Annu. Rev. Entomol. 1998. 43:619–43

EVOLUTION AND ECOLOGY OF SPIDER COLORATION

G. S. Oxford
Department of Biology, University of York, P.O. Box 373, York YO1 5YW, United Kingdom; e-mail: gso1@york.ac.uk

R. G. Gillespie
Center for Conservation Research and Training, University of Hawaii, 3050 Maile Way, Gilmore 409, Honolulu, Hawaii 96822; e-mail: gillespi@hawaii.edu

KEY WORDS: color, crypsis, genetics, guanine, melanism, mimicry, natural selection, pigments, polymorphism, sexual dimorphism

ABSTRACT

Genetic color variation provides a tangible link between the external phenotype of an organism and its underlying genetic determination and thus furnishes a tractable system with which to explore fundamental evolutionary phenomena. Here we examine the basis of color variation in spiders and its evolutionary and ecological implications. Reversible color changes, resulting from several mechanisms, are surprisingly widespread in the group and must be distinguished from true genetic variation for color to be used as an evolutionary tool. Genetic polymorphism occurs in a large number of families and is frequently sex limited: Sex linkage has not yet been demonstrated, nor have the forces promoting sex limitation been elucidated. It is argued that the production of color is metabolically costly and is principally maintained by the action of sight-hunting predators. Key avenues for future research are suggested.

INTRODUCTION

Differences in color and pattern among individuals have long been recognized as providing a tractable system with which to address fundamental evolutionary questions (57). Indeed, for decades, visible variation furnished virtually the only means with which to examine evolutionary changes at specific loci. In insects generally, and the Lepidoptera in particular, studies of color and pattern

0066-4170/98/0101-0619$08.00

have contributed major advances to our understanding of a number of key evolutionary phenomena. Classical studies include those on the nature and evolution of dominance (39), the power and mode of action of natural selection (75), the evolution of mimetic resemblances (39, 144), and the developmental rules underlying differences in patterns within and among species (97).

Spiders, in common with many other arthropods, occur in a very wide range of colors and patterns that vary both inter- and intra-specifically. Spiders are predators, and those in many families capture their prey using webs. Color patterns may therefore represent a trade-off between aspects of the spider's own predatory activity and the avoidance of falling prey themselves to the same or higher trophic levels. As a result, one might predict that a different balance of selective forces acts on color in spiders compared with that in herbivorous arthropods.

Over the last decade or so, there has been a growing interest in spider systematics (23), communication (150), neurobiology (5), behavior (138), ecophysiology (95), and ecology (149), as well as more general topics (38). With increasing information on phylogenetic relationships, examination of various behavioral, ecological, physiological, and other phenotypic attributes of many spiders within an evolutionary framework is now possible. Here we examine the chemical nature, taxonomic distribution, genetic control, and ecological and evolutionary significance of color variation in spiders.

PIGMENTS AND THEIR LOCALIZATION WITHIN SPIDERS

Unlike the chromes of many other invertebrates, those of spiders have been relatively little studied from a biochemical point of view. Only three major classes of pigment, ommochromes, bilins, and guanine, have been positively identified to date (66). Melanins, which are so widespread in other animals, appear to be absent in spiders (66, 69; but see 79). Carotenoids and pterins have also not been detected so far (63), although the former are present in some mites (56). Other pigments, apparently unrelated to these major classes, have been detected in spiders but have not been fully characterized.

Ommochromes

Ommochromes are derivatives of the amino acid tryptophan via kynurenine and 3-hydroxykynurenine and are responsible for a wide variety of colors (yellows, reds, browns, and black). Different colors are produced by different combinations of ommatins and ommins, and they may also depend on the redox state of the pigments and on the nature of conjugated proteins (136). In general, yellows, reds, and browns tend to be produced by ommatins, whereas dark browns to black are generated by a mixture of ommatins and ommins, with the latter predominating (137). Yellow coloration can also be produced by kynurenine and 3-hydroxykynurenine. Ommochromes are usually deposited as pigment granules within the cells of the hypodermis, immediately beneath the cuticle (66, 137), but in a number of species both xanthommatin and ommins can also be present in considerable amounts in the digestive mass (137).

Bilins

Bilins are blue or green pigments that consist of a linear arrangement of pyrroles. The green coloration of *Micrommata virescens* (Heteropodidae) is a result of micromatabilin in the hemolymph, interstitial tissues, and yolk of oocytes (68, 71). As with ommochromes, the final color produced is a function of both the pigment and its conjugates (65).

Guanine

Guanine is a crystalline purine excretory product (2), which, in many species, accumulates in specialized, peripheral cells (guanocytes) of the digestive diverticula lying directly beneath the hypodermis (90, 91, 135). Reflection of light off guanine crystals produces a structural whiteness, and so, strictly speaking, it should not be regarded as a pigment per se, although it is convenient to do so. Guanine deposits can contribute to the overall color pattern directly by showing through unpigmented patches of hypodermis and cuticle (38) or by forming a white background against which the colors and patterns of hypodermal pigments are maximally displayed (9, 107). In some genera, for example, *Tetragnatha* and *Leucauge* (Tetragnathidae), *Argyrodes* (Theridiidae), and *Theridiosoma* (Theridiosomatidae), the guanine is in the form of extremely thin plates that give the spider a silvery appearance (90; see photographs in 77, 88). Although usually restricted to the opisthosoma, guanine can also be deposited in the prosomal section of the diverticula (90), as in some *Cyclosa* (Araneidae) and *Tetragnatha* (Tetragnathidae) species (GS Oxford, unpublished observations). In species characterized by significant amounts of visible guanine, these deposits seem likely to be deployed for their contribution to overall coloration and not to be merely an indication of the inability of the spider to excrete the compound efficiently. Indeed a mechanism exists in spiders whereby the process of excretion can be blocked, which leads to an increase in the storage of guanine (24, 135).

Pigments of Unknown Chemical Affinity

Green pigments that are chemically unrelated to ommochromes or bilins have been detected as granules in hypodermal cells of the legs, prosoma, and abdomen of some species (68). Some pigments are located within the cuticle itself. For example, in *Diaea dorsata* (Thomisidae), an agranular green pigment of unknown chemical affinity is incorporated into the mesocuticle and, as such, is lost during moults (68). In these cases, the pigment appears to be localized (or, at least, is most visible) in the legs and prosoma where the cuticle is thickest. In *Holocnemus pluchei* (Pholcidae), a dark pigment deposited in dendritic cells beneath the hypodermis of both the prosoma and abdomen was initially identified as a "peculiar pheomelanin" (79). However, the chemical tests applied were not definitive, and the pigments were not extracted for positive identification; some of the properties shown were those expected of ommochromes (see also 137). The color and pattern of many species can be considerably modified by the distribution of hairs, many of which contain pigments. The nature of these pigments has not been studied. Finally, although pigment is not involved as such, in some species the exocuticle of the legs and prosoma is modified by a tanning process, and this is responsible for some brown coloration, which often acts in concert with hypodermal pigmentation to produce black (31).

In summary, pigmentation in spiders arises from a number of different sources, some related to excretory pathways. These pigments can be used in combination, and in different redox states, to produce a wide range of colors. In addition, layers can be superimposed upon each other, thereby masking or accentuating existing patterns.

STRUCTURAL COLORS

Structural colors occur as a result of the diffraction, scattering, or, more usually, interference of light by layers or surface sculpturing, usually of modified setae or scales (31, 41, 62, 74). For example, the white prosoma of *Argiope* spp. (Araneidae) is apparently a result of the total reflection of light from hairs (66). In two unrelated species, *Lycosa* sp. (Lycosidae) and *Josa* sp. (Anyphaenidae), areas of modified cuticle have been identified that act as light reflectors (76), the function of which is unknown. Structural colors can act alone or in concert with pigments within the hairs themselves or in the hypodermis.

TAXONOMIC DISTRIBUTION OF PIGMENTARY AND STRUCTURAL COLORS

Knowledge of the biochemical nature and localization of pigments in spiders is obviously still very incomplete, but it could prove a powerful tool with which to address a number of evolutionary questions. Taxonomically, ommochromes are widespread (66–69,136, 137; GS Oxford, unpublished observations), which suggests that their establishment as the primary pigment class appeared early in the evolution of the Araneoclada section of the Araneomorphae (in the sense of 23). Whether they are also found in the more primitive representatives of the Araneomorphae, and in the Mygalomorphae, is at present unknown, but they are certainly widespread in invertebrates generally (41). Bilins have been specifically sought in only very few species, and little can be deduced at present about their actual taxonomic distribution. Hypodermal green pigments are known to occur in the Araneidae, Dictynidae, and Tetragnathidae (68, 69; GS Oxford, unpublished observations), although within these families rather few species are involved. This raises the fascinating question of whether these pigments are chemically and phylogenetically related and are unexpressed in intervening families, or if they have evolved independently. Very few species have been investigated with regard to the presence of green pigments within the cuticle itself, but it is significant that, in contrast to green hypodermal pigments, they have so far only been found in members of the Thomisidae (68, 69; GS Oxford, unpublished observations).

Guanine is a major excretory product in all arachnids, but, surprisingly, only Millot (90) seems to have considered the differential use of guanine as an element of coloration in different species. He noted that guanine is deployed on all abdominal faces in brightly colored species such as *Enoplognatha ovata* (Theridiidae) and only on the dorsum of others [for example, *Araneus* spp. (Araneidae)], whereas in genera such as *Pholcus* (Pholcidae), *Amaurobius* (Amaurobidae), *Salticus* (Salticidae), and *Tegenaria* (Agelenidae), it is absent altogether. The utilization of guanine as a pigment occurs in a number of unrelated families, which suggests that the ability to accumulate it has developed (or been lost) several times. Indeed, the degree of guanine utilization may vary greatly between closely related species and even between individuals within species—the ecological significance of which has yet to be explored. In at least some species, the precise distribution of deposits within and between individuals is under genetic control and is tightly orchestrated with the disposition of overlying hypodermal pigments (107). Elucidating the relationship between these two developmentally independent components of coloration during ontogeny promises to be an important area for future research.

The deployment of hairs and other cuticular structures as determinants of color and pattern is taxonomically widespread. Hairs are particularly important in the Theraphosidae (*Avicularia avicularia*—140) and Salticidae (*Phiale* spp.—45, 46) but are also widely used in other families, for example, the Eresidae (66), Clubionidae (125), and Oxyopidae (12), to name but a few. The relationship between the pigments in hairs and those in the hypodermis is at present unknown but might prove to be of considerable phylogenetic and taxonomic interest. Indeed, why some taxa utilize hairs while many others use hypodermal pigments is not clear.

COLOR VARIATION IN SPIDERS—REVERSIBLE CHANGES

The coloration of many spiders is genetically fixed. However, in others, color may change to varying extents according to specific environmental conditions. Although a reversible color change is a reflection of an organism's physiology and is ultimately, therefore, genetically based, such changes do not have a direct, proximate genetic basis. Reversible color changes may occur at all ontogenetic stages in both sexes, or they may be restricted to certain developmental periods and/or to only one sex. Color changes can be either passive (food induced) or active (physiological, morphological, or behavioral). Active changes are almost always in a direction that increases the degree of crypsis of the spider on its current background (homochromy), and the nature and taxonomic distribution of these changes suggest that they may have evolved independently several times.

Food-Induced Coloration

Although many spider species are likely to take on the tinge of highly colored prey, the importance of the phenomenon and its possible adaptive significance, if any, is largely unknown. It is probably more common in young spiders, in which the deposition of hypodermal pigments and guanine may be incomplete, or otherwise translucent species, in which ingested pigments from colored prey are revealed through the opisthosomal wall. A striking example of food-induced coloration is found in the pale, translucent Hawaiian happy-face spider, *Theridion grallator* (Theridiidae) (50).

Environmentally Induced Color Changes

Environmentally induced color changes (other than by food) are traditionally divided into two types that reflect the physiological processes involved and the time required for the change to be effected. Reversible color changes can be described as morphological, if they take place over a period of days, or as physiological, if they are almost instantaneous (25). Morphological changes usually require the synthesis and degradation of pigments, whereas physiological changes involve alteration in the disposition of existing chromes, thereby affecting the overall appearance.

MORPHOLOGICAL COLOR CHANGE Relatively slow color changes that occur over a number of days have been most thoroughly investigated in the Thomisidae (3, 37, 42, 43, 49, 61, 134), although species in the Araneidae (9, 11, 14, 17, 85), Oxyopidae (49, 94, 127), Heteropodidae (70, 71), and Linyphiidae (135) have also been shown to be able to alter their overall darkness or color in response to changes in the environment. Species colored predominantly by scales or hairs would not be expected to be able to undergo morphological color changes, although this has not been investigated.

Background matching The flower-living crab spider, *Misumena vatia* (Thomisidae), has been studied in this context for over a century (3, 42, 43, 112, 115, 147). In this species, adult females can reversibly adjust the overall coloration of the opisthosoma between white and yellow to match their background, which in nature is usually flowers (112). The process of turning from white to yellow takes between 10 and 25 days, and the reverse change, 5 to 6 days (42). Yellowing is probably produced by the ommochrome precursors kynurenine and 3-hydroxykynurenine that accumulate in the hypodermis (137), and reversion to white is presumably a result of the degradation or movement of these compounds, which allows guanine to show through the opisthosomal wall (42). Similar changes occur in other families. For example, *Cyrtophora citricola, Araneus diadematus*, and *Araneus marmoreus* (Araneidae) can reversibly change the brightness of the opisthosoma as a result of exposure to varying light intensities (9, 11), and adult female *Araneus quadratus* (Araneidae) take on colors that accurately match their resting surfaces within 3 days (17). Similarly, gravid female green lynx spiders, *Peucetia viridans* (Oxyopidae), placed on different colored backgrounds are able to change their color over a period of 16–17 days (94, 127).

Morphological color changes vary from species to species and may well depend on the precise ecology of the sex and developmental stages involved. For example, in all the thomisids investigated to date, only the females appear to be able to undergo color adjustment. Many thomisid females utilize a sit-and-wait foraging strategy on flowers and, because they are relatively larger and sedentary, may be in particular danger from sight-hunting predators. Background matching may reduce this risk and, at the same time, render the spider less visible to their own potential prey species (15). Mature males are smaller and usually more darkly colored, and they spend more time wandering at ground level. More specific associations between habitat usage and the ability to undergo color changes may result from further work.

Darkening of cave spiders An interesting but relatively uninvestigated type of phenotypic color change concerns the darkening of species from caves on exposure to light. For example, in some linyphiid species with uniformly colored opisthosomas, individuals are usually darker in the twilight zone of caves than are those from totally lightless parts (CL Deeleman-Reinhold, quoted in 113). Some troglobitic species [e.g. *Troglohyphantes gracilis* (Linyphiidae)] seem to have lost the capacity to darken; individuals are pigmentless even in the twilight zone. However, *T. gracilis* and *Troglohyphantes roberti*, another troglobite, were found to darken in an artificial dimly lit environment (CL

Deeleman-Reinhold, quoted in 113). On dissection, darkening was shown to be a result of pigment deposited on interstitial tissues rather than in the hypodermis, which recalls the observations of dark sub-hypodermal pigments in *Holochemus pluchei* (Pholcidae) (79). Whether the pigmentation process of *Troglohyphantes* spp. is the same as that responsible for the darkening of troglophilic spiders remains to be seen.

Ultra-violet (UV) reflectance Background matching at other than visible (to humans) wavelengths can also be important. For example, *Thomisus labefactus* (Thomisidae) can alter its UV reflectance to match that of the flowers on which it sits, thus making it less visible to potential insect prey (134). Many, if not all, birds are known to be able to see in the UV range (7, 143), and these "color" changes may therefore also make the spider less vulnerable to its own predators.

PHYSIOLOGICAL COLOR CHANGE A number of spiders can change their color almost instantaneously when disturbed, a phenomenon apparently first recorded in an African *Argiope* species (Araneidae) (6) but now also reported in the Theridiidae (145), Tetragnathidae (37, 145, 151; GS Oxford, unpublished observations), Linyphiidae (14), and Philodromidae (73), as well as in other araneids (10, 16, 33, 34, 126, 130, 133). Immediate color change (darkening) of *Cyrtophora cicatrosa* (Araneidae) is a result of the retraction of guanocytes in the intestinal diverticula, which changes the overall background color of the opisthosoma from whitish to the brown of the digestive mass (10). Indeed, guanine retraction (or contraction) seems to be the basis of all physiological color change in spiders. The references cited above describe the most spectacular examples of this phenomenon; other species undergo lesser changes. For example, in *Tetragnatha polychromata* (Tetragnathidae) from Hawaii, the median dark stripe of the dorsal opisthosoma becomes slightly wider as a result of physical disturbance (GS Oxford, unpublished observations). In this case, the guanocytes that respond lie on either side of the cardiac region, and alterations in heart functioning might possibly play a direct role in mediating color change.

BEHAVIORAL COLOR CHANGE An unusual form of reversible color change has been described in *Cyclosa tremula* (Araneidae) (63). This species has a striking black and white disruptive pattern and rests in the center of an orb web decorated with greyish "imitation spiders" constructed from prey remains. If the spider is disturbed, it vibrates its body so rapidly that the black and white patches blur into grey, so that it resembles the false spiders above and below.

In conclusion, reversible color changes represent a number of mechanistic phenomena. In general, morphological changes occur in species that track a temporal shift in background colors (70) or need to adapt to a relatively constant, but spatially heterogeneous, environment. The species studied so far all occupy open habitats where crypsis is of particular importance, although many other spiders with similar ecologies apparently do not have the ability to change color. Physiological and behavioral changes, in contrast, are instantaneous reactions to immediate threats. Bristowe (14) pointed out that slow-moving web-builders, who may not be able to escape from predators by speed of movement, when disturbed tend to drop from their web, draw in their legs, and feign death. These species are often dull colored and cryptic on the ground surface, where they remain motionless for some minutes (14, 34). Physiological color change has presumably evolved in spiders exhibiting this "drop response" because the coloration appropriate in the web (or normal resting surface) differs from that ensuring crypsis on the ground. The taxonomic distribution of species in which physiological color changes have been demonstrated indicates that, in its extreme form, this phenomenon must have evolved independently several times. The evolutionary forces that have produced an ability to reversibly change color, and the extent to which it involves homology versus convergence, is unknown.

GENETIC VARIATION BETWEEN INDIVIDUALS

Although some species can alter their appearance in reversible ways, the majority display colors and patterns that are directly genetically determined and relatively impervious to environmental influences. The genetic control of color can conveniently be divided into two catagories—major genes and polygenes.

Major Gene Control (Genetic Polymorphisms)

Genetic polymorphisms are generated by the segregation of two or more alleles at (usually) one major locus. The locus concerned might be (*a*) autosomal with the morphs expressed in both sexes, (*b*) autosomal but with the expression of some or all morphs restricted to one sex (sex limitation), or (*c*) on the sex chromosome (sex linkage), in which case the frequencies of morphs will differ between the sexes.

Some of these polymorphisms are extremely complex. For example, the most spectacular example of color polymorphism in spiders is that exhibited by the endemic Hawaiian happy-face spider, *T. grallator* (Theridiidae). [The "happy-face" epithet derives from the dorsal opisthosomal pattern of one of the color morphs that resembles a smiling human face (see photograph in the Supplementary Materials section on http:\\www.AnnualReviews.org).] In the most intensively studied population (Maui), opisthosomal color is controlled by simple Mendelian alleles at a single autosomal locus or multiple closely linked loci, with the plain yellow morph recessive to all patterned morphs (53, 107); all morphs are found in both sexes. On Hawaii Island, however, some of the same morphs are sex limited (108, 109). Differences in the genetic basis of the color polymorphism have also been found on other islands (RG Gillespie & GS Oxford, unpublished observations). Because these changes are visibly displayed in the phenotype, the system provides an ideal model for investigating genetic shifts associated with island colonization and consequent population bottlenecks.

A similar, but less variable, color polymorphism is found in *E. ovata* (Theridiidae), where there are three distinct opisthosomal morphs (102, 123 but see 64). A two-locus model of inheritance has been proposed: One locus is concerned with color/pattern, and a second, closely linked regulatory locus controls the expression of the color locus during development (102). The regulatory locus determines when certain morphs are expressed ontogenetically and whether or not they are sex limited. As in the *T. grallator* system, the polymorphism of *E. ovata* has allowed insights into modifications of the genetic environment associated with drift and/or selection.

In our search of the literature for cases of color polymorphism, we have accepted only those examples in which (*a*) evidence shows that morphs are discontinuous and (*b*) distributions of morphs in both sexes have been investigated. Non–sex-limited polymorphisms have been reported in the Theridiidae (53, 54, 64, 80, 102, 104–107, 109–111, 123), Araneidae (11), Pisauridae (8, 92, 93, 151; T Yaginuma, personal communication), Gnaphosidae (119), and Salticidae (44, 98, 99). Sex-limited polymorphisms are described from the Theridiidae (64, 102, 103, 106, 108, 109), Araneidae (87, 146), Pisauridae (32), Oxyopidae (12, 13), and Salticidae (18, 45–48; G Uetz, personal communication). There are two general statements that can be made regarding color polymorphisms. First, sex linkage appears to be absent, although the chromosomal sex-determining mechanisms (e.g. 148) do not seem to preclude this mode of inheritance. However, sex limitation is quite common. The reasons for this are not clear; at least in *E. ovata*, different individuals in a single population can exhibit sex-limited and non–sex-limited versions of the same morph (103). Second, in those species in which dominance relationships have been elucidated, the general situation is that the bottom recessive morph is the most frequent in natural populations. This is a common feature of invertebrate color polymorphisms (60) and is predicted by some models of frequency-dependent selection (20).

Polygenic Control

The degree of polygenic control of color variation is impossible to determine without formal crossing experiments, and only three of these have been performed to date (59, 104, 139). The presence of substantial additive genetic variation (high narrow heritability estimates) in all three cases suggests that directional selection is weak or absent (36). However, this does not rule out the possibility that other modes of selection are operating. Temporally fluctuating changes in the fitnesses of different phenotypes (e.g. under apostatic selection) would be equivalent to stabilizing selection, and here the narrow heritability could take any value, depending on other genetic and environmental influences.

The long-term persistence of genetically determined color forms within a population implies that some form of balancing selection is operating. Persuasive evidence indicates that selection is indeed maintaining polymorphisms in *T. grallator* (RG Gillespie & GS Oxford, unpublished observations) and *E. ovata* (110) and continuous variation in *P. phrygianus* (59), but genetic drift can also be a powerful force that influences local morph frequencies (104, 124). What little work has been done on the genetics of color variation suggests that further study would be richly rewarded, for in many ways spiders offer ideal model systems for the investigation of a number of evolutionary phenomena.

COST OF COLORATION

Is the production of color in spiders costly? If the answer is yes, then the presence of constitutive pigments implies that selective forces favoring color more than offset the metabolic costs involved. One indirect approach to this question is to ask what happens in situations where color per se can be of no value. Animals living in semidarkness or total darkness often show predictable changes in a whole suite of characteristics, including the reduction or complete loss of eyes and of body pigmentation (29). Spiders are no exception to this generalization (49, 85). The genetic loss of pigment in a population of cave organisms could theoretically arise by one of two processes—natural selection or the random fixation of (neutral) mutations that disrupt the normal pathways of pigment biosynthesis (29). If loss of pigment in a subterranean environment is actively selected for, this would suggest that (*a*) the production of pigments entails a metabolic cost, (*b*) some visible aspect of pigmentation on the surface is actively selected for, and (*c*) pigments do not merely serve as convenient sinks for excretory products. If genetic drift is the cause of pigment loss underground, then the last two points also apply, with positive selection favoring pigmentation in surface-dwelling spiders.

Some spider species show a complete adaptation to cave living: They are blind and totally lack pigmentation, e.g. *Tartarus mullamullangensis* (Dictynidae) (85). In other cases, a cave-dwelling subspecies may lack pigment, whereas a surface-dwelling subspecies is fully pigmented, e.g. *Bathyphantes eumenis buchari* and *Bathyphantes eumenis eumensis* (Linyphiidae), respectively (131). However, these examples throw no light on whether features characterizing cave populations arose via selective or stochastic routes. A consideration of pigment variability within a species points tentatively in the direction of a selective loss of pigmentation with the adoption of a more underground existence. Růžička (132), for example, details variation with habitat in the degree of pigmentation of *Rugathodes bellicosus* (Theridiidae) in Czechloslovakia. At low altitude, the spider is found exclusively in mini-caves in the depths of stony debris, whereas higher altitude populations occur in more superficial situations. Correlated with this is a tendency for the frequency of the darkly pigmented form to increase with altitude: at $<$500 m, frequency $=$ 0.33 (n $=$ 6); at 500–1000 m, 0.67 (n $=$ 24); at $>$1000 m, 0.94 (n $=$ 17). These differences are significant ($\chi^2 = 6.31$, 1 degree of freedom; $0.025 > P > 0.01$; data for the two lowest altitude classes are combined). Here there is pigment variation in both broad habitat types, which suggests that it is genetic rather than environmentally induced, yet a smaller proportion of individuals in the mini-caves are darkly pigmented. Unfortunately separation of the effects of habitat and altitude is not possible in this example, and sample sizes are very low.

Among species that occur in both surface (epigean) and underground environments, it is not known how much, if any, gene flow occurs between these spatially separated populations. If gene flow is high, then the maintenance of pigmentary differences between the two environments would imply some form of selection, assuming that pigment variation is truly genetic. However, if gene flow between cave and epigean populations is small, which is more likely, nothing can be concluded regarding the presence or absence of selection for pigment loss in the cave. In this context, the ontogenetic change in coloration in the cave spider *Meta menardi* (Tetragnathidae) is informative despite the fact that it involves a change, and not a loss, of pigmentation. In Scottish populations of this species, second- and third-instar individuals live in the field layer and have a contrasting black and white dorsal pattern (118). At the end of the third instar, spiders abruptly vanish from the field layer and return to the rock debris mini-cave habitat of the adults, and at the same time their pattern changes to the much more uniform one possessed by mature individuals. Juveniles reared under laboratory conditions also show this color change at the appropriate instar, which indicates that it is genetically programmed and not light induced (118). The absolute correlation between habitat change and coloration suggests that the marked shift in the latter is, in some way, selectively advantageous.

The loss of pigmentation in cave-dwelling spiders, by whatever evolutionary mechanism, indicates that the continued presence of pigments in epigean populations is selectively maintained. There are also some indications that changes in levels of pigmentation along the epigean $\Rightarrow$ troglophile $\Rightarrow$ troglobite route are not merely a result of destruction of biosynthetic pathways by random mutations and subsequent genetic drift, but critical information is lacking. An estimate of the energy saved as a result of the loss of both pigmentation and eyes for a linyphiid species during the troglophile to troglobite transition was found to be ~5% over the spider's lifetime (120). This figure is necessarily very crude, and many assumptions are made in its calculation. Would it be a significant selective pressure? The answer depends on the effective size of the proto-troglobite population—if it was large, then selective differentials of this magnitude could be effective (28). Energy savings through loss of pigment alone would, of course, be smaller. Until selection for pigment loss is demonstrated directly, as has been done with regard to reduction in eye size in cave populations of the crustacean *Gammarus minus* (30), hypotheses of underground adaptation will remain tentative.

SELECTION FOR COLOR

Color is clearly adaptive in the majority of cases studied, and it appears to function in a number of ways, including crypsis/disruptive coloration, mimicry, aposematism, other forms of predator avoidance, and thermoregulation (see also 22). Several of these factors may operate concurrently so that coloration represents a compromise between conflicting selective forces, the nature of which will depend on the ecology of the species concerned. Sexual dimorphism for color is discussed as a separate issue.

Crypsis

In the section on environmentally induced color changes, we point out that changes in color are such as to make the spider more cryptic on its current background. The evolution of inducible color changes is almost certainly a result of selection by visually oriented predators or prey. By extending this argument, the colors and patterns and related physical and behavioral features (121) of those species that constitutively resemble their backgrounds are likely to have been selected for by the same process(es). Spiders have many enemies, of which perhaps the most important are insectivorous birds and spider-hunting wasps, both of which possess high visual acuity and color vision. In some cases, the matching of different background colors by different individuals of a species is extraordinarily close. There are, for example, several species that are variable in color but always seem to match the bark on which they are living, e.g. *Stephanopis cambridgei* and *Synalus angustus* (Thomisidae), *Dolophones conifera* (Araneidae), and *Tama fickerti* (Hersiliidae) (88). This would suggest either the very efficient selective removal of mismatched individuals by diurnal sight-hunting predators and/or that the spiders have some ability to alter their color according to background, as discussed above (85). Selection for crypsis in specific types of habitat has led to the convergent evolution of similar colorations in unrelated species. One can thus recognize specific adaptations for crypsis on flowers/leaves, grass/twigs, bark, underleaf surfaces, and the ground, although this list is by no means exhaustive.

CONVERGENT EVOLUTION OF COLORATION AND OTHER TRAITS Similar environments may cause convergence in a number of features that enhance crypsis. One striking example of this is provided by spiders that live under leaves in the tropics (55, 96). The Hawaiian happy-face spider, *T. grallator* (Theridiidae), builds a much reduced web beneath the leaves of broad-leaved native plants (55) and typifies the adaptations involved: translucent yellow background coloration, often with darker markings on the leg joints, which may serve to disrupt the outline of the legs. The legs are extremely long for the genus and unusually positioned so as to maximize contact with the leaf. During the day, the spider remains motionless and appressed to the leaf, thereby reducing shadows. Its coloration and flattened position make it highly cryptic in the green light transmitted through the leaf (55). Five other unrelated spider species living in the same Hawaiian forests have similar adaptations for under-leaf crypsis (55), as do at least four species from the forests of Panama (96). Of significance, the species revert from diurnal immobility to genus-specific postures at night, which suggests that the colors and other adaptations are for the avoidance of visually hunting, day-active predators.

A recent study has examined convergent evolution in a radiation of spiders in the spiny-leg clade of *Tetragnatha* in Hawaii (52). Representatives of this clade can be divided into green, red/green, and brown species, with each color group united by a number of morphological and ecological characteristics (51). However, molecular data suggest that these different color groups are either poly- or paraphyletic: Matching sets of taxa appear to have evolved independently on different Hawaiian islands. Convergence of this sort emphasizes the highly adaptive nature of particular coloration patterns, although the specific selective forces involved are unknown.

DISRUPTIVE COLORATION Disruptive coloration may be regarded as a form of crypsis in which the spider's characteristic shape is obliterated, often by contrasting patterns (34, 62). True crypsis and disruptive coloration may represent alternative adaptive strategies. Bold juxtaposed colors are common in many Salticids (62), where the tendency to wander over different backgrounds while searching for prey might preclude true crypsis. Paraxial stripes are common in a number of families (e.g. Salticidae, Theridiidae, Thomisidae, Oxyopidae, Lycosidae, Pisauridae, Dolomedidae, Philodromidae, and Sparassidae), where they may serve a disruptive function. Another situation where crypsis may be difficult is in orb-weavers that sit in their webs during daylight hours. Some have developed mimetic resemblances to dead leaves and sticks, but others have apparently adopted disruptive coloration. The spotting and striping on species such as *Argiope* (Araneidae) have been suggested to serve this function, without negating the thermoregularory role of the silver coloration (see below) (129). Crypsis and disruptive coloration are not mutually exclusive even within an individual. The flower spider *Diaea evanida* (Thomisidae), for example, has a bright, almost translucent, green cephalothorax and legs, but the opisthosoma is opaque yellow with a pair of paraxial reddish brown stripes (88). The anterior part of the body is cryptic on green leaves, but the posterior part is not and the stripes may be disruptive. The important point in all these examples is that the spider does not look like a spider from a distance.

MELANISM Note that the terms melanic and melanism as used here refer to the dark coloration of the individual and not to the presence of melanin-type pigments. Studies of the evolution of new cryptic coloration patterns in insects, and particularly in moths, as a result of human-made changes to the environment have yielded classical examples of natural selection in action (39, 75). Cases of apparent industrial melanism, although largely anectdotal, have been documented in a small number of spiders in the British Isles. In *Drapetisca socialis* (Linyphiidae), for example, the dorsal surface of the abdomen is normally pale yellowish green to grey with markings that make it very cryptic on the trunks of trees. However, in north Cheshire, which received aerial pollution from nearby industrial centers, up to 45% of individuals are uniform black, and selection for crypsis on the blackened trees has been suggested to be effected by various insectivorous birds (84). Similarly, melanic forms of *Ostearius melanopygius* (Linyphiidae) (82), *Salticus scenicus* (Salticidae) (83), and *Arctosa perita* (Lycosidae) (4) have been described living on industrially blackened backgrounds, and *Stephanopis altifrons* (Thomisidae), *Tama fickerti* (Hersiliidae), *Araneus eburnus*, and *Araneus rabiosulus* (Araneidae) (86) on naturally occurring dark surfaces, e.g. burnt wood.

These cases of possible evolutionary change should be treated with caution until it can be established that black coloration is not environmentally induced. Two considerations suggest that in at least some species it is not. First, *S. scenicus* lacks intermediate color forms. Second, in spiders whose coloration is predominantly produced by hairs and/or scales (salticids and lycosids), it is difficult to envisage a process whereby the pigments within these epidermal outgrowths could be altered in response to environmental cues. Intermediate color forms do occur in *O. melanopygius, D. socialis,* and possibly *A. perita,* although this does not preclude control by polygenic or multiple allelic systems.

Mimicry

Most studies of mimicry in spiders have been concerned with the imitation of ants, a topic that has recently been reviewed (89). A number of workers have suggested that spiders mimic a range of other organisms, alive or dead, and inanimate objects, for example, snails, beetles, Mutillid wasps, pill millipedes, dead leaves, sticks, bird droppings, prey remains, and the spider's own egg sacs (14, 25, 81, 100, 114, 121). In all these cases, color is an essential part of the deception. Mimicry may serve to deceive either predator or prey (or both).

Spiders monitoring orb webs frequently employ crypsis as described above, but they may also mimic inanimate objects like sticks or dead leaves, either on their own or as part of sometimes elaborate constructions. For example, many *Cyclosa* spp. (Araneidae) build vertical "sticks" of prey remains within the web but leave a gap in the center that is filled by the spider itself (14, 121).

Aggressive mimicry may allow spiders to escape visual detection by their prey. In flower-hunting thomisid spiders, aggressive mimicry might be involved in the normal color matching between the spider and its background (14). In this context, the eyes of potential predators and potential prey may have different spectral sensitivities, and a pattern that is cryptic to one might not be to the other (85). *Thomisus labifactus* (Thomisidae) can adjust its UV reflectance so that, while waiting in ambush on flowers, it is invisible to potential insect prey such as bees, even though it may mismatch in the visible spectrum (134). This suggests background matching for the purpose of predation. Some spiders resembling fresh wet bird droppings, which are attractive to insects (121), may gain a similar aggressive advantage. More recently, experiments have shown that visibility of both the contrastively colored ventral and the UV-reflecting dorsal side of the opisthosoma of *Argiope argentata* (Araneidae) increase insect prey caught in the web (26). The UV-reflecting surface may attract insects flying towards open spaces, and so, to some extent, the spider might be regarded as an aggressive mimic.

Aposematism

Most spiders are not dangerous or unpalatable enough to potential enemies with acute vision to benefit from warning (aposematic) coloration patterns, although apparent exceptions exist in species with powerful venoms or large jaws (14, 25). For example, *Poecilotheria* spp. (Theraphosidae), protected by their large jaws and urticating hairs, have black or brown venters and bright hairs on their fangs and/or legs and react to a potential enemy by displaying these attributes (14, 25). Species of *Latrodectus* (Theridiidae), with their striking black and red coloration, may also be aposematic (14, 85), and *Latrodectus tredecimguttatus* in Yugloslavia may act as an aposematic model for the pill woodlouse, *Armadillidium klugii*, and the pill millipede, *Glomeris pulchra* (81, but see 114). For none of these examples are there experimental data to suggest that the color patterns act as warnings to potential predators and that, as a result, the spider gains a measure of protection.

Other Forms of Predator Avoidance

At least some predators adopt hunting behaviors that result in their concentration on common species of prey and neglect of rarer ones (141). This process provides a powerful, frequency-dependent selective mechanism within species that show polymorphism in characters recognized by the predator (apostatic selection—19). Much evidence from both laboratory and field experiments now exists that demonstrates apostatic selection (1, 21), and it has been implicated in the maintenance of visible polymorphisms in the wild (e.g. 21, 101).

In some spiders, the adaptive function of rampant color polymorphism is difficult to imagine if not maintained by this form of selection. The highly polymorphic Hawaiian happy-face spider, *T. grallator* (Theridiidae) [see Major Gene Control (Genetic Polymorphisms) above] provides circumstantial evidence for the operation of apostatic selection. In all the major populations examined so far there is a significantly greater constancy in the frequencies of unpatterned (plain yellow) to patterned morphs (54; RG Gillespie & GS Oxford, unpublished observations) than expected from a model of population differentiation using neutral markers (allozymes) (RG Gillespie, GS Oxford, AWK Marumoto, unpublished observations). This suggests selective maintenance of the color polymorphism. Furthermore, in the most intensively studied population of *T. grallator* on Maui, RG Gillespie & GS Oxford (unpublished observations) found that, in a year when the unpatterned:patterned ratio was normal, wild-mated unpatterned females mated with unpatterned and patterned males in the proportions expected if mating was at random. However, in another year when the frequency of the unpatterned morph in the wild was unusually high, unpatterned females mated with patterned males significantly more often than expected from field frequencies, i.e. the common morph appeared to have a mating disadvantage. This phenomenon is probably not a result of female choice during mating but of higher predation pressures by insectivorous birds on males of the unpatterned morph while they move in search of mates. So far, apostatic selection in spiders has not been demonstrated experimentally.

Thermoregulation

General aspects of thermoregulation in spiders have been reviewed elsewhere (72, 122). Experiments and observations (128, 129, 142) suggest that the silver coloration of certain araneids, in conjunction with web and spider orientation, may help to prevent overheating. In a range of araneid species, dorsal surfaces tend to be silver or white, whereas ventral surfaces are mostly dark. However, in some *Leucauge* species (Tetragnathidae), which rest in nearly horizontal webs with the ventral side uppermost, the colors of the surfaces are reversed (129). Spiders can also optimize heating rates by behaviorally altering which surface (silver or dark) faces the sun (72). Over a longer time span, juvenile

Argiope trifasciatus (Araneidae) prevent overheating during the summer by web orientation and a silvery ventral coloration, whereas in the autumn, as the spiders mature, the ventral surface changes from silver to black and web orientation shifts so that the resident receives maximum insolation (142).

Thermal effects have also been implicated in the maintenance of genetically determined color variation within species. For example, melanic and non-melanic forms occur in some populations of *Pityohyphantes phrygianus* (Linyphiidae), and laboratory evidence shows that melanics have an activity advantage at low temperatures (58, 59). A weak association between the presence of black spots and a more advanced reproductive stage in individuals of *E. ovata* (Theridiidae) might also suggest a thermal connection (104, 110). Reference is occasionally made in the taxonomic and ecological literature to associations between the color of individuals within a species and the amount of light to which they are exposed. Possible reasons include differences in selection for coloration (e.g. in cave spiders) and/or crypsis, in addition to thermoregulation. Individuals of *Argyrodes furcata* (Theridiidae), for example, vary markedly in color, and this has been associated with the intensity of sunshine received (35). Within one area, individuals may vary from very pale grey to nearly black, with light spiders usually found in sunny situations and dark ones in the shade. Although the genetic basis is not known, this situation represents the reverse of that found in cave spiders, where paleness is associated with lack of light (see Darkening of Cave Spiders above).

Sexual Dimorphism

The remarkable sexual dimorphism for color and pattern exhibited by a large number of salticid and lycosid spiders has attracted attention for many years (e.g. 14, 27, 74, 116, 117). Where a species is sexually dimorphic for color, the mature male is usually more brightly colored than the female, although there are exceptions (40). The link between sexual maturity and the acquisition of bright colors in males has led to the hypothesis that these characters may have evolved by sexual selection (see 74 for a discussion of this and other hypotheses). This is a highly likely explanation because members of the Salticidae and Lycosidae, which exhibit marked sexual dimorphism, generally possess high visual acuity (40, 78) and color vision (40, 152). However, sexual dimorphism is also widespread in families without advanced vision, and here differences in appearance between the sexes are probably a result of males and females living in different habitats and acquiring colors appropriate to each (for example male and female thomisids—see Background Matching). Too few studies exist of differential habitat usage by males and females of sexually color-dimorphic species to be able draw general conclusions regarding the adaptive significance of this phenomenon.

FUTURE DIRECTIONS

Perhaps the most exciting avenue for future research on spider coloration is the relationship between color and habitat usage. In particular, intriguing associations are suggested by preliminary tests of ecological variables associated with color parameters (RG Gillespie & GS Oxford, unpublished observations). We have found that continuous variation in color is found more frequently in spiders that inhabit open areas, whereas color polymorphism occurs more frequently in forest habitats. In terms of microhabitat, continuous color variation and color polymorphism occur more frequently in spiders that inhabit vegetation and flowers rather than holes and rocky habitats. That true polymorphisms tend to occur in forest habitats may reflect the suggested role of bird predation in the maintenance of color polymorphisms. Continuous color variation, on the other hand, might be important for crypsis in spiders in more exposed habitats. If these speculations are true, one might argue that all species in forested areas should be polymorphic, and all those in open areas should show continuous variation for color, which is clearly untrue. However, the associations are worthy of further investigation.

The visible display of guanine appears to predominate in species that occur high in vegetation rather than low down. Coupled with the observations described earlier, in which physiological color changes associated with dropping from aerial webs frequently involve reduction in guanine exposure, this might suggest that the deployment of guanine as a pigment occurs primarily in situations where it can serve visual and/or thermoregulatory functions. Accordingly, it is much more important among spiders occupying more aerial habitats and is largely absent from species that occur on or near the ground. Again, this generalization has not been tested, but it suggests an interesting avenue for additional work. Related to these questions is the adaptive significance of sexual dimorphism for color in species with poor visual acuity.

Two other areas also deserve further exploration. Green pigments are sporadic in spiders, and investigation of their chemical nature and physical locations in a wide variety of taxa would indicate whether they have evolved independently or whether common, silenced, ancestral biosynthetic systems are from time to time “rediscovered” and utilized when conditions demand. Both mechanisms would be of evolutionary interest, and the former would also be of taxonomic importance. For the second area, a real dearth of data exists on whether intraspecific variation in color is genetic or induced. As a result, in many cases, evolutionary phenomena cannot be distinguished from phenotypic changes within individuals, and this precludes speculation regarding the immediate mechanism of adaptations to specific environmental challenges (natural selection versus phenotypic plasticity).

In conclusion, spider coloration is a complex phenomenon, with many possible agents involved in its manifestation. One particularly useful aspect of color is that, when under genetic control, the phenotype can frequently serve as a marker for the genotype. Hence, these systems may allow the investigation of the mode of selection acting on coloration. For example, estimates of population differentiation values can be generated for the color markers, and these can be compared with estimates derived from presumed neutral alleles (e.g. allozymes). Such methods can be used to test for selection between populations and also to reveal how selection operates differently on different sets of color (and other) characters.

ACKNOWLEDGMENTS

We thank J Koh, H Levi, D Penney, C Rees, G Roderick, G Uetz, and the late T Yaginuma for unpublished information and discussion. This work was supported in Hawaii by National Science Foundation Grant DEB 9207753 to RGG and GSO. GSO also acknowledges grants from The British Ecological Society, The Royal Society, The Bonhote Bequest, The Percy Sladen Memorial Fund, and The University of York.

Note: More details of the taxonomic distributions of pigment, reversible color changes, and genetic variation can be found in tables at the Annual Reviews home page (www.AnnualReviews.org) in the Supplementary Materials for the *Annual Review of Entomology*.

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