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20. *Visual Communication and Sexual Selection Among Butterflies*

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The wings of butterflies are adorned with a wealth of pattern and a display of colour unrivalled in the living world. Some butterflies have uniformly-coloured, unpatterned wings of white; others reflect yellow, orange, red, green, blue, violet, brown or black. The colours are produced in various ways (Fox & Vevers 1960), including selective absorption by pigments (Ford 1945), tyndall scattering (Huxley 1976) and thin-film interference (Simon 1971). In some species, the wings bear simple patterns, such as contrasting colour along the veins. In others multicoloured patterns of anastomosing lines, ripple patterns or eyespots are found (Nijhout 1980*a*). These complex patterns are genetically determined and developmentally controlled (Nijhout 1978, 1980*b*, 1981). The coloration and pattern of a butterfly's dorsal and ventral wing-surfaces may be the same or different. The two sexes may be identical, slightly different, or in some cases so distinctive that they were originally described in different genera. Wing colour may be seasonally, geographical or locally variable or polymorphic. Furthermore, closely related species may appear extremely different, while unrelated species can display nearly identical colour patterns (Vane-Wright 1971, 1979*a*,*b*).

Attempts to understand this panoply of spectral diversity have resulted in major contributions to our knowledge of the evolutionary process. The study of butterfly colour and pattern has played an important role in the development of the theories of both natural (Darwin 1859) and sexual selection (Darwin 1874, Hingston 1933), mimicry (Bates 1862, Müller 1878*c*, 1879, Carpenter & Ford 1933, Wickler 1968) and genetic polymorphism (Sheppard 1961*a*, Robinson 1971). In return, information from ecological, behavioural, genetic, developmental and evolutionary studies has contributed greatly to our understanding the significance of butterfly colour and pattern.

Butterfly wing colours and patterns serve several important functions. Unlike some colours associated with metabolically important compounds (e.g. haemoglobin, chlorophyll, cytochrome), butterfly wing pigments and structural colours must serve biophysical functions because they are located outside the metabolic pool, in the dead cellular skeletons of the wing scales. Certain colours absorb or reflect radiation effectively (Watt 1968). A butterfly may regulate its body temperature by positioning itself and its wings with respect to the sun (Vielmetter 1954, Clench 1966, Watt 1968, Findlay *et al.* 1983), but only the basal regions of the wings play an important role in thermoregulation (Wasserthal 1975, Douglas 1979). We must look elsewhere if we are to understand the function of the coloration of the remainder.

The colour patterns of butterflies have usually been discussed in the context of one or both of two contrasting, communicative functions: protection from predators (Poulton 1908, Cott 1940), and social signals used during courtship (Silberglied 1977). Darwin (1874) devoted a chapter to the Lepidoptera in *The descent of Man and selection in relation to sex*. He provided numerous examples and observations to support his view that, 'although many serious objections may be urged, it seems probable that most of the brilliantly coloured species of Lepidoptera owe their colours to [inter-]sexual selection, excepting in certain cases . . . in which conspicuous colours have been gained through mimicry as a protection.' Sexual selection on pattern and colour may oppose other selective forces, such as predation (e.g. Carpenter & Ford 1933, Stride 1956, 1958*b*, Brower 1963, Turner 1977*a*, 1978, Vane-Wright 1971, 1975, 1976, 1979*a*, Ch.23). A fuller understanding of the nature and intensity of sexual selection for colour and pattern in butterflies is therefore of great importance in evaluating other evolutionary processes.

†Bob Silberglied died in a tragic accident on 13 January 1982, a few days after submitting his final draft of this paper.

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Darwin's view that intersexual selection is of primary importance in the evolution of brilliant male butterfly coloration and sexual dimorphism has persisted with little change for more than a century. During this time a host of physiological and behavioural studies, both observational and experimental, have greatly augmented our knowledge of butterfly vision and its role in courtship. This paper explores the extent to which his view, which has been incorporated into numerous reviews, texts and theoretical discussions, is corroborated by our present knowledge of visual communication among butterflies.

Darwin's Views on Sexual Selection and Butterfly Coloration

Darwin (1874) was particularly impressed with sexual dimorphism as exhibited by many butterfly species, and by the disturbation of this phenomenon within genera. He was intrigued with the problem of why the sexes differ in some species, but not in close relatives. Were the colours and patterns attributable to direct effects of the environment in which the butterflies lived, were they largely protective, were they employed as attractive devices by the two sexes, or did they perhaps serve some unknown purpose? He pointed out that when the sexes differed, it generally affected the colour and pattern of the dorsal wing surfaces, those usually concealed when the butterfly is at rest. The male usually has the more beautiful, brilliant or striking dorsal coloration. According to Darwin, the female generally exhibits 'ancestral' features, from which the male pattern departs to greater or lesser degree. Thus females of closely related species tend to resemble one another more than do the males.

Darwin recognized that 'whenever colour has been modified for some special purpose, this has been, as far as we can judge, either for direct or indirect protection, or as an attraction between the sexes.' The similarity of the ventral wing surfaces in both sexes reflects the fact that they generally rest with the wings raised, with this surface exposed to view. The ventral surface is usually mottled or patterned in such a way as to resemble the background against which the butterfly rests, thus making it more difficult to detect.

That most nocturnal Lepidoptera were drab in coloration also impressed Darwin, as well as the fact that diurnal moths often have brilliant coloration. However, unlike butterflies, diurnal moths rarely exhibit strong sexual dimorphism. (The major exceptions involve sex-limited mimicry, e.g. *Callosamia promethea*, *Pericopis* spp.)

Darwin recognized that butterfly courtships are often prolonged. He knew that males are aggressive and competitive but more or less indiscriminate in their choice of mates, and that a female could refuse a courting male. The location of the colours, and the behaviour of the males, indicated to him an active function in display toward the opposite sex (Darwin 1880). Because butterflies exhibit colour preferences while feeding, and can be attracted to coloured decoys, he reasoned that they perceive and 'admire' bright colours. He believed that females were more excited by, and preferred, the more brilliant, beautiful males. By choosing mates on the basis of colour, females would select for males that departed from the duller ancestral pattern, resulting in the evolution of brilliant male coloration and striking cases of sexual dimorphism.

Though Darwin clearly perceived bright male coloration as being due to female sexual selection, he also discussed some evidence contrary to his view. He mentioned cases of matings to 'battered, faded or dingy males' (see also Ch.21) but dismissed these as being a result of protandry.

Wallace (1889) believed that the sexual dimorphism exhibited by many butterflies was often due to the acquisition of protective coloration by females, rather than to the development of brilliant colours in males by intersexual selection. However, the diversity of brilliant patterns of the males, and the similarity of closely-related females, argue strongly against this view, suggesting that protective coloration represents an ancestral character state that existed before the evolution of brilliant dorsal wing displays. Wallace felt that 'the varieties of colour and marking, forming the most obvious distinction between allied species, . . . have . . . in all probability been acquired in the process of differentiation for the purpose of checking the intercrossing of closely allied forms.' (It is difficult to understand how Wallace reconciled this "need for recognition" with his denial of female choice.) Both Darwin and Wallace argued that bright colours were not due to any special influence of tropical conditions.

In those few instances in which the females have the more brilliant patterns, Darwin suggested that the males prefer to mate with the more 'beautiful' females. When the sexes are alike, either the male has retained the ancestral colour pattern, or the male colours have been 'transferred' to the female (see Ch.23).

Darwin also recognized that mimicry affords a special explanation for the colours of many butterflies. When mimicry is limited to one sex, it is expressed in the female: the non-mimetic males generally retain the colour pattern typical of their phyletic group, from which the females depart. Darwin accepted Thomas Belt's explanation for this phenomenon, 'that the females had a choice of mates and preferred those that retained the primordial appearance of the group' (Belt 1874, see also Turner 1978).

Summarizing, Darwin (1874) said

> it is impossible to admit that the brilliant colours of butterflies, and of some few moths, have commonly been acquired for the sake of protection. We have seen that their colours and elegant patterns are arranged and

exhibited as if for display. Hence I am led to believe that the females prefer or are most excited by the more brilliant males; for on any other supposition the males would, as far as we can see, be ornamented to no purpose. With butterflies we have the best evidence, as the males sometimes take pains to display their beautiful colours; and we cannot believe that they would act thus, unless the display was of use to them in their courtship. Judging from what we know of the perceptive powers and affections of various insects, there is no antecedent improbability in sexual selection having come largely into play; but *we have as yet no direct evidence on this head, and some facts are opposed to the belief*. Nevertheless, when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance—that the female exerts no choice, and is not affected by the gorgeous colours . . . with which the male is adorned' (my emphasis).

The Evidence

Several kinds of direct evidence bear on Darwin's conjecture. For instance, we need to ask of butterfly vision: Over what spectral range do they see? Can they discriminate colours from one another? Have they a well-developed ability to distinguish among patterns? What other factors (e.g. depth perception, motion, polarization) are important in their vision?

Which characteristics of butterfly colour patterns might be used for visual communication? How are the mechanisms of colour production related to the qualities of visual stimuli? Which features are constant, and which variable, within and between species? Do male and female butterflies behave during courtship in a manner consistent with the use of optical signals? Do males rely on visual stimuli to choose among females? Do females refuse, and so choose among, males? If so, do they respond to the males' colours?

Butterfly Vision

> When physiological methods uncover color receptors in the compound eye, their biological significance in a color vision system is usually assumed, even in the absence of behavioral data
>
> (Goldsmith & Bernard 1974)

Spectral sensitivity

The spectral range visible to butterflies extends from the ultraviolet (Lutz 1924) through the red (Eltringham 1919, Schlieper 1928), fully encompassing the visible spectrum of humans as well as that of other insects. It is the broadest visible spectrum known in the animal kingdom (Silberglied 1979).

Colour vision

It has long been supposed that butterflies are sensitive to colour (Eltringham 1919). Flower constancy exhibited while feeding, and responses of males to dead specimens and coloured dummies, strongly suggested that they could distinguish hues. Simple choice experiments (e.g. Lutz 1924; see McIndoo 1929) also appeared to reveal colour preferences, but none of the early experiments controlled for differences in stimulus intensity (brightness). It remained for Ilse (1928; Kühn & Ilse 1925) to demonstrate that true colour vision (hue discrimination) exists in butterflies. Additional behavioural studies (e.g. Ilse 1937, Tinbergen *et al.* 1942, Tinbergen 1958, Crane 1955, Ilse & Vaidya 1956, Magnus 1958*a*, Swihart 1969, 1970, 1972*b*, C. A. Swihart 1971, Swihart & Swihart 1970) reveal colour preferences that may change with age and reproductive state, context, or learning.

Neurophysiological studies (it is extremely frustrating to find that several neurophysiologists rarely mention the sexes of the individual animals they so painstakingly study) have confirmed and extended these behavioural findings. Electroretinograms, single-cell recordings, optomotor responses and other data reveal broad sensitivity from less than 300nm in the UV through 700nm in the red, and more than one type of colour receptor in both butterflies and skippers (e.g. Swihart 1963, 1964, 1967*a*, 1970, Post & Goldsmith 1969, Schümperli 1975, Bernard 1979). Swihart (1969) has modelled colour vision as a dichromatic system in a skipper, and 'at least a trichromatic system' in a *Papilio*, a *Heliconius* and a *Morpho* (Swihart 1970, 1972*a*, *b*), but since his experiments (and those of Schümperli 1975) do not include the UV portion of the spectrum, such conclusions and models must be considered premature and incomplete. It is probable that more than three colour receptors are present in some butterflies, as in some moths (e.g. four in *Spodoptera exempta*; Langer *et al.* 1979). The complexities of receptor structure (Bernard & Miller 1970), function (Swihart 1973) and integration (Swihart 1965, 1968, 1970, 1972*b*) are such that a full understanding of the neurophysiological basis of butterfly colour vision is still a long way off. (See also Goldsmith & Bernard 1974, Horridge 1975, Mazokhin-Porshnyakov 1969, Menzel 1975.)

Building upon the foundation of Crane's work with *Heliconius*, Swihart (1963, 1964, 1965) studied the integration of visual information in the central nervous system of several species (Swihart 1967*a*). He had found that 'the behavioral sensitivity of [*H. erato*] seems . . . to be related not to any modification of the [visual] receptors, but rather to the development of [neural] pathways which "selected" the output of those receptors which

transduced information with special biological significance.' His findings generated the hypothesis that 'there was a selective advantage in developing neural mechanisms which demonstrate disproportionate sensitivity to the basic wing coloration, presumably because of the role played by such colors in releasing courtship behavior.' Studies on six species resulted in the discovery of a match between the spectral reflectance curve of the butterflies' wings, and the spectral efficiency curve for summated responses of high-order neurons in the medulla interna (Swihart 1967*a*). For example, the red and black *Heliconius erato* was found to have a peak response in the red, the green *Philaethria dido* and *Siproeta stelenes* a peak response in the green, and the iridescent blue *Morpho peleides* to have a maximal response to blue. He concluded that 'butterflies possess a neural mechanism which "selects" the output from various receptors in such a manner as to make the visual system respond maximally to stimulation with colors approximating the wing pigmentation.' It thus appears that colour preferences are effected by means of stimulus filtering in the butterfly brain. At the receptor level, contrast may be enhanced for biologically meaningful colours by selective back-reflection of narrow spectral regions from laminar tapetal interference filters (Bernard & Miller 1970, Bernhard *et al.* 1970, Miller & Bernard 1968, Ribi 1980).

Spatial resolution

The spatial resolution of a butterfly's eyes is related to the angular separation between ommatidia. However, the correspondence between interommatidial angles, and neurophysiological and behavioural measurements of resolution, is limited by complexities of ommatidial optics and receptor physiology (Goldsmith & Bernard 1974, Palka & Pinter 1975, Wehner 1975). In general, butterflies have a resolution of several degrees of arc, hundreds of times coarser than humans (0.5min of arc). From a behavioural standpoint, the amount of information obtained per solid angle of view is of greater interest than the simple angular resolution. Because the former is a squared function of the latter, the spatial information-gathering ability of butterfly vision may be tens of thousands of times lower than that of humans and other vertebrates. It is unlikely that pattern details of small objects, such as other butterflies, are resolved until they are extremely close (see Eltringham 1919, Mazokhin-Porshnyakov 1969, Yagi & Koyama 1963). Little is known about central processing of spatial information in butterflies (Swihart & Schümperli 1974, Schümperli 1975, Schümperli & Swihart 1978), but visual field organization and hierarchy generally resembling that of vertebrates has been found in some insects (Schümperli 1975, Wehner 1975).

The angle of view of butterfly eyes is very large, accounting in part for the difficulty of approaching alert species from any direction. One might think that the dorsal colours of a butterfly would not be visible to another that was below or in front of it (Wallace 1889). But the wide angle of view, the lowering of the wings to a nearly vertical position on the downbeat (Silberglied & Taylor 1978), and the forward projection of certain structural colours (Darwin 1880) make it likely that one butterfly can see the dorsal surface of another from most positions during flight. While there is little direct experimental evidence for depth perception in butterflies, a neurophysiological basis has been found in numerous protocerebral cells containing input from both eyes (Schümperli 1975).

The meagre behavioural data on pattern and spatial discrimination indicate that ovipositing female butterflies are capable of visually discriminating between leaves of different shapes (Rauscher 1978). They possibly detect eggs visually (Gilbert 1975; Ch.3) as well as chemically (Rothschild & Schoonhoven 1977, Ch.6). However, male *Hipparchia* butterflies do not discriminate among dummy butterflies of different shapes (Tinbergen *et al.* 1942, Tinbergen 1958), and pattern details play little role in species and sexual discrimination (Tinbergen *et al.* 1942, Tinbergen 1958, Crane 1955, Stride 1957, Magnus 1958*b*, Obara 1970, Rutowski 1977*a*) although there do appear to be some exceptions: *Papilio xuthus* (Hidaka & Yamashita 1975, 1976) and *Limenitis camilla* (Lederer 1960). In general, it does not appear that shape information is particularly important in the context of butterfly communication.

Temporal resolution and motion detection

The temporal resolution of the eye is generally measured in terms of the frequency at which successively presented images fuse. *Argynnis paphia* has been shown to have flicker fusion at about 150 images per second (A. Müller *in* Magnus 1958*a*,*b*), compared with about 40 per second in humans. It has been suggested that, for a moving insect or subject in view, the information gained from more frequent sampling of the visual environment may compensate to some extent for low spatial resolution.

A butterfly can detect a moving object if it differs in colour from the surrounding field, an ability that is greatly enhanced if a difference in brightness is also present (Kaiser 1975).

Polarization

Arthropod photoreceptors exhibit a general sensitivity to polarization, used at the behavioural level for orientation (von Frisch 1968). The iridescent reflection from the wings of some butterflies should

be strongly polarized at certain angles. To my knowledge, this phenomenon has not actually been demonstrated, and its possible role in visual communication is unknown.

Non-imaging photoreceptors

Such receptors might also play a role in communication. Adult butterflies lack ocelli, but extra-ocular photoreceptors have recently been reported on the genitalia of both sexes in a small but diverse array of species (Arikawa *et al.* 1980). This 'anatomical provision for hindsight' (C. M. Williams) may serve some function during copulation.

Butterfly Colour Patterns

The colours and patterns of butterfly wings have been responsible for their great popularity among scientists, collectors and the general public. Attention has been given to the nature and synthesis of pigments, the mode of production of structural colours, the development and genetics of wing colour and pattern, and the role of visual signals in communication with vertebrate predators. However, the signal properties of butterfly colours and patterns, as related to communication, are as yet poorly understood. It is not intended to provide a comprehensive review of this formidable subject, which has been reviewed in general terms by Hailman (1977) and Hamilton (1973). Rather, a few features of butterfly coloration especially pertinent to the topic of this paper will be discussed. Readers are referred to the voluminous literature on butterfly coloration for reviews of other aspects (e.g. Crane 1954, Graham 1950, Nijhout 1978, 1981, Papageorgis 1975, Poulton 1908, Robinson 1971, Schwanwitsch 1924, Silberglied 1977, 1979, Turner 1977*a*, 1978, Vane-Wright 1975, 1976, 1979*a*).

Ultraviolet patterns

The human observer describes butterfly colours in terms of our system of colour nomenclature, which is inadequate for the task because butterfly vision includes an ultraviolet (UV) component. With some exceptions, diurnal terrestrial vertebrates do not see UV, so this spectral region may provide a 'private channel' for communication among insects (Silberglied 1979). A butterfly's wings may reflect little or much UV; as with 'visible' colours the reflection may be produced by scattering in the absence of UV-absorbing pigments, or by physical means. A great variety of UV patterns exists, even in 'visibly' concolorous groups such as pierids and satyrines, and striking differences in UV patterns between otherwise similarly coloured species occur in many genera (e.g. *Colias*, Silberglied & Taylor 1973, 1978; *Gonepteryx*, Mazokhin-Porshnyakov 1957, Nekrutenko 1968; *Phoebis*, Allyn & Downey 1977; *Pieris*, Bowden 1977; *Prepona*, Descimon *et al.* 1973–74) (cf Wynne-Edwards 1962: 34). Sexual dimorphism is more pronounced in the UV than in the 'visible' spectrum; local polymorphism, geographical variation and other colour phenomena also occur (Silberglied 1979). Since insect compound eyes are maximally sensitive in the UV, as much attention should be paid to UV patterns as potential sources of behaviourally meaningful signals, as to 'visible' reflection patterns. Furthermore, since vegetation generally absorbs UV, reflection in this region serves to maximize colour contrast in terms of insect vision.

Iridescence

Iridescence is usually defined as 'exhibiting a rainbow-like display of colours'. Most cases of iridescence in butterflies are attributable to reflection from multiple thin-film interference filters present in the outer layer of wing scales (Mason 1926–27, Anderson & Richards 1942, Simon 1971). In most such cases, including spectacular examples such as *Morpho* and many lycaenids, the range of reflected colour lies in the blue-to-violet end of the 'visible' spectrum; further investigation usually reveals intense UV reflection as well (Ghiradella *et al.* 1972, Ghiradella 1974). Due to the mechanism of colour production, such colours change in hue and intensity as the angle of the wing changes during flight (Crane 1954). At any particular angle, the reflection is of very high spectral purity and thus unlike other reflected light in the terrestrial environment. To an observer watching through a narrow spectral window (e.g. a television camera with a narrow-band filter; Eisner *et al.* 1969) or with species whose reflection barely enters the 'visible' spectrum (e.g. *Apatura* spp.), these butterflies are conspicuous at considerable distances as their wing reflection flashes 'on' or 'off'. The reflection may also be partially polarized at certain angles.

Such iridescent patterns are widespread among butterflies, especially in the three largest families, Lycaenidae, Nymphalidae and Pieridae. In pierids and some other groups, these spectacular patterns of iridescence are nearly always totally invisible to the human eye, as the reflection does not pass beyond 400nm into the violet. Iridescence, whether 'visible' or UV, is largely restricted to the dorsal wing surfaces, and is far more strongly developed in males.

Light colours

A large number of species are light in colour; nearly all of the Pieridae, for example. White and other light colours also provide contrast with vegetation, and the suggestion has been made at various times that white may be aposematic (Wallace 1889, Kettlewell 1965, T. Eisner, pers. comm., C. L. Remington, pers. comm.). In light coloured butterflies, the ventral wing surfaces are usually darker and bear cryptic

patterns and colours. Where sexual dimorphism occurs among light-coloured species, the males usually have a uniform field of colour, while that of females is infuscated or obscured by other markings.

Orange and red

Orange and red patterns must be considered to have potential signal value, since butterflies, unlike other insects, can see these colours. Red has been demonstrated to have a communication function in *Heliconius* (Crane 1955).

Sexual dimorphism

When the sexes differ in coloration, females usually have a protective pattern, either more cryptic or more mimetic than males. The male pattern is often visible from a greater distance than that of the female, even in cases where the latter is mimetic of an aposematic unpalatable model. Female coloration also appears to be more variable, as has been shown quantitatively in moths (Fisher & Ford 1928).

Variation and polymorphism

In species with local polymorphism, either both sexes are polymorphic, or only the females. Male-limited polymorphism is virtually unknown in butterflies (Brower 1963, Turner 1978). Some species are polymorphic on a seasonal basis. The males of polymorphic species cannot use a single, narrow, visual searching-image for females. When both sexes are polymorphic, females likewise cannot use a single colour pattern to recognize conspecific males. Where geographic or seasonal variation or polymorphism occurs, there must be some compensation in the use of visual signals, by corresponding variation in the signal-receivers' behaviour (Burns 1967), a broad range of, or multiple, acceptable signals, constancy of the signal component (Rutowski 1981), or less reliance on visual signals for communication (Richards 1927, Brower 1963).

Mimicry

Mimetic species cannot use visual signals exclusively for communication, or confusion with similarly-coloured species would result. In sex-limited mimicry, the male cannot use visual signals alone for the recognition of conspecific females, but females could use them to recognize males. Brower (1963; see also Ch.25), in a brief but seminal discussion of sex-limited mimicry, suggested that in Müllerian mimicry where both sexes are mimetic, 'scent plays a more important role in courtship than sight.' It is alternatively possible that mimetic species use distinctive patterns of UV reflection for sex- and species-recogition (Remington 1973, Silberglied 1979).

A wide range of problems involving the use of visual signals by variable, polymorphic or mimetic species awaits investigation. For example, what visual signals are employed by male *Papilio dardanus*, and do these signals vary geographically with the female morphs? If red coloration is critically important in *Heliconius erato*, what signals are used by the yellow and blue Colombian *H. e. chestertonii*, the only subspecies that lacks red markings (see Turner 1975*a*)? How do similarly coloured sympatric congeners (e.g. *Adelpha* spp.) tell one another apart?

Butterfly Courtship

The courtship of butterflies is a complex ritual, involving the exchange of visual, chemical and tactile stimuli. While it differs in detail from one species to another, a general sequence of behaviour is followed by most species (Scott 1973*d*, Hidaka 1973, Silberglied 1977).

Courtship is usually initiated by the male. Males locate females by using one or both of two behaviour patterns: 'waiting' for females in locations where they are likely to be encountered, or 'seeking' females by active, persistent search of the habitat (Magnus 1963; these behaviours have also been named 'perching' and 'patrolling' by Scott 1973*d*, 1974*b*). Both types of behaviour may be found within a species (Dennis 1982), or in an individual at different times (Davies 1978).

Actual courtship begins in response to the sight of the female. It is easy to study the initial approach behaviour of males, by using 'dummies' of various sizes, shapes and colours (e.g. Crane 1955, Magnus 1958*b*, Petersen *et al.* 1952, Petersen & Tenow 1954, Silberglied & Taylor 1978, Stride 1957, 1958*a*, Tinbergen *et al.* 1942, Tinbergen 1958). The visual stimuli required to attract a male are surprisingly unspecific in many species. Movement, colour and size are usually important, while shape and detail of pattern are not (but cf. Lederer 1960, Hidaka & Yamashita 1975, 1976). Males of some species fly after anything that might be another butterfly, including falling leaves, birds, or a moving butterfly net. Further male behaviour appears to depend on the response of the chased object—other males may be chased away, birds avoided, and females courted.

In *Colias*, only a stationary visual stimulus is needed to release the entire sequence of male courtship behaviour, so that males may actually copulate with paper dummies (Silberglied & Taylor 1978). In other species (*Argynnis*; Magnus 1950, 1958*b*), the male requires motion and olfactory cues before continuing his courtship.

The later stages of courtship depend on the receptivity of the female. In those species carefully studied to date, olfactory signals released by the male are usually required for successful mating (e.g. Brower *et al.* 1965, Lundgren & Bergström 1975, Magnus 1950, Pliske & Eisner 1969, Rutowski

1977*b*, 1978*a*, 1980*a*, Stride 1958*a*, Tinbergen *et al.* 1942, Tinbergen 1958; cf. Pliske 1975*b*; for reviews see Scott 1973*d*, Silberglied 1977 and Ch.25). The more elaborate behaviour associated with courtship appears at this stage, when the male disseminates his odour(s) in the vicinity of, or directly upon, the female's antennae. Depending on the species, the male may dust her antennae during flight or while she is resting (*Danaus gilippus*; Brower *et al.* 1965), rub her antennae with one or both wings (Tinbergen *et al.* 1942, Temple 1953), or perform other specialized, species-specific behaviours (Crane 1955, 1957).

Most females encountered by males have already mated, and in most cases mated females respond negatively towards males. This negative response is characterized by 'rejection postures', 'ascending flights', and other behaviours which vary in detail from one species to another (Scott 1973*d*, Stride 1958*b*; see also Rutowski 1978*a*,*b*, Edmunds 1969), Chovet 1983). Males usually persist for a while in spite of the rejection posture, and a female that initially rejects a male may later accept him (Petersen & Tenow 1954).

In the final stage of courtship, the male positions himself alongside the female and probes laterally and ventrally along her wings with his abdominal tip, in an attempt to locate and couple with her genitalia. In most species, there is no visible indication that the female has accepted the male, other than absence of rejection posturing. In a few cases the female may be seen to adjust her position and lower her abdomen (Rutowski 1977*b*).

In some species, a receptive female may initiate courtship with a 'solicitation' flight towards a male (Crane 1955, Stride 1956, 1958*b*; Ch.21, Lederer 1960, Rutowski 1980*b*, 1981). Courtship may also be said to be initiated by the female in those few species where a sex-attractant pheromone is used (see also Ch.25). Such cases sometimes involve mating by the pharate or teneral female. Facultative mating with teneral females is common in many butterflies; in these circumstances the female may be unable to reject a male and prevent insemination (Taylor 1972).

In most species, the female becomes unreceptive after mating, and rejects subsequent matings for some time. Because the number of matings by a female may easily be determined by counting the number of spermatophores in the bursa copulatrix, substantial data exists on female mating frequency (Burns 1968; Ch.22). In general, females mate at most only a few times; large numbers of matings are very unusual (Ehrlich & Ehrlich 1978). Thus most mating attempts by males are not successful. Unsuccessful courtships may result from general female unreceptivity, female coyness or female preference (Ch.21).

While mating behaviour is usually initiated by males in response to visual stimuli, subsequent courtship behaviour is more complex. The male may require olfactory stimulation or he will not persist, and the female generally requires male olfactory stimuli before accepting (Ch.25). Tactile stimuli may be exchanged, especially in the later stages just prior to and during copulation. The role of visual stimulation during the later phases of courtship is poorly understood. In particular, the question of whether the female 'chooses' the male (or the male 'chooses' the female) on the basis of visual stimuli is not easily answered (see also Ch.21).

Visual Signals affecting Male Behaviour

The responses of male butterflies to visual stimuli have been studied in virtually every experimental investigation of butterfly courtship behaviour. Generally, dead specimens or 'dummies' have been used as stimuli, and the number of approaches by males counted as a measure of attractiveness. Such experiments are simple to perform, and the results have generally been consistent from one such study to another. One of their drawbacks is that little information is gained about the response of males to colour and pattern in later stages of courtship. Another problem with 'approach tests' is that the males' behaviour may easily be misinterpreted: males may be attracted to stimuli for reasons other than courtship (e.g. feeding, aggression, roosting, puddling, etc.). Some of these difficulties are circumvented by studying the behaviour of males toward living females in flight cages, or on tethers (e.g. Crane 1955, Brower 1959, Rutowski 1981, Silberglied & Taylor 1978).

Another method used to assess the importance of visual stimuli to males, compares mating frequencies of female colour phenotypes in polymorphic species relative to the frequencies of these morphs in the population (e.g. Smith 1973, Burns 1966, Pliske 1972; Chs 21, 22). Such data are obtained from mating pairs collected under field conditions, or from spermatophore counts in wild-caught females of the various morphs. While of great value in documenting assortative mating or sexual selection, this work does not necessarily identify the colour patterns as the signals used by male butterflies in mate choice. The correspondence between colour phenotypes and mating success may also be due to differences between female morphs in vigour, behaviour (coyness), pheromone production, longevity, or other properties correlated with or genetically linked to pattern loci.

In general, males are attracted to visual stimuli coloured most like the conspecific female (but see also Ch.23). The detailed pattern of the butterfly need not be duplicated in the more attractive dummies; only colour and UV reflection need

resemble the female (e.g. Magnus 1963, Stride 1956, Obara 1970, Obara & Hidaka 1968, Silberglied & Taylor 1978). Often the ventral wing colour, exposed by the female when at rest, is most attractive. Both saturation and intensity of the colour make important contributions to a dummy's attractiveness. It has sometimes been possible to make artificial dummies that were more attractive than female specimens (Magnus 1958*b*, Silberglied & Taylor 1978).

In sexually dimorphic species, the colour of the male may be *deterrent* to other courting males, rather than neutral or attractive (but see also Ch.23). This was first discovered by Stride (1956, 1958*b*), who added the white of male *Hypolimnas misippus* wings to otherwise attractive female dummies. Males initially attracted to some of these dummies departed immediately, rather than persist in courtship. It is significant that the most pronounced deterrent effect was produced when he used white pieces of males' wings (rather than white areas from another species or an artificial material), which are intensely UV reflecting and iridescent (see also Ch.21 concerning this work). Rutowski (1977*a*) found that the UV flash of sitting, fluttering male *Eurema lisa* inhibited further courtship attempts by other males; courting males did not distinguish males lacking UV from females. In *Colias*, Silberglied & Taylor (1978) found that simply adding UV-reflection to an attractive dummy produced a 30- to 50-fold decrease in its attractiveness. They also found that mating males of *C. eurytheme* and *C. philodice* expose their hindwings when approached by another male; in *C. eurytheme* this action produces a sudden flash of intense UV-reflection that is surely repellent to the intruder.

In some species, male coloration elicits agonistic behaviour in other males. The deterrent or intimidating effect, of male colour on the behaviour of other males, is probably 'turned off' (or interpreted differently) during puddling behaviour, a predominately male activity (Arms *et al.* 1974).

Where studied, motion has been shown to significantly increase the attractiveness of a dummy (e.g. Tinbergen *et al.* 1942, Crane 1955, Magnus 1958*a*,*b*). In Magnus' classic experiments with *Argynnis paphia*, motion of the dummy was necessary to hold the attention of the male. He found that more and more effective super-normal stimuli could be created by increasing the degree of flicker in the dummy's apparent motion, until the flicker-fusion-frequency of the butterfly's eye was reached.

Size is another important stimulus. A graded response to size has usually been found, with low responses to dummies of the appropriate colour smaller than the female, good responses to dummies of the same size, and super-normal responses to giant dummies (Tinbergen *et al.* 1942, Tinbergen 1958, Silberglied & Taylor 1978). Males do not appear to discriminate against dummies shaped differently from the female, unless the differences assume extreme proportions (Tinbergen *et al.* 1942).

The details of wing-pattern usually do not contribute to the attractiveness of a dummy, except where the pattern affects the saturation or intensity of the entire wing. Thus the minor sexual differences of pattern found in genera like *Colias* (light spots in the dark borders of females), *Pieris*, etc. probably do not matter to males, at least in the initial attraction (Rutowski 1981).

Ethological studies of species with female polymorphism have sometimes demonstrated male preference for dummies resembling one of the morphs relative to others. Yellow females of *Pieris bryoniae* are less attractive than white ones (Petersen 1952). Magnus (1958*b*) found that the dark female form 'valesina' was less attractive to male *Argynnis paphia* than the normal phenotype. Extrapolating from the result that white is inhibitory to male *Hypolimnas misippus*, Stride (1956) tried to account for the rarity of its 'alcippoides' form (but cf. Edmunds 1969*b*, Smith 1976*a*, Ch.21). Burns (1966, 1967) used spermatophore counts from field-collected females to argue that male preferences maintain the non-mimetic female morph in *Papilio glaucus* (but cf. Prout 1967, Pliske 1972, Levin 1973, Barrett 1976; Ch.22). Male *Anartia fatima* are more attracted to dummies with white bands than to those with yellow bands; in this species the colours are not under genetic control, but change gradually from yellow to white with age (Emmel 1972, 1973*a*, cf. Taylor 1973*b*, Young & Stein 1976, Silberglied *et al.* 1979). The data and interpretation of several of these studies have been subject to dispute. I will discuss (below) only the relevance of dummy experiments to male mating behaviour under natural conditions.

Visual Signals affecting Female Behaviour

> Literally not one particle of evidence [exists] that the female is influenced by colour.
>
> (Wallace 1877)

> There is no proof to date for the assumption that any visual selection in favor of normally colored males takes place by butterfly females.
>
> (Magnus 1963)

In contrast with the numerous studies of the role of visual stimuli in male courtship behaviour, few attempts have been made to obtain similar information about females. There are many reasons for this. Male butterflies are aggressive in initiating courtship attempts, but females usually are initially passive or preoccupied with other activities. Any study of female courtship behaviour requires sexually active males. Second, 'determined' approaches can be used to bioassay attractive visual stimuli for males, but such tests can rarely be performed with females.

The coy responses of females are such that only actual copulation (or in rare cases where it is recognizable, solicitation flights or acceptance behaviour such as exposing the abdominal tip; Rutowski 1977*b*, 1981) can be used to compare the relative acceptability of various male phenotypes. Because females become unreceptive after mating, each can be used only once, so many virgin females are required. Third, many species have polymorphic females, and the experimenter may use the various female forms, dead specimens or even paper dummies as stimuli for courting males. But since males are rarely polymorphic, and because active males are required to test female responses, the investigator must modify living males with various experimental treatments to produce different colour or pattern phenotypes. Fourth, most experiments involving choice by females, between males from different groups, must be conducted in cages to keep the butterflies from dispersing, but many species will not behave normally in such an environment. Only those individuals that do not spend all their time trying to escape can be used, so large numbers must be reared to produce a cage-adapted population. Fifth, since mating behaviour changes with age, all experimental groups of each sex must be 'balanced'—they must have the same age distribution. Sixth, I have found that in nearly every experiment of this kind, untreated males mated more frequently than did treated control males of the same colour. This is probably due to minor injury of the latter during handling and treatment (see also Ch.4). A comparison between experimentally colour-modified males, and normally coloured, but *un*treated control males, is generally meaningless. Both untreated and treated control groups, as well as one or more experimental groups, should be included in the design of such experiments. For these and other reasons, few have attempted to perform them.

Crane (1955) and Rutowski (1981) used 'angling' techniques to assay for female responses to tethered males and artificial dummies. This method can succeed only if there is a visible bioassay for female acceptance behaviour.

Field data, on assortative mating in polymorphic species, are of limited value in determining the importance of male colour to females. Non-random mating and/or sexual selection are not necessarily due to visual discrimination and choice, even when there are coloration differences between phenotypes. While male phenotypes may differ in their relative representation in mated pairs, such a result may arise because of differences between morphs in thermal properties, vigour, courtship activity, competitiveness, pheromone production, longevity, etc. The rarity of male polymorphism is a serious practical limitation to the use of this technique, but it has been employed by Smith (1975*c*, 1980, 1981, Ch.21) in *Danaus chrysippus*. The method may also be used in species like *Chlosyne lacinia*, in which several colour forms occur sympatrically in both sexes. Field mating data may suggest that visual discrimination is occurring, but only experimental studies can test for the operation of visual signals.

Given these limitations, it is not surprising that data on female colour preferences are few, and needs to be augmented by additional studies of other species. Anyone with large cultures of living butterflies has the opportunity to test the ideas presented below. Experimental studies of the role of colour in mate selection in 'visibly' dimorphic species are particularly desirable.

Crane (1955) was the first to attempt the experimental study of the role of colour in female acceptance behaviour. She painted both sexes of *Heliconius erato* various colours, and observed the behaviour of other butterflies towards them. She claimed that 'the farther the altered color of the forewing from the normal scarlet in the spectrum, the less notice is taken of the butterfly, either by the opposite sex or as a general subject for social chases.' But she also remarked that 'positive courtship responses, sometimes including copulation, were obtained at least once for each color change effected in each sex', and that 'females were in general less influenced [in behaviour] by color change than were males.' Her discussion of this experiment includes no indication of sample size for each colour beyond 'at least one butterfly of each sex', and she did not include treated control individuals. She describes difficulties with variables of weather and the physiological state of the butterflies, and the reader is presented with a generalized summary of the results rather than quantitative data. It is not clear that social interactions were fully separable from sexual behaviour. Finally, most of her discussion of the role of colour deals with the responses of males.

Another series of experiments performed by Crane (1955) used cloth dummies angled from bamboo wands. The *single* female tested responded 'positively' to red and orange, but minimally or not at all to other colours. The 'female's responses were . . . gauged from the strength of her courting behavior, shown by the degree of abdomen elevation, extrusion of yellow gland, apposition of forewings and fluttering of hindwings.' But this is a description of female rejection behaviour (L. Gilbert pers. comm., J. Mallet pers. comm.). One may not conclude that female *H. erato* discriminate between males on the basis of colour.

Stride (1958*b*) studied the responses of female *Hypolimnas misippus* to two kinds of modified males. Two 'black' males had their white spots blackened chemically, a treatment that did not affect the UV-blue iridescence. Three 'colourless' males had most of their wing scales removed. Males were tested

individually in a large flight cage containing six virgin females in each test. None of the 'colourless' males mated successfully (18 courtships), while both of the blackened males were successful (three courtships). All four untreated control males mated (four courtships). Unfortunately, Stride did not include a treated control group, so there is no way to evaluate the traumatic effect of scale removal. He did not control for odour (Brower 1963), so the results may have been affected by disruption of a chemical communication system involving wing-born pheromones (cf. Silberglied & Taylor 1978, Rutowski 1980*a*, Grula *et al.* 1980). His sample size is too small for statistical analysis. Nevertheless, the all-black males mated successfully, so one can probably agree with Stride's conclusion that 'the white spots on the wings of the males played little part in the courtship of the butterfly.' There was no female selection against males lacking the most conspicuous 'visible' pattern element.

Rutowski (1981) used his 'angling' technique to study solicitation flights of female *Pieris protodice*. By removing UV-absorbing pterins from the wings of males, he produced dummies that resembled females. He found that females use the UV-absorption of males as a sexual recognition signal. No colour modifications were performed in the 'visible' spectrum.

In *Danaus chrysippus*, a species in which both sexes are polymorphic, males heterozygous at a locus affecting colour pattern have a significantly higher mating success than either homozygote (Smith 1981, Ch.21). However, the minor colour differences between the heterozygote and one of the homozygotes are probably too small, in my opinion, to be acted upon by visual selection. Smith partly attributes the difference in mating success to inter-male competition, mediated through the interaction of climatic conditions and the thermoregulatory properties of these colour patterns.

Silberglied & Taylor (1978) reported an extensive series of experiments on two species of *Colias*. Their goal was to identify the basis of conspecific assortative mating by females. The experiments, performed in flight cages, involved large numbers of receptive females of both species, both untreated and treated control males as well as experimental groups, and balance for age distribution.

Colias eurytheme has orange, UV-reflecting males, while male *C. philodice* are yellow and UV-absorbing. Males of the yellow species were coloured orange by means of felt-tipped pens, and the males of the orange species yellow, by transplanting the discal area of the wings, of a yellow-winged, UV-reflecting strain of hybrid origin, onto the corresponding area of *C. eurytheme*. Females were still fully discriminatory: they mated conspecifically, and they *accepted* the peculiarly-coloured conspecific males as frequently as they did the normally-coloured treated control males of their own species. In another experiment, males *C. eurytheme* (Colour plate 4A) and *C. philodice* (Colour plate 4B) dyed orange, red, green, blue and black mated as frequently and as conspecifically as did treated control individuals!

The only visual component, the modification of which had any effect on female mating behaviour, was the ultraviolet reflection of *C. eurytheme*. Regardless of their 'visible' colour, males of this species whose UV reflection had been destroyed, suffered a significant drop in the number of successful conspecific matings. Yet they were not accepted by *C. philodice* females, even though the males of *C. philodice* are UV-absorbing, and even though *C. philodice* females accept their own males in any colour. In short, the females of *C. eurytheme* responded only to the UV component of wing coloration, and the females of *C. philodice* acted as though they were totally blind to the male colours or UV reflection!

The olfactory basis of mate selection has since been identified in these *Colias* species (Rutowski 1980*a*, Grula *et al.* 1980). So far as female discrimination is concerned, olfactory cues are far more important to the females of these species than are visual signals (Silberglied & Taylor 1978). It is significant that the females of these species are polymorphic for colour, while the males are not. This colour distribution agrees with the idea of stronger female than male sexual selection stabilizing coloration of the opposite sex. But the experimental results directly conflict this suggestion.

I have since carried out one additional experiment on the role of colour in female choice, this time with the brilliant red Neotropical species *Anartia amathea* (Colour plate 4C). It was performed in collaboration with Annette Aiello at the Smithsonian Tropical Research Institute, and is published here for the first time. The experiment meets all of the criteria discussed at the beginning of this section.

Freshly-eclosed but hardened *A. amathea* were used. Virgin females were mixed with equal numbers of males, divided into three groups: untreated control (red), treated control (red), and experimental (black). Treatment involved painting the dorsal wing-surfaces with clear (Ad Marker (R), Jacksonville, Florida: Warm Gray 1) or black (same brand, Super Black) felt-tip pens. The butterflies were released into a flight cage and subsequent matings recorded. Because there were three groups for each sex, there were nine mating combinations possible. The results are presented in Table 20.1.

Only 21 matings were obtained, so the number in each cell is very small. For both logical and statistical reasons (the total number of matings in each cell is the result of two phenomena: male attraction/courtship of females and female acceptance/rejection

Table 20.1. A mating experiment on sexual selection for colour in the brilliant red butterfly *Anartia amathea* (Nymphalidae)

	Females			
	Red (untreated control)	Red (treated control)	Black (experimental)	TOTAL
Males:				
Red (untreated control)	5	3	1	9
Red (treated control)	3	2	0	5
Black (experimental)	4	3	0	7
TOTAL	12	8	1	21

The experiment was performed in a 3m × 3m × 2.1m screened cage on Barro Colorado Island, Panamá, with stocks collected in the Darién region of eastern Panamá, in 1976.

behaviour, and the small sample size in each cell), the results in each of the nine cells cannot be meaningfully compared with one another. However, if we compare the number of matings by group within each sex, a distinct picture emerges.

Notice first the number of matings by females in each of the three groups. Black (experimental) females did not mate as frequently as did either of the red females (one-tailed binomial test of black vs. red treated control females, $P = 0.02$; Siegel 1956). It is highly unlikely that the acceptance/rejection behaviour of females is changed by painting them a different colour. The only logical conclusion is that the males spent little time courting them compared with the red females. This is entirely consistent with what we know about the role of colour in male behaviour.

On the other hand, notice that those females that mated did *not* discriminate between the red and black males (one-tailed binomial test of black vs. red treated control males, $P = 0.44$) (or if they did, they might have preferred the black!). Thus females did *not* choose on the basis of the red colour—the most conspicuous feature of the wings and the only colour present. A devil's advocate might argue that they prefer black, but this is hardly what we are concerned with when we speak of the brilliant colours that have been or could be so nicely explained by female sexual selection. This brilliant red butterfly sees red (Bernard 1979), and the males respond to red. Because the male has the more brilliant red coloration, it is only logical that it be the result of female selection. Yet it is clear even from this minor experiment that such is not the case.

Brower *et al.* (1971) have argued convincingly that *A. amathea* is an 'incipient mimic' of *Heliconius erato/melpomone*. This contention is supported by their experimental data which show that predators, having learned to discriminate *H. erato*, will also sight-reject *A. amathea*. Thus the red coloration might be 'explained' on that basis. But the male of *A. amathea* has a more brilliant red and a darker black, and would probably be a better mimic. Unless the red of the male serves some other role, we have a case in which the male is the better mimic than the female, which would be a unique situation so far as I am aware (Carpenter & Ford 1933).

Discussion

Is it possible, or wise, to attempt to make generalizations about the use of visual signals for communication among the 10 000–15 000 species of butterflies? I believe it is, because they all have to deal with the same problem: recognition of and communication with conspecific individuals. Their vision is constrained by the same solar spectrum. Their use of colour is limited by biosynthetic versatility, as well as by the activities of visually-oriented predators. Diverse solutions to the problem are found, including the discarding of visual communication for many functions. But a general picture of the use of visual signals by butterflies has emerged from the confusing wealth of species, colour patterns and behaviour.

Before proceeding, it is well to emphasize that exceptions will be found to such generalizations, and that the exceptional cases, when studied in depth, often serve to confirm, refute or qualify the hypotheses generated. Since so few intensive studies of butterfly communication have been carried out, I cannot hope to convince—only to raise doubt where it should exist, about the classical interpretation of the role of butterfly colour patterns in communication.

The two functions—protection from visually-oriented predators, and social signals used during

courtship—may at first seem to be mutually exclusive, because the former often requires patterns that are difficult to detect (crypsis) or are confusing (mimicry), while the latter demands a high signal-to-noise ratio and uniqueness with respect to species and sex. But it should also be remembered that these functions involve different visual systems: the vertebrate lens-eye and the lepidopteran compound eye. It is possible that some patterns serve both functions by taking advantage of the differences between these visual systems (Silberglied 1979).

Vision and Pattern

Butterfly vision is characterized by excellent colour discrimination across an extremely broad visible spectrum, low spatial resolution and high sensitivity to motion or flicker. Colour contrast is increased in particular spectral regions by physical devices (e.g. tapetal reflection) and neurophysiological mechanisms (stimulus filtering). The ability of the insect's eye to detect a moving object is strongly enhanced by brightness- as well as colour-contrast. At the behavioural level, butterflies are capable of discriminating quite subtle differences of hue, intensity and saturation (e.g. the difference between greenish-yellow and yellowish-green on the ventral hindwings of male and female *Colias*; Silberglied & Taylor 1978), and of learning (C. A. Swihart 1971, Swihart & Swihart 1970).

Hence the extremely brilliant patterns that characterize the dorsal surfaces of so many male butterflies probably are not required for communication by any intrinsic limitations of the visual system. For iridescent colours, the change of hue with angle of the wing, narrow spectral reflectance at any given angle, abrupt intensity change with angle at any given wavelength, and strong ultraviolet component (and possible polarization) that contrasts strongly with vegetation, are features that would serve well as *signals for long-range communication*. *Morpho* can easily be seen from low-flying aircraft; the gleam of their wings, as they sail above the forest canopy, makes them appear as giant, blue, flashing beacons. Describing *M. rhetenor*, H. W. Bates (1864) reported that 'when it comes sailing along, it occasionally flaps its wings, and then the blue surface flashes in the sunlight, so that it is visible a quarter of a mile off.' Where iridescence is not involved, the flicker of the alternating dorsal and ventral surfaces exposed by beating the wing, often enhanced by colours that contrast well with the green of vegetation, might perform the same function. The patterns of females, being more variable and less conspicuous, ought not to be as apparent over the same visual distances as are those of the males.

The mode of colour production in butterflies allows for an overlay of transparent scales producing structural colour over a base of pigmented scales. As a result, these two types of coloration may evolve and be expressed independently of one another. We see a striking example of this in males of *Hypolimnas misippus* and related species, where a patch of intense ultraviolet reflection overlays both white and black. In terms of insect vision, this produces a white bull's-eye, surrounded by a ring of pure ultraviolet in a field of black. While the pigments have not been studied, only melanin or some other dark pigment would be required to achieve this effect, because white is produced by diffuse scattering, and the UV reflection by a transparent interference filter overlay. Thus, a remarkable range of coloration, with diverse optical properties, is made possible by the combination of pigmentary and structural colours. A glance through a collection reveals the extent to which these possibilities have been realized.

Thus we find two solutions to the problem of providing increased or decreased brightness- and colour-contrast. Reflectance over much of the spectrum may be increased (or decreased) (the pierid/satyrine solution). Alternatively, a particular colour may be increased (or decreased) in intensity beyond anything found in the habitat, by optical interference (the iridescence solution). The latter allows for the combination of intense reflection (or absorption) with *any* underlying visible coloration, and/or restriction of iridescence to the ultraviolet. The use of dark borders around a brilliant iridescence (as in most *Morpho*, some *Hypolimnas*, many *Colias*, etc.) provides a high-contrast edge to the intense colour field borne on the wings.

A visual signal may be effective in any spectral region that coincides with the spectral sensitivity range of the receiver. In butterflies we should expect to find important visual signals scattered from the UV to the red. Feeding and mate-finding behaviour are mediated in part by visual signals throughout the spectrum, and the butterfly's responses to differences of hue, saturation and intensity are most evident in these contexts. However, a surprising number of important signals involving sexual communication are effected through bright coloration at all wavelengths (white), UV-reflectance and iridescence. Many of these appear to be all-or-none signals, such as 'I am a male' or 'go away'. They differ from the full-spectrum group in that the signal's function is of great value to the sender as well as to the receiver.

Iridescent colours and/or ordinary high-intensity reflection, as well as large size, are characteristic of butterflies of open spaces, where long-range signalling may be important. The most spectacular examples of such colours are found in wide-ranging pierids and nymphalids that frequent the upper canopy, and species that use treefall gaps, shafts of sunlight and other openings in the forest. Such colour

patterns are relatively less well developed in the satyrines, ithomiines and other groups that frequent deep forest or dense vegetation. While there are numerous exceptions, I believe most lepidopterists would agree with these generalities (cf. Hingston 1933, Papageorgis 1975).

Courtship and Intersexual Selection

Male and female behaviour during courtship agrees well with observations on other organisms, and with recent sexual selection theory (see Blum & Blum 1979, Maynard Smith 1978, O'Donald 1980, Parker 1974, Rutowski 1982, Thornhill 1976, 1979, 1980, Trivers 1972, West-Eberhard 1979, Williams 1975). Males are aggressive toward rivals, and persistent in locating and courting females, while females are coy and effective at rejecting males. Female mate-rejection behaviour has been described in numerous species (Scott 1973*d*). A male butterfly usually cannot rape an unreceptive, rejecting female unless she is teneral (Taylor 1972).

Female rejection behaviour is elicited by courting males in a variety of situations. Recently fertilized females are generally unreceptive. A receptive female may respond with rejection behaviour in the initial stages of courtship, or she may respond negatively if the courting male lacks appropriate signals (e.g. another species with different pheromones). While UV visual signals are employed in a few cases, pheromones are almost always involved; a male that has been experimentally deprived of the necessary pheromones is usually rejected (e.g. Tinbergen *et al.* 1942, Tinbergen 1958, Pliske & Eisner 1969; Ch.25).

Male butterflies depart immediately after copulation: there is no behavioural post-mating investment by males on behalf of their offspring. Males do not control access to resources. Besides gametes, the male's only contribution toward his offspring is the spermatophore and its contents, which in one species have been shown to be metabolized by the female and incorporated into the contents of eggs (Boggs & Gilbert 1979; but see also Chs 3, 6).

If a female were somehow to assess male quality during courtship, in terms of potential paternal investment, she would have to do so on the basis of the spermatophore he would produce if she accepted him. Older males that have previously mated produce smaller spermatophores, and also place the female at risk to predation due to prolonged copulation times (Rutowski 1979, L. E. Gilbert, cited in Thornhill 1976, Silberglied, unpublished). But because of her low visual resolution, it is unlikely that a female can discriminate between young and old males on the basis of colour pattern or wing wear. Most of a female's efforts in a generally short life are spent locating suitable hostplants for oviposition (Watt 1968; Ch.6). A female is unlikely to waste valuable time selecting among males on the basis of colour or pattern, features that are likely to be poor predictors of age and male quality (cf. Thornhill 1980). A female that mated with a male who produced a small spermatophore (or who was judged unsatisfactory on any other grounds) could always remate sooner than she otherwise would. (Because strong sperm precedence exists in butterflies, a male should produce large spermatophores to prevent this—Ehrlich & Ehrlich 1978; see also Rutowski 1978*a*, 1978*b*.) Another male adaptation that may perform a similar function is the antiaphrodisiac pheromone (Gilbert 1976). The female should minimize the time to copulate with a healthy male, so as to get on with oviposition—and the identification and health of a male may be better determined by chemical signals than by visual ones (Rutowski 1978*b*, 1981; Ch.21). Chemical signals may be more reliable at close range than visual ones, due to variation in lighting conditions and in the relative positions of sender and receiver. Initial rejection behaviour by receptive females may also be interpreted as a means of assessing male vigour or potency (Rutowski 1979).

Butterfly Coloration and Male Behaviour

Male butterflies definitely use colour as a signal to recognize females. This has been demonstrated in nearly every experimental study. But generally males do not encounter more than one female at a time, and they respond to anything that *might* be a female by approaching it. In natural conditions, males must decide whether to chase sequentially presented stimuli that might be conspecific females. A wild male rarely chooses between different stimuli presented simultaneously, as is usually the case in 'dummy' experiments. Males make inspection flights in response to a much broader range of visual stimuli than one might predict on the basis of results of approach tests.

Unlike females, males may mate many times; variance in the number of matings by males is probably quite high. Because receptive females are scarce and competition among males is high, one should not expect to find strong male discrimination against conspecific receptive females. In fact, males often persistently court, and sometimes mate with, females of other species and even on rare occasions with other males (Tilden 1980, Silberglied, unpublished).

It is unusual to find unmated older females (Ehrlich & Ehrlich 1978), even in species having female polymorphism with 'unattractive' forms such as 'valesina' of *Argynnis paphia* (Magnus 1958*b*) and 'turnus' of *Papilio glaucus* (Burns 1966, 1967; cf. Prout 1967, Pliske 1972, Levin 1973; Ch.22). Such

females may or may not attract as many males, over as great a distance or as often, as 'normal' phenotypes, but it is unlikely that the availability of willing males is ever limiting, or that copulation by such females is significantly delayed. Females may also compensate for lower attractiveness to males by performing 'solicitation' flights.

For these reasons I do not believe that the colour preferences shown by males, under experimental conditions, necessarily translate into significant sexual selection on female colour in the field. There exists a graded response to sign stimuli, but it is in the male's best interest to mate at every opportunity, and to drive away or avoid competing males. A male's colour preferences serve him well in *locating* conspecific females, in shunning or thwarting rivals, and in wasting less time with members of other species. But because opportunities for choice between receptive females rarely occur, male colour preferences probably do not serve to stabilize female pattern to any great extent (Magnus 1963, Pliske 1972). The high variability of female coloration, and female polymorphism, are indirect reflections of this (cf. Richards 1927).

Butterfly Coloration and Female Behaviour

It is not surprising that we know so little of female preferences in butterflies. This situation is a reflection of the difficulties involved with such experiments, including the few female behaviours that can be used to measure the relative acceptability of males, the requirements that receptive (i.e. virgin) females be used and that a separate female be used for each data point (i.e. mating), and the fact that many, if not most, species do not mate readily in cages. There has also been a widespread assumption of colour discrimination by females, hence little interest in such experiments. Yet all experiments of this type point to the fact that colour is used less by females than by males, as a basis for discrimination, that females use colour little, if at all, and that when females use visual cues, these are primarily in the UV (Silberglied & Taylor 1978, Rutowski 1981).

However, I do not deny that females choose. They exhibit effective rejection behaviour, especially after mating and during other periods of unreceptivity. The evidence simply does not support choice on the basis of 'visible' colour characters. Olfactory and ultraviolet signals are used. Perhaps if we were as receptive and attentive to olfactory stimuli as we are to bright colours and complex patterns, we would appreciate the fragrant world of male butterflies as a sensory nirvana surpassing even their kaleidoscopic adornments.

A hypothesis cannot be proven; one can only attempt to refute it by means of experiment and observation. Darwin's hypothesis is that female choice is based on male colour. Experiments have been designed to try to disprove this hypothesis. Females have been offered choices among males bearing different colours. They exhibited little preference, if any, and at most far less preference for colour of their mates than do males. Hence the hypothesis is falsified, in spite of its logic, in spite of its apparent success at accounting for many colour phenomena in butterflies, and in spite of its attractiveness to evolutionary theorists.

The argument might be made that sexual selection is operating, and that females are choosing males on the basis of colours not changed in the experiments (e.g. the black of *Colias* spp. and *Anartia amathea*). However, the question is, to what extent are the *spectacular* patterns and colours of butterflies, as we see and interpret them, a product of sexual selection by females? Ultraviolet signals and dull 'background' colours are not at issue here; the former were unknown to Darwin, and the latter have never been suggested as products of intersexual selection.

Male Intrasexual Selection — an Alternative Hypothesis

> The season of love is that of battle.
>
> (Darwin 1874)

If female colour preferences are unimportant selective forces on male coloration, we are left with the problem of accounting for the peculiar sexual distribution of colour and pattern in butterflies. The problem is now more acute, for the old argument is now reversed: if colour is more important to the male than to the female, we should expect females to be less variable in colour than males.

I would like to suggest an *alternative hypothesis*, one that may explain the distribution of many butterfly colour patterns, and yet be in accord with the experimental and observational data on butterfly courtship. I believe that *intrasexual communication between males* (see also Ch.23), rather than intersexual or interspecific communication, *is the major selective agent responsible for brilliant male coloration*, low male colour variability, lack of male-limited polymorphism, and absence of male sex-limited mimicry.

Darwin (1874) recognized conflict between males as the other important component of sexual selection, but his discussion of characters produced by intrasexual selection was concerned primarily with physical structures, such as the horns of beetles, narwhals and moose. He was aware of aerial battles between males in some butterfly species, but did not link such observations with sexual dimorphism for colour or pattern. Darwin appreciated that inter-male displays figure in the evolution of bird coloration, but he did not consider brilliant butterfly wing colours as important signals used for communication

between males. He instead attributed them almost entirely to intersexual selection by females.

The alternative hypothesis, of male intrasexual selection, as an important factor in the evolution of butterfly sexual dimorphism, is not new. Wallace (1877, 1889), Hingston (1933) and Huxley (1938*a*) refuted intersexual selection in general, in favour of intrasexual selection among males. In particular, Hingston (1933) discussed the anomalous distribution of colour and pattern in butterflies. He presented a wide variety of observational evidence in support of his view that the brilliant dorsal colours of many male butterflies function in fighting. To Hingston, male butterflies engage in 'psychological warfare', 'a battle of bravado, gesticulation and threat'; 'their colours are . . . their weapons'.

Other recent authors have mentioned male interactions as a possible factor in the evolution of sexual dimorphism, but usually without further elaboration or supporting evidence (e.g. Turner 1978). Vane-Wright (1980), reviewing possible combinations of sexual interactions between butterflies, has also suggested that colour patterns might play a role as male-male signals (see also Ch.23). The hypotheses presented by Wallace, Hingston and Huxley are in accord with many of the observable facts of butterfly colour distribution. Inter- and intrasexual selection are not mutually exclusive agents. In many cases, they serve equally well to 'explain' the same observations. Until recently, it has not been possible to weigh the relative importance of intersexual versus intrasexual selection, due to lack of direct evidence. Now, having demonstrated experimentally that female selection on male colour is weak at best, we must evaluate the evidence regarding male intrasexual selection on colour and pattern. This evidence comes from diverse sources, including field observations and experiments, as well as from the physical nature of colour and its distribution among butterfly species.

The male is the active, mate-locating sex in butterfly courtship. If brilliant colour had evolved as a signal facilitating mate location, we would expect to find it better developed in the female. This is not the case. Colours detectable at a great distance are not necessary for female choice, because butterfly courtship usually takes place in a space of less than one cubic metre.

Fighting between males has been reported in numerous species (Baker 1972*a*, 1978, Davies 1978, L. E. Gilbert in Maynard Smith & Parker 1976, Joy 1902, Richards 1927, Hingston 1933). The behaviour can be observed at food sources as well as in other, but not all, contexts (cf. puddling, migration; Shapiro 1970). In a few stout-bodied species, the wings are modified as weapons (e.g. *Charaxes* spp.; Owen 1971*a*), and physical damage may be inflicted during flights (Darwin 1874). But direct physical contact should be avoided, for such action may result in a pyrrhic victory, in which the winner may be as badly damaged as the vanquished. Selection for effective alternatives, such as ritualized threat displays, would be expected. The signals need not be visual—loud snapping noises accompany inter-male fights in *Hamadryas* (Darwin 1839, Swihart 1967*b*).

Males of many butterfly species are 'territorial' (Baker 1972*a*, 1978; see also Silberglied 1977). Such behaviour is best developed in species exhibiting 'waiting' mate-location behaviour (cf. Scott 1973*d*). Territorial defence in butterflies probably serves to prevent access by rival males to sites at which receptive females fly. (Among birds, food resources, perches, and nests are also defended.) For this reason, butterfly 'territories' are not necessarily fixed in location from day to day, or even from one time of day to another (Baker 1972*a*, Owen 1971*a*, Davies 1978). These differences between butterfly and bird territoriality have served to complicate discussions with semantic problems and confound researchers looking for strict analogies (e.g. Ross 1966, Scott 1973*d*). In species that 'hilltop' males defend prominences to which receptive females fly in search of mates (Shields 1968, Scott 1974*b*). In territorial or aggressive species, brilliant male colour may serve to intimidate rivals for prime locations. Males that are victorious in such encounters would receive a disproportionate share of matings, resulting in selection for stronger male signals.

Male butterflies of many species make inspection flights whenever anything that might be a female appears (e.g. Tinbergen *et al.* 1942, Lederer 1960, Stride 1957). As a result, frequent male-male interactions occur, especially in species exhibiting 'seeking' mate-location behaviour (though also in 'waiting' species). Mating success in such species should be related to the efficiency with which an area is searched for females. It would be of advantage to a male to identify his sex to other 'seeking' males from a great distance; thus reducing time wasted in fruitless homocourtships. It would be of advantage to the signal receiver for the same reason, and also because his time may be better spent searching areas not recently explored by another cruising male (cf. Rutowski 1981). While such behaviour may result in greater dispersion of males throughout the habitat, its explanation is based on individual advantage rather than group selection (Wynne-Edwards 1962).

Experimental evidence also supports the hypothesis that males respond to one another's colours. Colour patterns are more important to males than to females. Not only are males attracted to visual stimuli resembling females in approach tests, they are *repelled* by visual stimuli resembling other males (Obara 1970, Stride 1958*a* (but see also Ch.21), Rutowski 1977*a*, 1981, Silberglied & Taylor 1978). White, UV reflectance and iridescent colours seem to be most

important in this regard. Some species have special displays in which the male's dorsal colours are exhibited while sitting (e.g. 'flutter response'; Obara & Hidaka 1964, Rutowski 1977*b*, 1978*a*; see also David & Gardiner 1961). Another striking example is illustrated by the stereotyped rejection behaviour of mating male *Colias eurytheme*, in which the hindwings are flashed at approaching intruders (Silberglied & Taylor 1978). However, to my knowledge no one has performed an experiment to determine if colour may affect the outcome of inter-male combats between butterflies.

Males of the Grayling butterfly studied by Tinbergen and his colleagues (Tinbergen *et al.* 1942, Tinbergen 1958) are unusual in discriminating colours while feeding but not in relation to social interactions. This lack of colour use is consistent with the lack of intense colour and absence of strong sexual dimorphism in this species.

Like birdsongs, brilliant butterfly colours may serve as agonistic devices, used for threat, intimidation and rejection. The attractive, alluring, seductive characteristics of male butterflies, required for successful courtship are their odours. Male pheromone glands are widespread in nocturnal as well as diurnal Lepidoptera, and their pheromones, unlike female sex-'attractants', are chemically diverse (Ford 1945, Silberglied 1977; see also Ch.25). Intersexual selection has probably played the dominant role in the evolution of these scent organs and their secretions—not in the evolution of brilliant male colours.

Darwin (1874) noted the close analogy between the secondary sexual characters of birds and insects, especially in terms of beautiful colours and the distribution and nature of sexual dimorphism. 'Whatever explanation applies to the one class probably applies to the other; and this explanation . . . is sexual selection.' However, Darwin treated male coloration in birds largely as adornment evolved under intense intersexual selection. This view has not been supported by recent studies. According to Rohwer *et al.* (1980), 'bright plumages are evolved strictly for aggressive signalling. We know of no good support for the alternative hypothesis that bright coloration serves in female attraction or as an isolating mechanism.' In contrast, Baker & Parker (1979) concluded that 'bird coloration has evolved almost entirely in response to predation-based selective pressures. Although plumage and coloration are involved in species and sex recognition systems, they have not evolved in response to sexual selection pressures.' Thus, while ornithologists do not fully agree on the selective agents responsible for bird coloration, intersexual selection no longer has their enthusiastic support (but cf. Burley 1981 and Ch.21; see also Hingston 1933). Butterflies also differ from birds in the clearer physical partitioning of communicative and protective functions onto the dorsal and ventral wing surfaces, exposed, respectively, during display or at rest (Darwin 1874).

Baker & Parker (1979) also support the hypothesis that 'bright colours may commonly be favoured when an individual is anyhow obvious (e.g., through activity), and where it represents an "unprofitable" prey for a predator', as was suggested for insects by Jones (1932; see also Young 1971, Gibson 1980). Flash coloration—the sudden appearance of colour during flight and its sudden disappearance at rest—may startle or confuse predators. These and other 'predation hypotheses' do not conflict with, and are not mutually exclusive of, the suggested role of intrasexual selection as the major selective factor producing brilliant male coloration. They do not explain why brilliant coloration should be so advantageous for the male, but less so for the female. These hypotheses should be supported to the extent that they are in agreement with experimental data, but are unlikely to account for the phenomena of male brilliance, low variation, etc. Colour may also play other roles (e.g. interspecific signalling in social aggregations, such as puddling) that do not conflict with these conclusions.

Another hypothesis that has been proposed to account for brilliant male coloration is the so-called 'handicap principle' (Zahavi 1975). This suggestion, that females prefer to mate with males that have survived *in spite of* the 'handicap' of brilliant coloration, has serious theoretical flaws (Maynard Smith 1976, 1978, O'Donald 1980; cf. West-Eberhard 1979, Thornhill 1980). But even if that was not the case, Zahavi's hypothesis would predict female choice based on male colour. This prediction is not supported by the experimental evidence.

The concept of intersexual selection on colour pattern has figured prominently in discussions of butterfly systematics, genetics, behaviour, mimicry and evolution (e.g. Carpenter & Ford 1933; Wickler 1968, Vane-Wright 1971, Scott 1973*d*, Silberglied 1977, Turner 1977*a*, 1978). Some theories developed using this concept do not depend on male-female communication as a selective force, and may easily be modified by the partial or complete substitution of intrasexual for intersexual selection. Others will require major revision. Male intrasexual selection cannot account for all interesting colour phenomena in butterflies, many of which are better understood in the contexts of thermoregulation, camouflage, mimicry, and in some cases (especially UV), intersexual selection. These agents are not mutually exclusive, but act in concert, sometimes one or another playing a more important role, producing infinite variations, concerti and symphonies on the themes of colour, pattern and vision.

Summary

Butterflies have a visual spectral sensitivity extending from the ultraviolet to the red, the widest known among animals. They have excellent colour vision, and exhibit both innate and learned colour preferences. Butterfly wings bear diverse colour patterns, and colour is used by butterflies during feeding, oviposition and sexual behaviour. Nevertheless, there is little evidence to support Darwin's argument that intersexual selection, in the form of male and female mating preferences, acts as a potent force in the evolution of 'visible' butterfly coloration.

For males of many species studied, the colour of the female provides an important visual stimulus for mate-location and recognition. However, male behaviour is probably not an important selective factor in determining female colour, and males do not often discriminate between potential mates on its basis. This is so because male colour preferences are relatively broad, females are usually encountered and courted one at a time, the number of receptive females encountered usually limits male reproductive success, and males can mate many times. Female variation and polymorphism, sex-limited mimicry and low pattern diversity among females of closely related species provide indirect evidence that males' preferences probably do not act as important stabilizing selective forces on female colour and pattern.

Female butterflies exhibit well-developed rejection behaviour. The bases for discrimination by females have been little studied, and there are very few data on colour preferences. Available data reveal that female colour preferences are weak or absent, or are at most even less precise than those of males. The only visual signals on the males' wings that have been shown to affect female behaviour lie in the ultraviolet. As determinants of female acceptance behaviour, olfactory stimuli appear to be far more important than visual.

The brilliant colour patterns of male butterflies have signal properties that would serve well for long-range communication. It is suggested that male-male interactions may be the major selective agent in the evolution of bright colours and iridescence in males, low variability of male coloration, lack of male sex-limited mimicry, and several other general colour phenomena in butterflies. Recognition of other males, and advertisement of his own sex, are advantageous for a male in the contexts of agonistic, territorial and mate-location behaviour. This suggestion is consistent with conclusions of recent reviews of the evolution and function of bird coloration.

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