Polymorphism of melanic ladybirds maintained by frequency-dependent sexual selection

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Sexual selection, whether by female preference or male competition, is almost inevitably frequency-dependent. Female preference gives rise to a 'rare male effect', by which the rarer male phenotypes gain a relatively greater selective advantage. In addition to this effect, the proportion of females expressing a preference may also be frequency-dependent.

Frequency-dependent expression of mating preference can arise in at least two ways: (1) when females encounter a succession of courting males while searching for a male they prefer; (2) when females chose a male from within a lek. Models of mating behaviour reveal a clear distinction between the frequency dependence in the expression of female preference and the frequency dependence in the consequent selection of the males. When expression of preference is highly dependent on frequency, the selection of males is constant or only slightly frequency-dependent: constant expression of preference produces high frequency dependence of selection. Analysis of general models shows that genetic polymorphisms can be maintained under a wide range of conditions.

The ladybird, *Adalia bipunctata*, is polymorphic for several melanic and non-melanic phenotypes. Females have a genetically determined preference for melanic males. Non-melanic phenotypes mate assortatively. By estimating the parameters of a detailed model of natural selection, sexual selection and assortative mating, it has been shown that the *Adalia bipunctata* polymorphism will be maintained at frequencies observed in the wild.

KEY WORDS:—Natural selection – sexual selection – female preference – assortative mating – frequency-dependence – *Adalia bipunctata* – ladybirds – polymorphism – melanism.

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INTRODUCTION

Sexual selection, whether by female preference or male competition, is almost inevitably frequency-dependent. Female mating preference necessarily gives rise to frequency-dependent selective advantage. Each female with a preference has fewer preferred males to choose from when they are rare than when they are common: a preferred male mates more often when he is rare (see O'Donald, 1977, 1980). Female preference thus produces a 'rare male effect', which has so often been observed in experiments on the relative mating success of different genotypes at high and low frequencies. A rare male effect has frequently been observed in *Drosophila* (see, for example, Ehrman, 1972; Spiess & Ehrman, 1978; Spiess & Schwer, 1978; Spiess & Kruckeberg, 1980), in the two-spot ladybird (Muggleton, 1979; O'Donald & Muggleton, 1979; Majerus, O'Donald & Weir, 1982a), in a parasitic wasp (Grant, Snyder & Glessner, 1974) and in the guppy (Farr, 1977).

Spiess & Ehrman (1978) and Spiess (1982) suggested that the rare male effect of *Drosophila* occurred because females would avoid choosing to mate with male genotypes whose courtship they first received. In this 'avoidance model', females usually express a preference for rare male genotypes which they less often encounter. Partridge (1983, and Partridge & Hill (1984)) discuss models of male competition that might give rise to frequency-dependent mating. Indeed, Charlesworth & Charlesworth (1975, 1981) showed that competition among males in leks or small groups must always produce at least some frequency dependence in selective advantage.

The frequency dependence in the Charlesworths' model is usually positive: the advantage gained increases with increasing frequency of the advantageous males. The advantageous genotype is thus selected to fixation: polymorphisms are unstable. This is the opposite of the rare male effect which represents an advantage that increases with increasing rarity: common males lose their advantage by being common. The negative frequency-dependent selection thus maintains each phenotype in the population. Polymorphisms are necessarily stable.

O'Donald (1980) fitted models of preferential mating to data of the rare male effect in *Drosophila*. Different models produce different frequency-dependent effects. The goodness of fit of the models can therefore be tested by data of matings at different frequencies (O'Donald, 1980). Unfortunately, very different models sometimes produce very similar effects. For example, in Spiess and Ehrman's avoidance model, the female preference is itself frequency-dependent: the proportion of females expressing a preference increases as the preferred males decline in frequency. This can lead to probabilities of matings similar to those of a model in which constant proportions of females express preferences for the different male phenotypes (O'Donald, 1983). Fitting these models to data does not discriminate them statistically.

In Spiess and Ehrman's avoidance model, two variables are frequency-dependent: one is the proportion of females that express a preference; the other is the selective advantage of the preferred males. To some extent, the expression of preference must often be frequency-dependent: a female with a preference for a very rare male phenotype will have little chance of meeting a male she prefers; failing to do so, she will eventually mate with some other male. The proportion of females expressing a preference will depend on the chances of meeting

preferred males, hence on their frequencies. But, regardless of how preference may be expressed, preferential mating will normally produce a frequency-dependent selective advantage. This rare male effect in the selective advantage should not be confused with a frequency-dependent expression of the behaviour which causes the sexual selection.

Mating preferences of Adalia bipunctata

Partridge (1983) has denied that female choice or preference is the cause of sexual selection and the rare male effect in *Drosophila*. In repeating Spiess and Kruckeberg's experiments on matings between homozygous and heterozygous genotypes in *Drosophila*, she failed to obtain a rare male effect (Partridge & Gardner, 1983; Spiess & Kruckeberg, 1980). There can be no doubt, however, that female preference causes the rare male effect in matings of melanic and non-melanic phenotypes of *Adalia bipunctata*. *Adalia bipunctata*, the two-spot ladybird, is polymorphic for the colour and pattern of elytra and pronotum. There is a wide range of distinct morphs, from red to almost completely black, determined by a multiple allelic series with at least 11 alleles. The melanic forms (black with red spots) are dominant to the non-melanics (red with black spots), but distinct heterozygotes are produced in combinations with some of the rare alleles. Five morphs may be found in certain English populations: *sublunata* (phenotype L, allele s^{lu}), black with two red spots; *quadrimaculata* (phenotype Q, allele s^{m}) black with four red spots; *sexpustulata* (phenotype X, allele s^{p}), black with six red spots; *typica* (phenotype T, allele s^{t}) red with two black spots; and *annulata* (phenotype A, allele s^{a}), red with two extended black spots. Genetic studies (described in Hodek, 1973) suggest there is an ordered hierarchy in dominance as follows:

$$s^{lu} > s^{m} > s^{p} > s^{t} > s^{a}.$$

Muggleton (1979) analysed data of mating pairs and individual ladybirds classified as melanic and non-melanic. He found that melanics were at a frequency-dependent advantage: at lower frequencies a relatively greater proportion of melanics were mating than were present in the population as a whole. Majerus, O'Donald & Weir (1982a) observed mating pairs both in a wild population at Keele and in experimental population cages at fixed frequencies of *quadrimaculata* (Q) and *typica* (T) phenotypes. They also made direct observations of the matings in mating chambers. The experiments were all carried out using samples taken from the Keele population or stock derived from the samples from Keele. The frequencies of the matings of Q and T males were consistent with a model combining sexual selection with assortative mating of the two phenotypes (Karlin & O'Donald, 1978). By fitting this model, it was estimated that 23% of all females express a non-assorting preference for Q males and 16% of Q females express an assorting preference for Q males. Both population cage and mating chamber experiments gave closely similar estimates. From data of mating frequencies in the wild population at Keele, 21% of females prefer melanic (M) males (M includes all melanic phenotypes L, Q and X). Very large samples taken at Keele in the following year (1982) gave the estimate that 20.3% of females prefer melanic males (O'Donald *et al.*, 1984). The samples from Keele also show strong assortment in the matings of T and A

phenotypes, which population cage experiments with A and T have recently corroborated.

Other experiments using unselected Keele stock have all produced consistent estimates of the mating preference for Q males (Majerus, O'Donald & Weir, 1982b).

Although our data are completely consistent with a model of female preference, they are not sufficient to exclude specific models of frequency-dependent male competition. The decisive proof of female preference was obtained by a selection experiment (Majerus, O'Donald & Weir, 1982b). In a selection line derived from females that had mated with Q males, the proportion of females expressing a preference for Q males rose rapidly, reaching 55% in the fourth generation of selection. Selected females tested with unselected males from the Keele stock showed the high level of preference of the selected line. Unselected females tested with males from the selected line showed the 20% level of preference of the unselected Keele stock. Thus we had selected some female behavioural characteristic giving rise to preferential mating with Q males. The females' preference was genetic.

A MODEL OF PREFERENTIAL MATING OF LADYBIRDS

In a model of preferential mating (O'Donald *et al.*, 1984) the three melanic phenotypes have been treated as a single phenotype preferred by the same group of females. Strictly, the model applies only to the phenotypes Q, T and A for which experimental data and estimates of preferences have been obtained. The phenotypes, alleles, their frequencies and preferences, have been given the following symbols:

	Q	T	A
Phenotypes	Q	T	A
Alleles (with dominance ordering)	$s^m >$	$s^t >$	s^a
Phenotypic frequencies	π_1	π_2	π_3
Preferences:			
non-assortative	α_1	α_2	α_3
assortative	a_1	a_2	a_3

The non-assortative preferences are expressed by all females regardless of their phenotype. The assortative preferences are expressed only by females with the same phenotype as that of the males they prefer. As in the Keele population, phenotypic frequencies are the same in both sexes. Table 1 shows the frequencies of preferential matings.

From Table 1, the females left to mate at random are Q at frequency π_1

Table 1. Preferential matings of males

	Q	T	A
Females Q	$\alpha_1\pi_1 + a_1\pi_1$	$\alpha_2\pi_1$	$\alpha_3\pi_1$
T	$\alpha_1\pi_2$	$\alpha_2\pi_2 + a_2\pi_2$	$\alpha_3\pi_2$
A	$\alpha_1\pi_3$	$\alpha_2\pi_3$	$\alpha_3\pi_3 + a_3\pi_3$
Totals for each phenotype	$\alpha_1 + a_1\pi_1$	$\alpha_2 + a_2\pi_2$	$\alpha_3 + a_3\pi_3$

Table.2. Total mating frequencies for male phenotypes

Phenotype	Total frequency of matings
Q	$\alpha_1 + a_1\pi_1 + \pi_1(1 - \theta - a_1\pi_1 - a_2\pi_2 - a_3\pi_3)$
T	$\alpha_2 + a_2\pi_2 + \pi_2(1 - \theta - a_1\pi_1 - a_2\pi_2 - a_3\pi_3)$
A	$\alpha_3 + a_3\pi_3 + \pi_3(1 - \theta - a_1\pi_1 - a_2\pi_2 - a_3\pi_3)$

$(1 - \theta - a_1)$, T at frequency $\pi_2(1 - \theta - a_2)$, and A *at frequency* $\pi_3(1 - \theta - a_3)$, where $\theta = \alpha_1 + \alpha_2 + \alpha_3$. These females mate with Q, T and A males at frequencies π_1, π_2 and π_3. Matings in *Adalia bipunctata* are polygynous: Q, T and A males, having mated once or several times preferentially, are still available to mate randomly. Combining preferential and random matings, we obtain the total mating frequencies for each male phenotype (Table 2).

Table 3 shows that the average number of matings by a single male of each phenotype is a measure of his relative fitness determined by sexual selection. The sexual selection, determined by the non-assortative preferences α_1, α_2 and α_3, is strongly frequency-dependent. For example, if $\alpha_1 = 0.1$, $\pi_1 = 0.01$, then the non-assortative preference for Q produces $\alpha_1/\pi_1 = 10$ matings for each Q male in addition to a small proportion of assortative and random matings. But, if Q increases in frequency to $\pi_1 = 0.9$, the number of non-assortative preferential matings drops to $0.1/0.9 = 0.111$. The overall selective advantage of Q is much less at the higher frequency. This numerical example explains the point we stressed in the introduction: a constant (non-assorting) preference produces frequency-dependent sexual selection. Assortative preferences have the opposite effect. They are expressed only by females who possess the preferred phenotype, and hence in proportion to its frequency. Therefore they produce a constant selective advantage as Table 3 shows.

Maintenance of polymorphism

The ladybird data we have already obtained show that Q males are chosen preferentially and without assortment by the females. In addition, all three phenotypes probably mate assortatively to some extent. Only the Q phenotype would thus gain a frequency-dependent advantage. This could balance a polymorphism with either A or T but not with both: either A or T would have a constant selective advantage over the other, and one of them, A or T, would be eliminated. To maintain all three phenotypes in a balanced polymorphism, at

Table 3. Relative fitness as measured by number of matings

Phenotype	Relative fitness
Q	$\alpha_1/\pi_1 + a_1 + K$
T	$\alpha_2/\pi_2 + a_2 + K$
A	$\alpha_3/\pi_3 + a_3 + K$

$K = 1 - \theta - a_1\pi_1 - a_2\pi_2 - a_3\pi_3$

least two must gain a frequency-dependent advantage from the rare male effect. If we assume that T males are also preferred non-assortatively, as well as the Q males (since, in the Keele population, T has a slight advantage over A), we are left with the general model in which α_3 is the only parameter assumed to be zero (no general preference for A). This is the most general form of the model for which analytical results can easily be obtained (O'Donald *et al.*, 1984). There are two alternative equilibria: either the three phenotypes are maintained at stable frequencies:

$$\pi_1{}^* = \alpha_1/(a_3 - a_1)$$
$$\pi_2{}^* = \alpha_2/(a_3 - a_2)$$
$$\pi_3{}^* = 1 - \pi_1{}^* - \pi_2{}^*$$

or one of the phenotypes, A or T, is eliminated, when equilibrium is given by the solution of

$$\pi_1{}^2(a_1 - a_2) + \pi_1(\theta - a_1 + a_2) - \alpha_1 = 0$$

Both these solutions obviously entail monomorphism if the equilibrium frequency is $\pi_1{}^* > 1$. In most cases of polymorphism, all three phenotypes coexist at equilibrium (see O'Donald *et al.*, 1984, for analytical details).

If only the Q phenotype is preferred non-assortatively $(\alpha_2 = \alpha_3 = 0)$, then, as we have explained, either A or T must be eliminated. One of the following alternative equilibria is attained. If $a_3 > a_2$, then:

$$\pi_1{}^* = \alpha_1/(a_3 - a_1)$$
$$\pi_2{}^* = 0$$
$$\pi_3{}^* = 1 - \pi_1{}^*$$

If $a_2 > a_3$, then

$$\pi_1{}^* = \alpha_1/(a_2 - a_1)$$
$$\pi_2{}^* = 1 - \pi_1{}^*$$
$$\pi_3{}^* = 0$$

Since neither A nor T are subject to frequency-dependent selection in this case, one must have an overall, constant advantage, and eliminate the other. If $a_3 > a_2$, A has the advantage and T is eliminated: if $a_2 > a_3$ T has the advantage and A is eliminated. It is easy to see that the point $\pi_1 = 0$ is unstable so that Q will always enter the population. Q has its greatest frequency-dependent advantage when it is very rare. Thus if Q enters the population, it will increase in frequency until its advantage has eventually declined to exactly balance the advantage the other phenotype or phenotypes gain from their assortative mating. If $\alpha_1 > (a_3 - a_1)$, $(a_2 - a_1)$ Q always retains an advantage right up to the point at which $\pi_1 = 1$: the population then becomes monomorphic for Q. A polymorphism is maintained whenever $0 < \alpha_1 < (a_3 - a_1)$, $(a_2 - a_1)$. This is the condition for both the existence and stability of the polymorphism.

In the wild population at Keele M (i.e. $L + Q + X$), T and A phenotypes are all present at apparently stable frequencies. Our analysis thus shows that to maintain these three phenotypes, we must have preferences α_1 and α_2 for both the M (including Q) and T phenotypes. Clearly some other factors are required to explain the small proportion of the L and X melanics in the population, possibly by separate mating preferences in their favour (Karlin & O'Donald, 1981).

FREQUENCY-DEPENDENT EXPRESSION OF PREFERENCE

We have seen that constant expression of a non-assortative preference produces a frequency-dependent selective advantage of preferred males. More realistically, we should expect that the expression of preference would also be frequency-dependent. A female will be less likely to mate preferentially if the males she prefers are rare: having failed to meet a preferred male in a number of encounters with courting males, she will eventually give up after these disappointments and mate with the next courting male she meets. This concept gives rise to the 'Encounter Models' of sexual selection (O'Donald, 1978, 1980; Karlin & Raper, 1979).

Encounter model of female response

Suppose that a female may respond at two levels to male courtship. She has a lower threshold of response to the males she prefers. Having been stimulated by male courtship to the level of this threshold, a preferred male will then elicit her mating response. But she will have to be stimulated to a higher threshold to respond to other male phenotypes. Encounters with courting males will bridge the gap between the two threshold levels of stimulation. If she meets a preferred phenotype of male in the course of these encounters, she naturally mates with him. But if she fails to encounter a preferred male, she continues to reject other male phenotypes until her level of stimulation reaches the higher threshold: then she mates with the next courting male of any phenotype.

O'Donald (1978) originally formulated these models in terms of fixed numbers of encounters required to stimulate a female to mate at random. More general models can be formulated in which the number of encounters required for random mating varies between females, following some general probability distribution with generating function $\phi(x)$ (Karlin, O'Donald & Majerus, in prep.). Consider the Q males at frequency π_1 in the population. The probability of not meeting a Q male in n encounters is $(1-\pi_1)^n$. If a_n females require n encounters with non-preferred males before mating at random, the overall probability that females with a preference for Q mate at random is given by:

$$\sum_{n=0}^{\infty} a_n(1-\pi_1)^n = \phi(1-\pi_1)$$

where ϕ is the probability generating function of the distribution of n as before. Females with low values of n are prepared to accept only a few disappointments before mating at random. 'Choosy' females, on the other hand, still continue to search for a preferred male after many disappointments. ϕ thus represents the distribution of the females' 'strength of preference'.

More generally, we should allow for the possibility that the distribution of the strength of each preference is different. Table 4 lists the probabilities of expressing preferences for each phenotype. Females with preferences, who eventually mate at random after not having encountered a preferred male, contribute equally to the matings of each male like the females without any preferences. The relative number of matings achieved by a male of each phenotype is given by the expressions in Table 5. The assorting preferences a_1, a_2 and a_3 are assumed to be constantly expressed.

Table 4. The probabilities of expressing preferences for each phenotype

Phenotype	Probability of expressing preference
Q	$\alpha_1 [1 - \phi_1(1 - \pi_1)]$
T	$\alpha_2 [1 - \phi_2(1 - \pi_2)]$
A	$\alpha_3 [1 - \phi_3(1 - \pi_3)]$

If females were prepared to accept only one disappointment before mating at random, then we should have:

$$\phi_1(1 - \pi_1) = 1 - \pi_1$$

so that Q would have relative fitness

$$\alpha_1[1 - (1 - \pi_1)]/\pi_1 + a_1 + k$$

or

$$\alpha_1 + a_1 + k$$

In this case the preference for Q is expressed as $\alpha_1 \pi_1$ in simple proportion to frequency, hence giving rise to a constant selective effect. Polymorphisms cannot be maintained in this simple case. A general analysis shows that polymorphisms can be maintained provided that $\phi_1'(1)$, $\phi_2'(1) > 1$. The quantities $\phi_1'(1)$, $\phi_2'(1)$ are mean numbers of encounters, which must be greater than one for polymorphic stability (Karlin, O'Donald & Majerus, in prep.). Polymorphisms can also be maintained even in the case when $\phi_1'(1)$, $\phi_2'(1) = 1$, provided that ϕ_1 and ϕ_2 represent bimodal distributions—for example, if some females are very choosy, while others accept few or no disappointments before mating at random.

Lekking model

A similar model to the encounter model describes the mating system in which females encounter males at leks where display and courtship takes place. If ϕ is now the probability generating function of the numbers of males in each lek, then the quantities:

$$1 - \phi(1 - \pi_1), \; 1 - \phi(1 - \pi_2), \; 1 - \phi(1 - \pi_3)$$

are the probabilities that a lek contains at least one Q, T or A male and, hence,

Table 5. Relative number of matings achieved by a male of each phenotype

Phenotypes	Relative fitness
Q	$\alpha_1[1 - \phi_1(1 - \pi_1)]/\pi_1 + a_1 + k$
T	$\alpha_2[1 - \phi_2(1 - \pi_2)]/\pi_2 + a_2 + k$
A	$\alpha_3[1 - \phi_3(1 - \pi_3)]/\pi_3 + a_3 + k$

that a female can mate preferentially. This gives a result similar to the encounter model with $\phi_1 = \phi_2 = \phi_3 = \phi$.

The encounter and lekking models produce complicated frequency-dependent fitness functions of the form:

$$[1 - \phi(1-\pi)]/\pi$$

As we have seen, in the simple case when females accept only one disappointment before mating at random.

$$\phi(1-\pi) = 1 - \pi$$

and preferential mating has a constant effect on fitness. Thus, as females become less choosy, they express their preference with greater dependence on frequency, while the resulting selection of males becomes less frequency-dependent. More choosy females are more constant in expressing their preference, producing greater frequency dependence in the selection.

SEXUAL SELECTION OF LADYBIRDS

Estimates of preferences

Our experiments and field observations have produced consistent estimates of mating preferences. These results may be summarized as follows.

(i) Original population cage experiments on matings of Q and T at experimentally determined frequencies of individuals gave estimates (Majerus, O'Donald & Weir, 1982a):

$\hat{\alpha}_1 = 0.23$ (highly significant)
$\hat{a}_1 = 0.16$ (nearly significant: $\chi^2 = 3.51$; $P = 0.061$)

(ii) In selection experiments on the female preference for Q, control lines, tests on controls and the initial generation of the selected line gave estimates (Majerus, O'Donald & Weir, 1982b):

$$\hat{\alpha}_2 = 0.27, 0.27, 0.28, 0.21, 0.23, 0.19, 0.22$$

rising to $\hat{\alpha}_1 = 0.57$ in the fourth generation of the selection line.

(iii) Field data of very large samples from Keele gave estimates (O'Donald et al., 1984):

$$\hat{\alpha}_1 = 0.203, \hat{a}_3 = 0.44$$

In estimating a_3, we assumed there was no assorting preference for T ($a_2 = 0$), since T shows no assortment in matings with Q in population cages.

If expression of preference is frequency-dependent, the estimates of α_1 will depend on the frequencies of the Q males available to be chosen by the females. Both in our selection experiments and in the unselected control lines (concurrently run with the selected line), we were always careful to maintain a fixed ratio of $Q:T$ males in the population cages and to sample with replacement. Suppose, in accordance with the encounter model, a proportion $1 - \phi_1(1-\pi_1)$ of the α_1 females express their preference for Q males. Since π_1 is held constant, the proportion expressing the preference is always the same

proportion of α_1. This will hold for any frequency-dependent function of the expression of preference. We chose the ratio $3:7$ for $Q:T$. This gives an efficient estimate statistically and is also very close to the actual ratio of $Q:T$ in the wild population at Keele.

We thus obtained the following estimates of parameters:

$\hat{\alpha}_1 = 0.203$ (from the large sample of field data)
$\hat{a}_2 = 0.16$ (from population cage experiments)
$\hat{a}_3 = 0.44$ (from the field data)

Our analysis of the model shows that with these parameters T would be eliminated, leaving Q and A at equilibrium:

$$\pi_1^* = \alpha_1/(a_3 - a_1) = 0.72$$
$$\pi_3^* = 0.28$$

Fitting the model

In order to obtain the observed frequencies of T and A in the Keele population we must have:

$$\alpha_2 = 0.199$$

Even with this preference for T, the frequency of melanics would still be much too high.

Creed (1971) found that in some urban populations the frequency of melanics declined after smoke abatement zones had been introduced: melanics were at a disadvantage as a result of natural selection. When natural selection is incorporated into the model, an analytic solution no longer appears to be obtainable. Computer simulation shows that with parameter values:

$$\alpha_1 = 0.203 \quad a_1 = 0.162$$
$$\alpha_2 = 0.199 \quad a_1 = 0$$
$$a_3 = 0.44$$

and a selective disadvantage of melanics of:

$$s = 0.143$$

an equilibrium is attained at:

$$\pi_1^* = 0.342$$
$$\pi_2^* = 0.452$$
$$\pi_3^* = 0.206$$

as in the wild population at Keele.

The estimate $\hat{a}_1 = 0.162$ for the assorting preference of Q is not quite significant statistically, nor is it supported by any evidence of assortative mating of Q in the wild. If we assume, therefore, that $a_1 = 0$ and use the values

$$\alpha_1 = 0.203 \qquad a_1 = a_2 = 0$$
$$\alpha_2 = 0.199 \qquad a_3 = 0.44$$

in the computer model, equilibrium is attained at the frequencies of the Keele population when melanics are at a disadvantage in natural selection of:

$$s = 0.0734$$

We are pleased to be able to report that at the Population Genetics Group meeting in Southampton on 3–6 January 1984, John Muggleton told us that in urban and suburban areas in England the selective disadvantage of melanics is about 10%. This estimate thus corroborates our own theoretical calculations of the range of values of s that would give rise to the observed frequencies in the urban and suburban environments round Keele.

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