P. zelicaon*, produce as many fertile eggs when isolated after one mating as when mated repeatedly (Levin 1973; Sims 1979). However, this needs to be investigated in *P. dardanus* because Watanabe (1988) found that multiple matings significantly increased fecundity in the yellow swallowtail, *P. xuthus*, showing that it is not safe to generalize across species within the same genus. Finally, studies of paternity following multiple matings in *P. dardanus* show that females are unlikely to gain better genes for their offspring through sperm competition because the last male to mate fertilizes the majority of eggs (Ae 1962; Clarke & Sheppard 1962).

We hypothesize, then, that the simultaneous maintenance of *hippocooides*, *trimeni* and possibly also *lamborni* can be explained as follows. *Hippocooides* females have a frequency-dependent selective advantage owing to the supposed lower levels of predation they suffer through being Batesian mimics. However, their fitness is reduced by high levels of male harassment. In contrast, the andromorphs, *trimeni*, have a selective advantage owing to the lower harassment they receive, but this advantage is offset by the increased predation they suffer through not being Batesian mimetic. The selective advantage to *trimeni* might also be frequency-dependent if it arises through male mimicry or rarity rather than just reduced conspicuousness, because if andromorphs became more common males would be selected to approach

male-like butterflies. The rare third morph, *lamborni*, might also be maintained by a similar frequency-dependent selective advantage that it obtains by mimicking faded males. Since faded males are less common than yellow males this hypothesis is consistent with the low frequency of *lamborni*. If correct, this would be the first case of polymorphic intraspecific mimicry; however, the idea remains to be tested. In summary, we can potentially explain the stable maintenance of the three female morphs of *P. dardanus* found on Pemba Island in terms of frequency-dependent selective advantages that arise directly from their different wing colour patterns. We hope we have shown that it is unnecessary to turn to 'constraints' explanations such as heterozygote advantage, as Ford (1965) did, for the stable maintenance of non-mimetic morphs in many populations of *P. dardanus*.

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