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Portraits of Evolution: Studies of Coloration in Hawaiian Spiders

GEOFF S. OXFORD AND ROSEMARY G. GILLESPIE

Color variation, when genetically determined, provides a visual tool with which to investigate natural selection. Here we examine how color variation in two spider systems in the Hawaiian Islands can be used to understand evolutionary phenomena at both population and species levels. First, the happy-face spider (*Theridion grallator*) shows a number of discrete color morphs, the frequencies of which are very similar among populations, although the genetic basis for them differs between islands. These observations permit intriguing insights into the evolution and maintenance of color polymorphism. Second, we consider the adaptive radiation of Hawaiian *Tetragnatha* spiders. Here the spectacularly diverse array of color forms is found within closely related species on each island, with similar sets of colors evolving independently in each locale, suggesting selection is acting to maintain such diversity.

Genetically determined color variation provides an immediately tangible link between a genotype and an externally expressed phenotype and, as a result, has long been used to probe evolutionary questions. In insects generally, and in Lepidoptera in particular, studies of color and pattern 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 (Ford 1975), the power and mode of action of natural selection (Kettlewell 1973), the evolution of mimetic resemblances (Turner 1970), and the developmental rules underlying differences in patterns within and among species (Nijhout 1991).

Color polymorphism is variation that is determined genetically at a small number of major loci (Ford 1940) and is classically divided into two categories: balanced and transient. In *balanced polymorphisms*, morph frequencies can remain constant over long periods of time, usually as a result of an equilibrium between advantages and disadvantages of the different morphs. Indeed, balanced polymorphisms often transcend species boundaries, for example, the color and pattern variation in the spiders *Enoplognatha ovata* and *E. latimana* (Oxford and Reillo 1993).

THE DISCRETE COLOR POLYMORPHISMS IN SPIDERS ALLOW THE STUDY OF EVOLUTION “IN ACTION”

Transient polymorphisms are those that are not maintained in a balanced state over extended time periods. Perhaps the best-known situation is when one color morph replaces another over time (which may be comparatively short, depending on the relative advantage of the favored allele) as a result of *directional selection*. In other situations, one ancestral color morph can give rise to two or more descendant color morphs as a result of *disruptive selection*, a phenomenon well known in adaptive radiations. For example, populations may diverge in allopatry (that is, when geographically separate from each other), with disruptive selection acting on color variants when the two ecologically similar color forms regain sympatry (overlap geographically), as has been observed for morphological characters in *Anolis* lizards (Losos et al. 1998) and cichlid fish (Ruber et al. 1999). Alternatively, selection on a single population for adaptation to different habitats (or microclimates within a habitat) within a particular locality can lead

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to polymorphism (Mather 1955). If disruptive selection is strong, the subpopulations of the different habitat-specific color morphs may cease to exchange genes and evolve sympatrically into separate species (Thoday and Gibson 1962). In either case, color polymorphism is implicated in the process, and its existence may be identified by examining the evolutionary end products.

Consider coloration in spiders. Like many other arthropods, spiders display a wide range of colors and patterns that vary both inter- and intraspecifically. As a group they have been relatively neglected, until recently, as possible models with which to study evolutionary processes. However, investigations of spider coloration have a long and distinguished history. For example, one of the very early studies of sexual selection was based on the sexual dimorphism for color and pattern exhibited by many jumping spiders (Salticidae; Peckham and Peckham 1889, 1890). This work served to underline the principles espoused in Charles Darwin's book on the subject published just a few years earlier (Darwin 1871). Perhaps the most common explanation for many of the color patterns exhibited by spiders is for avoidance of predation (Foelix 1982). Spiders can use color to hide from (crypsis) or confuse predators (Oxford and Gillespie 1998); here color is generally associated with a specific habitat. Therefore, the existence of discrete color polymorphisms makes it possible to elucidate the selective forces acting on color and hence the evolution of ecological affinity.

Two different selective forces, selection for balanced polymorphism and disruptive selection acting on transient polymorphisms, are well illustrated by spiders in the Hawaiian Islands. Islands have long been recognized for their importance in studies of the genetic differentiation of populations and the processes involved in speciation (Darwin 1859). Remote oceanic archipelagos, in particular the Hawaiian Islands, provide opportunities to observe the effects of colonization, isolation, and population differentiation replicated over time and in a defined geographical and temporal sequence (Simon 1987). The Hawaiian archipelago consists of four independently formed high islands: Kauai, Oahu, Maui Nui (Maui, Molokai, and Lanai, formed as a single land mass), and Hawaii. This arrangement allows comparison of taxa on different islands. In the case of both spider systems, *Theridion grallator* and *Tetragnatha* spp., similar arrays of color forms are found on each island and, in the case of *Tetragnatha* at least, have evolved largely independently. The implication is that selection maintains the balance of color forms, within a species in the case of happy-face spiders (balanced polymorphism), and among several species in the case of the Hawaiian *Tetragnatha* (the product of selection acting on a transient polymorphism). We now consider these systems in more detail.

Balanced polymorphisms

The mechanism through which selection acts on color per se can be studied most easily in situations where variation exists as an integral property of populations, that is, in balanced polymorphisms. Such genetic polymorphisms have provided

the basis for many of the advances in our understanding of ecological genetics made during the 20th century. The Hawaiian Islands offer an ideal opportunity for studying the maintenance and adaptive significance of color variation within spider populations, as well as the interaction between genetic drift and natural selection. These aspects have been studied in some detail in the endemic Hawaiian happy-face spider *Theridion grallator* (Araneae, Theridiidae). The species occurs on the islands of Oahu (largest population to date known from Mt. Kaala summit, elevation 1220 m), Molokai (largest population in Kamakou Preserve, elevation 1110 m), Maui (largest population in Waikamoi Preserve, Haleakala, elevation 1360 m; other populations on Puu Kukui, West Maui, elevation 1387 m, and in Auwahi on the south slope of Haleakala, elevation 1370 m), and Hawaii (populations in the Kohala mountains, 1152 m; the Saddle, 1600 m; and Kilauea, 1190 m). These are all sites of native Hawaiian wet-to-mesic forest, with a canopy generally dominated by *Metrosideros polymorpha* (Myrtaceae) and *Acacia koa* (Leguminosae), and the subcanopy by *Broussaisia arguta* (Saxifragaceae), *Clermontia arborescens* (Campanulaceae), *Cheirodendron trigynum* (Araliaceae), *Coprosma* sp. (Rubiaceae), *Ilex anomolum* (Aquifoliaceae), *Myrsine* spp. (Myrsinaceae), and *Pelea* spp. (Rutaceae). Populations of *T. grallator* are patchily distributed, and at most sites they occur at very low densities.

The spiders build very small, flimsy webs consisting of a scanty, two-dimensional layer of silk covering the entire underside of a leaf. During the day, the spiders are usually tightly appressed to the underside of the leaf, but at night they often hang well below the leaf from silk threads. They capture insects on the underside of a leaf and feed in situ. The most common prey items are small adult flies of the families Dolichopodidae and Drosophilidae (Gon 1985). Upon maturation, a male is often found sharing a leaf with a penultimate instar female just prior to her final molt; mating occurs immediately after the female's molt. The female deposits an egg sac after a few weeks and guards it aggressively (Gillespie 1990). When the eggs are ready to hatch, the mother loosens the silk of the egg sac to free the emerging spiderlings. Once emerged, the spiderlings feed communally on prey caught by the mother for the next 6–8 weeks, at which time the mother may die or abandon her offspring. Young spiderlings then disperse from the maternal leaf and shortly after commence their usual existence as single occupants on the underside of a leaf.

Theridion grallator is highly variable for color. The commonest color morph is Yellow, which makes up about 70% of any population. The other 30% is composed of a selection of genetically determined, "patterned" morphs generated by patches of red, white, or black pigments superimposed on a yellow background (Figure 1). It is possible to assign the majority of color morphs to one of the following broad categories: Yellow, Red front, Red back, Red front and back, Red lines, Red ring, Black ring, Red/black ring, Red blob, Red/black blob, and White (Gon 1985, Gillespie and Tabashnik 1989, Oxford and Gillespie 1996a). The yellow background of any morph can

be modified through ingestion of highly pigmented prey (Gillespie 1989), although this phenomenon is unlikely to be of any evolutionary significance. The common name *happy-face spider* comes from the pattern of red and black shown by the color morph Red front. The genetic control of some of

these color morphs has been determined using laboratory mating experiments and also collections of mothers, with their associated offspring, from the field. Initially the focus was on spiders from the Waikamoi population on Maui. Here it was found that the progeny always segregated for the parental alleles and in Mendelian ratios (Gillespie and Tabashnik 1989, Oxford and Gillespie 1996a). Yellow is recessive to all patterned morphs. Among the patterned morphs, the dominance hierarchy is approximately proportional to the amount of pigmentation on the abdomen: the more red, black, or white pigment, the higher the allele is in the dominance hierarchy. Thus Red blob is dominant to all other red morphs, and White is dominant to all morphs. Some morphs are codominant, for example, crossing Red lines with Red front and back produces the Red ring pattern. Evidence to date indicates these morphs are controlled by a single autosomal locus, expressed equally in both sexes (Oxford and Gillespie 1996a). The system of genetic control of the color polymorphism on Maui is therefore fairly straightforward.

Hawaii populations of *T. grallator* contain morphs superficially almost identical to those found on Maui, and they occur at similar frequencies. However, their underlying genetic control differs markedly (Oxford and Gillespie 1996b). On Hawaii there is clear evidence for two unlinked, autosomal loci (I and II) controlling the color variation (Figure 2). Moreover, on Hawaii some color forms, found in both sexes on Maui, are restricted to either males or females. Thus, Yellow and Red front appear to be controlled by just one allele on Hawaii, with the former expressed in females and the latter in males. Red blob (females) and Red ring (males) form another such pair. As a further complication, there is good evidence that the two sets of sex-limited phenotypes are controlled by alleles at different loci. These patterns of gene expression are retained, on the whole, in the offspring from interisland crosses; sex-limited morphs derived from



Figure 1. Color morphs of the Hawaiian happy-face spider, *Theridion grallator* (Araneae, Theridiidae). Top row, left to right: Yellow (Waikamoi, Maui); Yellow (Mt. Kaala, Oahu), Yellow (Saddle, Hawaii), Red Front (Kamakou, Molokai), Black lines (Auwahi, Maui). Second row: Red front (Saddle, Hawaii), Red front (Mt. Kaala, Oahu), Red/black lines (Mt. Kaala, Oahu), Black lines and Red back (Auwahi, Maui), Red back (Auwahi, Maui). Third row: Black midline (Mt. Kaala, Oahu), Red front and back (Kohala, Hawaii), Red lines (Waikamoi, Maui), Red lines and Red front (Waikamoi, Maui), Red/black ring (Maui). Fourth row: Red/black ring (Puu Kukui, Maui), Red blob (Waikamoi, Maui), Red blob (Mt. Kaala, Oahu), White (Waikamoi, Maui).

Hawaii behave on a mixed-island (Maui–Hawaii) genetic background exactly as they do in pure Hawaii crosses. The only exception is that the full expression of the commonest male-limited morph from Hawaii (Red front) depends on the presence of an X chromosome of Hawaii origin (Oxford and Gillespie 1996c). Less-detailed studies of spiders from other populations on Hawaii suggest that these genetic characteristics probably are common islandwide. Certainly Yellow seems to be confined to females, and Red front to males, wherever populations have been sampled.

How are the substantial differences in the genetics of color between Maui and Hawaii to be explained? The sequential formation of the Hawaiian Islands (see Carson and Clague 1995) means that the source of Hawaii populations of *T. grallator* is most likely the adjacent and next oldest island, Maui (as has been proposed for many Hawaiian taxa; Wagner and Funk 1995). Preliminary molecular evidence suggests that *T. grallator* has indeed colonized the island chain from Oahu (the oldest island inhabited by *T. grallator*) to Maui and Molokai, and then to Hawaii. The simplest hypothesis for the genetic difference is that the Hawaii population was initiated by a very small number of immigrants from Maui. Genetic changes

within this tiny founder population produced the mode of inheritance found on Hawaii today. As the initial population expanded to fill suitable habitats, the new genetic architecture underlying the color variation spread across the island. This hypothesis is tentative, as it is possible that there are small, uninvestigated populations of the spider on Maui that have the Hawaii pattern of inheritance, and that it was from one of these that the colonizing spiders came. Even if this is the case, it leaves unanswered the question of how the multiple genetic changes occurred, whether in an isolated Maui population before the colonization of Hawaii or during the founding event itself. Intriguingly, preliminary evidence from the island of Oahu suggests that the genetics of the polymorphism there may be different again. If substantiated, this may indicate that the Maui–Hawaii genetic transition was not the first to have affected the control of the polymorphism during the evolutionary history of *T. grallator*.

Selection on balanced polymorphisms

The frequencies of morphs within a natural population are determined by a number of evolutionary factors, predominantly chance (genetic drift) and natural selection. *Genetic drift*

is a stochastic change in allele frequencies as a result of sampling. The effect is much more profound in small populations, for example, when a new population is established by a small sample of founding individuals (known as the founder effect; Templeton 1980). We now know that genetic drift represents a potent force in molecular evolution (Graur and Li 2000), but to what extent it has an influence on highly visible, phenotypic variation is still a contentious issue. As a result of genetic drift, intraspecific variation tends to be distributed between populations, rather than within any one population.

There are several ways in which natural selection can operate to maintain color variation within a population, the three commonest being heterozygote advantage, disruptive selection between populations with migration between them, and various forms of negative frequency-dependent selection. Heterozygote advantage has been demonstrated in only very few cases. Disruptive selection in different environments with gene flow between them is a likely explanation for the distribution of pale and melanic forms of the moth *Biston betularia* in rural and industrial areas of Britain (Majerus 1998). Negative frequency-dependent selection, acting via a number of disparate mechanisms, is probably responsible for the maintenance of the majority of poly-

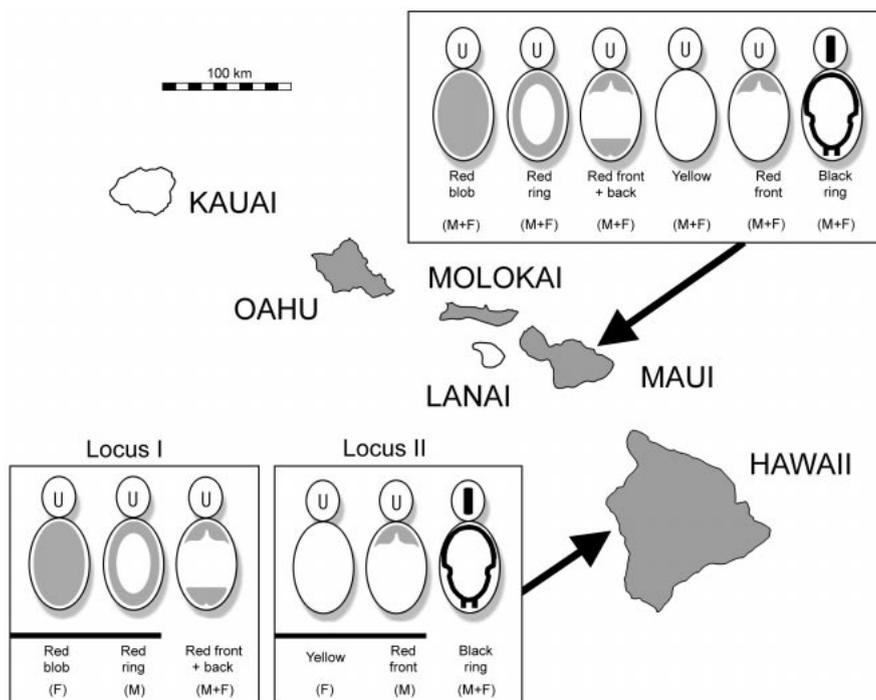


Figure 2. Distribution of the Hawaiian happy-face spider, *Theridion grallator*, and the genetics of its color patterns. The shaded islands are those occupied by *T. grallator*. The panels indicate the genetics of just six of the numerous color morphs that have been examined from both Maui and Hawaii. The Maui color morphs all seem to be determined by alleles at one locus, and they are found equally in both sexes. On Hawaii, two unlinked loci are present (loci I and II), with the color morphs distributed between them as shown. Single alleles appear to control the Red blob/Red ring and Yellow/Red front pairs of morphs (indicated by the lines beneath), which are differentially expressed in females (F) and males (M), as indicated. Adapted with permission from Oxford 1999.

morphisms in the wild. Here, the fitness of a genotype (or allele) is a negative function of its frequency in the population, so that when it is rare it is at an advantage and when common, at a disadvantage. In these cases the fitness associated with a genotype is not fixed and changes according to the genetic composition of the population.

In the case of *T. grallator*, color diversity is predominantly contained within populations with rather little variation between them. Therefore, the question is whether there is any evidence that the polymorphism is maintained by natural selection, and if so, what the adaptive significance of the spectacular variation is. As mentioned earlier, the Yellow morph (Yellow females and Red front males on Hawaii) accounts for about 70% of individuals in the populations studied in detail so far (Gillespie and Tabashnik 1990). The remaining 30% comprises a mix of different patterned morphs, each at rather low frequencies. The apparent constancy of the Yellow-to-patterned morph ratio across populations could be produced in two principal ways, by gene flow or selection. There may be high levels of gene flow within and among islands, such that all populations come to have roughly the same morph frequencies. This has been shown not to be the case (Gillespie and Tabashnik 1990). Rather, studies indicate that the color variation shows significantly less differentiation between populations than neutral markers (allozymes), indicating some sort of overall selection for similar Yellow-to-patterned ratios (Gillespie and Oxford 1998).

What might the nature of this selection be? It has been suggested that a form of frequency-dependent selection may be involved (Gillespie and Oxford 1998). In two separate years the offspring from wild-mated Yellow (i.e., homozygous recessive) females from the Waikamoi population on Maui were scored to determine whether they had mated with a Yellow or a patterned male. In one year, the Yellow-to-patterned ratio was approximately 7:3, and females were shown to have mated with males in almost exactly these proportions; mating seemed to be at random with respect to color. In the second year, the frequency of the Yellow morph was higher than normal, at 85%. Then, Yellow females were found to have mated with the rarer, patterned males about twice as often as would be expected, given the frequency of patterned morphs in the population. These data suggest that the rare, patterned males were at a mating advantage compared to the unusually common Yellow males.

This apparent rare-male mating advantage can arise through a number of different mechanisms. For example, during courtship, females may favor rare males, that is, those that are different from the most frequently encountered morph, as has been demonstrated in some *Drosophila* species (Salceda and Anderson 1988). A direct, rare-male mating advantage of this sort is unlikely in *T. grallator*, as population densities are low and the chance that two males will court a female simultaneously, allowing her a choice, is therefore small. Also, *T. grallator* belongs to a spider family with poorly developed visual acuity (Land 1985), and courtship almost certainly depends mainly on vibratory and olfactory, rather than visual,

signals. Perhaps a more likely explanation for the rare-male advantage hinges on a behavioral response of predators to their prey. The quest for food may lead to the situation whereby a visually hunting predator forms a search image for the most common color morph in the prey species, and as a result, this morph suffers disproportionately high predation relative to its actual frequency in the population (Gillespie and Oxford 1998). It follows that the rarer morphs gain an advantage by being preyed upon less often than expected. The rare morph then increases in number, and at some point the predator switches its preference to this now common morph. This is apostatic selection, a form of negative frequency-dependent selection (Allen 1988).

In *T. grallator*, the Yellow form is highly cryptic and very difficult to see against the filtered green light that penetrates the leaves under which the spider lives. This, in conjunction with morphological and behavioral attributes (Oxford and Gillespie 1998), suggests that predators do represent an important selective agent. Many of the Hawaiian honeycreepers occupying the same forests as *T. grallator* specialize on insects and spiders and search visually for them, so they may be key predators in this system. Female happy-face spiders are largely sedentary; it is the mature males who move to find mates. It is known that moving prey are almost inevitably more conspicuous to predators and therefore more vulnerable than stationary prey (Avery and Krebs 1984). One can hypothesize, therefore, that apostatic selection acts more strongly on reproductive males than on females. If the frequency of the Yellow morph is higher than normal, birds may develop a search image for this morph and, as a consequence, prey more on Yellow males, thus the pool of males that eventually find mates is enriched with the rarer, patterned morphs. This would have the effect of shifting morph frequencies back toward the apparent equilibrium of 7:3, Yellow-to-patterned morphs. The equilibrium frequencies presumably reflect a balance between the advantages of being cryptic and the disadvantages of being common.

Balanced polymorphism: Synthesis of current knowledge

It has long been recognized that differences in genetic background between populations can influence the expression of major color alleles, and indeed that different genetic architectures can exist within a species. For example, on different Scottish islands, dominance of a melanic form of the lesser yellow underwing moth, *Noctua comes*, is achieved by the accumulation of different modifier genes; when crosses were made between moths from different islands, dominance became incomplete (Ford 1955). More major differences are found in the genetic control of the color polymorphism in the two-spotted lady beetle, *Adalia bipunctata*, from western and central Asia and from Britain (Majerus 1994). Finally, most meadow spittlebug (*Philaenus spumarius*) populations contain a number of melanic morphs at relatively high frequencies in females, which are virtually absent in males (Halkka and Halkka 1990). By contrast, in what was an

industrially polluted area of South Wales, these same morphs are found with nearly equal frequencies in the two sexes (Stewart and Lees 1987, 1988).

In the case of the Hawaiian happy-face spider, the shifts in the genetics underlying the color polymorphism are much more extreme than in any of these other examples. Not only have two loci in spiders on Hawaii been derived from what appears to be a single locus in spiders on Maui, but sets of apparently composite alleles controlling sex-limited morphs have evolved at each of the two loci in Hawaiian spiders. The precise relationship between these contrasting genetic systems is not clear at present, but the single locus in spiders on Maui is probably a supergene (a number of closely linked loci affecting color and pattern), and this may provide the basis for at least one of the genetic differences between spiders from different islands (Oxford and Gillespie 1996a). Thus, if a number of closely linked loci control the polymorphism on Maui, recombination within them, coupled with a translocation or inversion event, could yield two effectively unlinked loci. Supergenes have been postulated as the bases for color polymorphisms in other arthropod taxa, for example, ladybirds (Majerus 1994), spittlebugs (Halkka and Halkka 1990), and mimetic butterflies (Ford 1975).

In the happy-face spider, there may have been even greater genetic revolutions than we currently recognize. The probability of a large number of color forms colonizing Hawaii from Maui is small given the fact that Yellow, the homozygous recessive morph, occurs at frequencies of 70% or so in Maui populations. However, most of the color morphs found on Maui are also present on Hawaii. There is a possibility that at least some of the morphs on Hawaii are not of Maui origin but have arisen in situ. Molecular analyses of the color loci are needed to explore this hypothesis further. The establishment of a full color polymorphism on Hawaii, despite the probable loss of alleles during the founder event, suggests selective maintenance of the variation, a conclusion consistent with recent data (Gillespie and Oxford 1998). Despite these genetic upheavals, there is no evidence for any reproductive isolation between Maui and Hawaii Island populations (Oxford and Gillespie 1996c).

Transient polymorphisms

The Hawaiian spiders in the long-jawed orb-weaving genus *Tetragnatha* (Tetragnathidae) provide an example of what might be an end product of disruptive selection acting on habitat-associated color polymorphism. These spiders have undergone spectacular adaptive radiation in the islands. Outside the archipelago, *Tetragnatha* has a worldwide distribution (Levi 1981), yet it is also one of the most homogeneous genera of spiders. In Hawaii, however, the tetragnathids span a tremendous spectrum of colors, shapes, sizes, ecological affinities, and behaviors (Gillespie et al. 1994, 1998). Many species are web builders, with striking patterns, colors, and structural modifications of the abdomen that allow concealment within specific microhabitats. Some species have structural modifications that appear to allow specialization for

specific prey types. One entire clade (the spiny-leg clade) has abandoned web building and, with the development of long spines on the legs, has adopted a cursorial predatory strategy (Gillespie 1991).

Species of the spiny-leg Hawaiian *Tetragnatha*, on each island, can be characterized as green, leaf dwelling; maroon, moss dwelling; large brown, bark dwelling; and small brown, twig dwelling. However, phylogenetic analyses indicate the species on any one island are generally most closely related to each other, and each of the different ecomorphs appears to have evolved independently on the different islands (Gillespie et al. 1997). Therefore, we envisage a scenario being enacted on each island whereby discontinuous variation in coloration arises in these spiders through mutation, either in a single population or in closely related populations that have diverged reproductively in allopatry. The color polymorphism is then subjected to strong selection in divergent directions, resulting in a set of three to four discrete ecomorphs (Figure 3). On different islands, convergence has led to the formation of similar sets of ecomorphs, which suggests that the disruptive selective forces are similar from island to island.

Selection on transient polymorphisms

How might selection act on transient polymorphism so as to cause diversification? Because the Hawaiian Islands formed at different times and were populated chronologically, we can examine population-level phenomena associated with species proliferation. As described above, *Tetragnatha* has diversified within older islands, but what about younger islands? Preliminary evidence suggests that recent colonists on the youngest island (Hawaii) appear to undergo expansion in ecological range. Colonization is probably a time when genetic variability increases and polymorphisms develop. Strong disruptive selection acting on the different morphs may lead to local adaptation and specialization within different ecological environments (Gillespie et al. 2001). This in turn may allow these spiders to proliferate into an array of closely related but visibly monomorphic species, as can be found on the next oldest island, Maui.

The inferred mechanism of speciation in the situation outlined may be allopatric, parapatric, or sympatric. If speciation is *allopatric*, the color differences probably arise in allopatry but are accentuated when two close relatives are reunited in sympatry after initial divergence in allopatry. Alternatively, selection may act on polymorphism to cause divergence into contiguous habitats, in *parapatric* speciation, or into overlapping habitats but different microhabitats, in *sympatric* speciation. Parapatric divergence as a result of adaptive shifts has been most clearly documented for cave faunas (Howarth 1981, Arnedo and Ribera 1999). Sympatric speciation based on divergent selection and ecological shifts has been demonstrated for flies on different hosts (Bush 1994), as well as beetles in different microhabitats (Chown 1990). This mechanism of speciation has now been implicated in adaptive radiations, including that of cichlid fish in the African rift lakes (Johannesson 2001). However, whether allopatry, para-

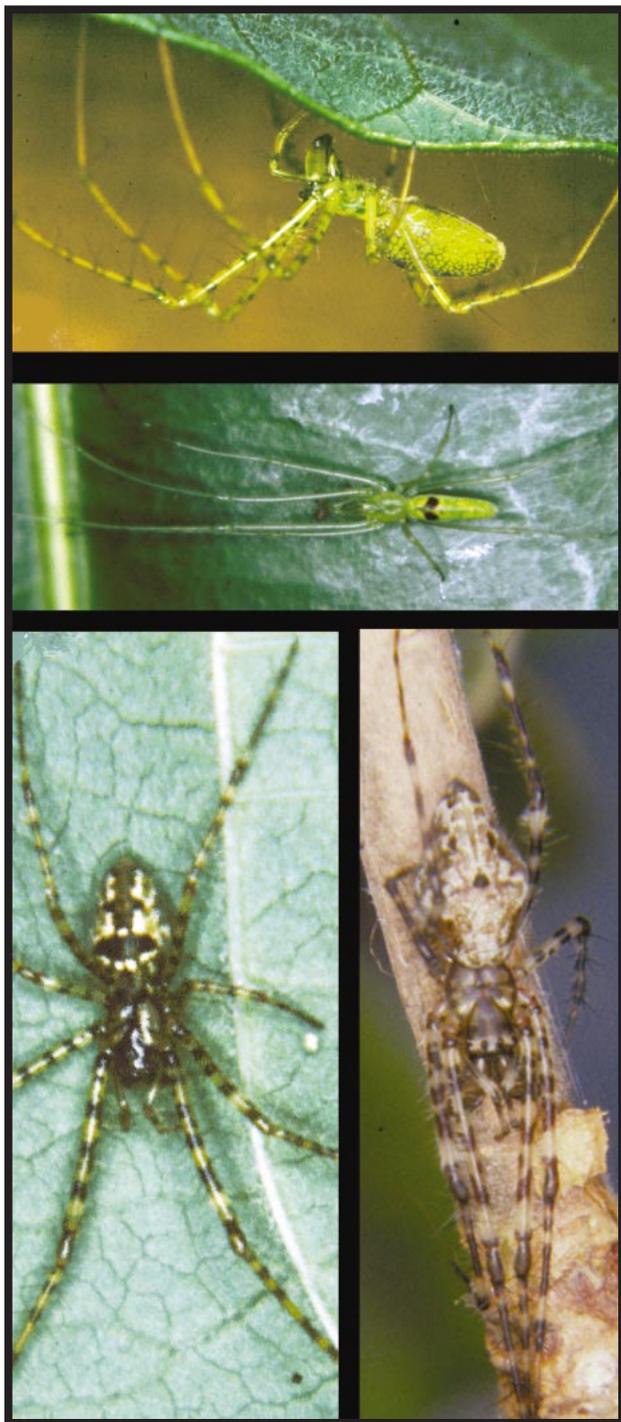


Figure 3. Ecomorphs of Hawaiian spiny-leg *Tetragnatha*. *Tetragnatha waikamoi* (top) and *T. brevignatha* (second from top) represent the “green” ecomorph; these species have nonoverlapping ranges and are not sister taxa. Likewise, *T. pilosa* (bottom left) and *T. quasimodo* (bottom right) represent the “large brown” ecomorph. They do not overlap at all: *T. pilosa* is on Kauai only, *T. quasimodo* is on all other islands, and they are only distantly related within the spiny-leg clade of Hawaiian *Tetragnatha*.

patry, or sympatry is involved in initial population differentiation, divergent natural selection has frequently been discussed as the ultimate cause of adaptive radiation (for review see Schluter 1996). The Hawaiian *Tetragnatha* system indicates that divergent selection on color has played an important role in the evolutionary history of the lineage, probably as a result of predator-mediated selection for crypsis.

Conclusions

Color polymorphisms are very useful in providing a visible manifestation of the genetic differences upon which selection acts. The Hawaiian Islands offer an ideal situation in which to study the nature of the selective process because they were formed at different times and are chronologically arranged. Spiders carrying a subset of the ancestral gene pool arrive on an island and are subjected to selection. In most situations, evolution seems to proceed faster than immigration. If immigration provided the array of color forms filling the various ecological roles, color morphs would be more closely related to similar morphs on nearby islands than to the dissimilar morphs on the same island. However, many color forms appear to have evolved *de novo* on most islands, resulting in physically similar, yet genetically unique, sets of color morphs on each island. For the highly polymorphic *T. grallator*, it is likely that at least some of the patterned color morphs have arisen independently on different islands. Likewise, in Hawaiian *Tetragnatha*, a similar set of color ecomorphs has appeared *de novo* on each island. Therefore, in both these spider systems, the end product is similar sets of color morphs on different islands. The difference between the two is that color arises within a population in the case of *T. grallator*, but within a lineage (between species) in the case of *Tetragnatha*.

Many questions are yet to be answered. For *T. grallator*, the possibility of genetic differences between Oahu populations and those on the other Hawaiian islands remains to be investigated. If genetic differences are substantiated in this model system, it would imply that genetic revolutions during founding episodes are a relatively common, and important, evolutionary phenomenon. Further work also is required to understand the genetic basis for the changes that occur subsequent to colonization of new islands, for example, the molecular differences affecting color determination in spiders from Maui and Hawaii, described above. For *Tetragnatha*, the genetic constraints or switches underlying the repeated evolution of similar sets of color forms in the same environments are yet to be explored. Indeed, elucidation of the genetic mechanisms underlying these color changes would provide insight into the mechanisms underlying adaptive radiation, not only in these spiders but also in other lineages (such as cichlid fish and *Anolis* lizards) that display similar evolutionary phenomena.

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