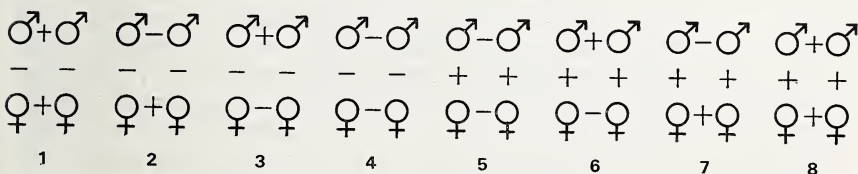# A classification of sexual interactions, and the evolution of species-specific coloration in butterflies

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Sexual dimorphism in butterflies (Bernardi, 1974; Vane-Wright, 1975) has often been considered the product of *epigamic* sexual selection (Belt, 1874; Brower, 1963; Turner, 1978). Females are thought to select extravagantly or ancestrally coloured males. Males are promiscuous, allowing females to adopt those patterns best suited for survival. However, most authors do not differentiate between the two types of sexual selection, epigamic and *intrasexual* (Huxley, 1938). The possibility of intrasexual use of colour by butterflies has been largely disregarded.

My approach is to classify the sexual interactions that could possibly exist within species, and then examine the behaviour of particular organisms to identify their signalling requirements. Three binary combinations of individuals are possible: male, female, and mixed. Sexual interactions between members of a pair can be positive (co-operative) or negative (non-co-operative). Within a population, three binary combinations, each with positive or negative interactions, give $2^3 = 8$ possible interaction situations.

$\male + \male$	$\male - \male$	$\male + \male$	$\male - \male$	$\male - \male$	$\male + \male$	$\male - \male$	$\male + \male$
$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$
$\female + \female$	$\female + \female$	$\female - \female$	$\female - \female$	$\female - \female$	$\female - \female$	$\female + \female$	$\female + \female$
1	2	3	4	5	6	7	8

Class 1 would represent some form of 'sex war'; I do not know of a good example. Class 2 occurs, for example, in beehives, when workers eject drones. Class 3 is the reverse of 2. Class 4 represents a sexual taboo, as may occur in mammals 'out of season'. Class 5 indicates simultaneous sexual competition amongst both sexes. Class 6 represents male leking behaviour, and Class 7 is the reverse of this. Class 8 describes sexual co-operation.

In butterflies, except for communal roosting in some species, there is no evidence of female co-operation. Classes 1, 2 and 7 can thus be eliminated, and 8 regarded as of minor importance. Class 3 describes co-operative 'mud-puddling' by male butterflies, where females are rejected or ignored. Class 4 probably does not apply. Class 5

occurs when females seek to be mated, the males behaving agonistically towards each other. Class 6 (male leking) may occur in some species e. g. ithomiines).

Thus only class 3 and 5 situations appear important for butterflies. For many species this decribes how males divide their time between co-operative herding ('mud-puddling') and agonistic territoriality.Although males initially locate females visually, females of any appearance get mated, because the males are promiscuous. Thus long-distance (intrasexual) specific signalling is plausibly a fundamental requirement for males, but not for females. The males of sympatric species will tend to evolve stable, but different visual signals.

Closely related butterflies often differ sharply in male coloration, and this is frequently associated with sexual dimorphism (weak or strong), or partial female-limited polymorphism (Vane-Wright, 1975; 1979). In such cases the females may be more cryptic, mimetic of other species, or male-like. It is suggested that this last possibiliy may be realised through 'pseudo-sexual-selection' and a mechanism of intra-specific mimicry (Wickler, 1968; Vane-Wright, 1976). Male-like females tend to elicit a stronger male response than non male-like females (Magnus, 1963). I suggest this is caused by mistaken identity, males being unable to distinguish (at a distance) such females from other males. In species which use male coloration for long distance signalling, this will act as a selective pressure for females to become male-like. This process may involve morph 'decoupling' (Vane-Wright, 1979). Imagine a sexually dimorphic species, the male having a unique signal pattern. A male-like morph is then added to female pattern range, through the postulated pseudo-sexual-selection. Such a *decoupled* morph is unlikely to be identical to the male; it is essentially a male mimic. If all non-male-like morphs are eventually eliminated, the species becomes weakly dimorphic for the species-specific male colour pattern. Such polymorphism pathways (Vane-Wright, 1979) can be demonstrated by phylogenetic analysis (e. g. yellow *Papilio dardanus)* and by biogeographic analysis (e g. red *Appias nero),* and may illustrate one way by which sharply discontinuous, species-specific colour patterns are evolved in closely related butterflies.

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