

Sun, surf and spiders: taxonomy and phylogeography of Hawaiian Araneae

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Summary

The isolation of the Hawaiian archipelago has resulted in a fauna that shows high levels of endemism, and an associated vulnerability to anthropogenic disturbance and alien species invasion. Most of the initial collections of Hawaiian spiders were made by R. C. L. Perkins, and the species described by Eugène Simon. Some groups are represented by single (or a few) species, and may be relictual, or evolutionarily recent introductions. Major radiations are now known in the following groups: (1) the genus *Theridion*, a poorly known group, except for the single species *T. grallator*; (2) the genus *Tetragnatha*, which has been the focus of studies by R. G. Gillespie and colleagues; (3) the genus *Argyrodes*, which has been the subject of recent studies by M. A. J. Rivera; (4) representatives of Thomisidae and Philodromidae, which were studied by T. W. Suman, with more recent phylogenetic studies of the Thomisidae being conducted by J. E. Garb; and (5) representatives of Lycosidae, best known for their cave adaptations discovered by F. G. Howarth. Preliminary evidence from some of these radiations, based on morphological and/or molecular data, suggests that founder events (and the associated isolation) and adaptive shifts have been involved in species proliferation for at least some groups.

Introduction

Remarkable suites of endemic and often rare species are characteristics of isolated land masses. This is particularly true of the Hawaiian Islands, where extreme isolation has been associated with accentuation and acceleration of the processes of both evolution and extinction. The biota is well known for its extraordinarily high levels of endemism: species frequently occupy minute distributional ranges. At the same time, anthropogenic disturbance, either direct or indirect, is causing rapid species decline. No other area in the USA has such a high proportion of endemic species nor suffers the impact from as many new invading species as Hawaii. As a consequence, the archipelago represents a microcosm for studies in evolution and conservation.

The Hawaiian Islands

There are several geographic features that render the Hawaiian Archipelago an unparalleled scientific laboratory for studying processes of evolution. First, the extreme isolation of the Hawaiian Islands has allowed repeated and explosive diversification of species from a single ancestor, often accompanied by radical shifts in morphology, ecology and behaviour. These radiations are associated with high frequencies of endemism: more than 81% in birds and an extraordinary 99% in terrestrial molluscs and arthropods (Eldredge & Miller, 1995; Miller & Eldredge, 1996). Second, the tremendous topographical range and consequent environmental diversity (wet and dry habitats; bogs, shrublands and forests; elevations from tropical coastlands to alpine deserts) provide a huge

ecological spectrum for species differentiation. Third, the series of islands provides a replicated system for examining within-island patterns of species formation across similar ranges of environmental extremes. Finally, because the islands are arranged by age from Kauai (oldest) to Hawaii (youngest), the archipelago allows examination of species, formation within an identifiable chronological framework (Carson & Clague, 1995). The initial stages of population subdivision can be found on the youngest island, with the dynamic volcanic state of the island providing shifting barriers to gene flow (Carson, 1990). Later stages in species formation can generally be found on the older islands. Upon this palette, the primary factors responsible for generating the high diversity of endemic species are: (1) small population sizes, (2) species interactions, and (3) habitat fragmentation.

History of arachnology in Hawaii

The pioneering work on the Hawaiian fauna was carried out by R. C. L. Perkins, who was sent out to the islands from the UK in the late 1800s. He spent over ten years in Hawaii, collecting just about everywhere, and against all odds: "I was obliged to carry a limited supply of oil and a small oil stove on account of the difficulty or impossibility of making a fire . . . during the continuous and heavy rains . . . for the purpose of cooking rice. This with coffee and sugar and one or two kinds of tinned meats (in addition to a tent, clothing and apparatus) will be found as much as the collector will care to pack in so rough a country, and I found the stove and oil a sore burden, very reluctantly assumed." (Perkins, 1913).

Perkins's contribution to Hawaiian biology was such that his work is still a primary reference for many of the Hawaiian insect groups. Unfortunately, by his own admission, his collection of spiders was very inadequate. He spent more than half his time collecting birds, the rest of the time looking for insects, the spiders all being collected while he was involved in pursuit of the latter.

Perkins sent his collection of Hawaiian spiders to Eugène Simon at the Muséum National d'Histoire naturelle in Paris. Despite the paltry representation of many species, Simon recognized the extraordinary nature of the

Hawaiian spider fauna. "The fauna of this archipelago could be considered to be strongly specialized and rich relative to its area . . . The diverse groups of arachnids here are very unevenly distributed. Of the 40 or so families which are generally recognized today, 31 are completely lacking [from the native fauna]." (Simon, 1900). He recognized the speciose nature of closely knit lineages in the genera *Theridion* (Theridiidae, described ten endemic species), *Tetragnatha* (Tetragnathidae, described seven endemic species), *Sandalodes* (Salticidae, described eight endemic species) and several lineages in the crab spider families Thomisidae and Philodromidae. Simon also recognized that many (if not all) of the taxa with distributions outside Hawaii were probably introduced. Recognition of this has become increasingly important as the onslaught of alien species has risen dramatically in recent years. Understanding of the biological associations and evolutionary origins of species that currently occur on the islands is critically important to the interpretation of any biogeographic study.

Until very recently, the only work that had been carried out on the native Hawaiian spiders since the time of the *Fauna Hawaiensis* (Simon, 1900, 1904; Perkins, 1913) was that of Ted Suman (1970), who worked on the crab spider families Thomisidae and Philodromidae. Here, we discuss some of the recent work that has been, and is being, conducted on Hawaiian spiders, a group that is providing fascinating insights into patterns and processes of evolution.

The biogeographic pattern that predominates in most Hawaiian taxa is a tendency for both species proliferation and population differentiation to occur in a step-like manner down the island chain from the oldest to the youngest islands. In addition, species (or populations) tend to have the narrowest ranges on the older islands (Gillespie, 1997). Species on the youngest island (Hawaii) tend to be widely distributed over the island (in some groups these species are shared with Maui). A number of different within-island patterns have been superimposed on these general patterns. Here we discuss two broad categories of patterns found in the native Hawaiian taxa: (1) Singleton species—single representatives of a lineage throughout the islands, and (2) Species radiations.

Singleton species

A number of species of spiders have been described recently from Hawaii that have widespread distributions and have not differentiated in the archipelago. This is particularly true at low elevations, where almost all of the spiders are introduced. It is also likely that all of the native Hawaiian spider fauna is endemic. Among the endemic fauna are a number of lineages represented by single species. These may be recent introductions, or relicts from largely extinct radiations.

Single representatives among relictual taxa. Certain taxa are characterized by a suite of apomorphies, which, in some cases, has even caused them to be placed in monotypic genera. For example, *Doryonychus raptor* (Tetragnathidae) has abandoned the web-building behaviour characteristic of the family, and developed long claws at the ends of the tarsi of leg pairs I and II. The claws are employed in a unique behaviour whereby insects are impaled directly from the air (Gillespie, 1991b, 1992b). *D. raptor* has all the features characteristic of the genus *Tetragnatha*, but is phylogenetically basal (Gillespie *et al.*, 1994). Accordingly, this information, coupled with its extraordinarily specialized foraging behaviour and confinement to very small pockets of forest on the oldest of the main Hawaiian Islands (Kauai), suggests that the species may be a relict of a previously diverse radiation of *Tetragnatha* (Grimaldi, 1988; Gillespie, 1991a).

Recent introductions. Lack of diversity in some groups may be due to recent introduction into Hawaii. For example, the few native lowland representatives of the genus *Tetragnatha* (*T. hawaiiensis* clade) have been found to group outside the main radiation of Hawaiian *Tetragnatha*. This may be because this group has arisen from a relatively recent colonization of the archipelago. As described above, this may be an artefact of possible extinction of lowland relatives of *T. hawaiiensis*.

Species radiations

Species radiations are a characteristic feature of the Hawaiian Islands. Among spiders, the major radiations appear to have occurred in: (1) the genus *Tetragnatha* (Simon, 1900;

Gillespie, 1991a, 1992a, 1994); (2) the genus *Argyrodes* (Simon, 1900; Rivera, in prep.); (3) representatives of the crab spider families Thomisidae and Philodromidae (Suman, 1970; Garb, in prep.); (4) the genus *Theridion* (Simon, 1900); and (5) representatives of the wolf spider family Lycosidae (Gertsch, 1973). Radiations may also exist in the genus *Sandalodes* (Salticidae) and *Cyclosa* (Araneidae), although there is little conclusive evidence for these groups. Recent work by Gustavo Hormiga (pers. comm.) suggests that there are more species in the genus "*Labulla*" (Linyphiidae) than the two originally described by Simon (1900).

Systematic status of radiations

1. *Theridion*. Radiation within the genus *Theridion* is well known, but again, little work has been done on this group, and many species remain undescribed. Nearly all recent work on this genus has been on the colour polymorphism of a single species, *T. grillator* (see below).

2. *Tetragnatha*. The radiation of Hawaiian *Tetragnatha* was "rediscovered" in 1987. At that time information on the endemic Hawaiian spiders in the family Tetragnathidae was based on old descriptions of only nine species (Karsch, 1880; Simon, 1900) in the genus *Tetragnatha*, and one in the monotypic genus *Doryonychus*, *D. raptor*. Although *D. raptor* is highly modified in gross body morphology, its eye and genitalic structure is typical of *Tetragnatha* (H. W. Levi, pers. comm.). An additional nineteen species of Hawaiian *Tetragnatha* have now been described (Gillespie, 1991a, 1992a, 1994) and another 52 taxa have been collected and are in the process of description (Gillespie, in prep.). Unlike that of their continental congeners, the tetragnathid radiation in Hawaii spans a tremendous spectrum of colours, shapes, sizes, ecological affinities, and behaviours. Many species are web-building, with striking patterns, colours and structural modifications of the abdomen that allow concealment within the specific microhabitats that they occupy (Gillespie & Croom, 1995; Gillespie *et al.*, 1997). Some species have structural modifications of the cheliceral armature which allow specialization on specific prey types. In terms of foraging strategy, several groups have abandoned the characteristic web-building behaviour

of the genus. Most notable among those species that do not build webs is *D. raptor*, which uses elongated tarsal claws to impale prey, as discussed above (Gillespie, 1991b, 1992b). One entire clade of sixteen species (the "spiny leg" clade) has abandoned web building, with the concomitant development of long spines along the legs and the adoption of an extremely vagile, cursorial predatory strategy (Gillespie, 1991a). The majority of the species in the Hawaiian radiation fall into two clades: this spiny leg clade and a large and diverse clade of web-building species (Gillespie *et al.*, 1994).

3. *Argyrodes*. Simon (1900) described only two species in the currently recognized composite genus *Argyrodes*: *A. hawaiiensis* and *A. (Ariamnes) corniger*. Exline & Levi (1962) incorporated the genus *Ariamnes* into *Argyrodes*. The former is a short-bodied kleptoparasitic species, considered to belong to the *A. argyrodes* species group as defined by Exline & Levi (1962). *A. corniger* is a long-bodied species, currently considered to belong to the *Ariamnes* species group. Recent studies have shown that the genus *Argyrodes* has many more species than were described by Simon, and represents another of Hawaii's diverse radiations of terrestrial arthropods. Both short-bodied kleptoparasitic forms and long-bodied free-living solitary forms comprise an estimated 15–20 endemic species occurring in the islands. The short-bodied species are most often found as kleptoparasites on the webs of *Labulla* species, and appear to be specialized on those webs. Both molecular (see below) and preliminary morphological data suggest that the kleptoparasitic forms are monophyletic, representing a single introduction to the archipelago (M. A. J. Rivera, work in progress). The long-bodied *Argyrodes* display a wide array of both colour and body form variation, although the genitalic structures appear to be relatively conserved. M. A. J. Rivera is currently examining the long-bodied *Argyrodes*, using both morphological and molecular information to determine monophyly.

4. Thomisidae and Philodromidae. These two families, once considered subfamilies within the Thomisidae, are well represented in Hawaii. The original work on the Hawaiian Thomisidae by Karsch (1880), Koch (1883), Keyserling (1890), and Simon (1900), resulted in fifteen newly

described species placed in the genera *Misumena*, *Diaea*, *Synema*, and *Mecaphesa*. *Misumena*, *Diaea*, and *Synema* are cosmopolitan genera, while *Mecaphesa* is endemic to Hawaii. A more recent revision of the Hawaiian thomisids by Suman (1970) moved *Misumena* and *Diaea* into the cosmopolitan genus *Misumenops*. Suman's revision resulted in recognition of several new species, giving twenty-one total described species (seventeen species in *Misumenops*). Therefore, based on this later revision, there are at least three potential clades (*Misumenops*, *Mecaphesa*, and *Synema*) among the Hawaiian thomisids. The described differences between these genera rely mainly on eye arrangement, carapace setation, carapace shape, and abdomen shape. *Mecaphesa*, which likely represents a sister group of the Hawaiian "*Misumenops*", has only three species. Of the described Hawaiian *Synema*, Lehtinen (1993) argues that the genitalia of both male and female are much closer to the genitalia of all Hawaiian "*Misumenops*" than to those of the type species of *Synema*. However, because both *Misumenops* and *Synema* genera are broadly defined, they are extremely species-rich and are in need of future revision (Lehtinen, 1993). Accordingly, placement of the Hawaiian thomisids into several genera may be erroneous. In particular, Lehtinen (1993) has suggested that they may form a monophyletic group belonging to the genus *Mecaphesa*. We are currently addressing the monophyly of the group and generic relationships using mitochondrial DNA sequences and morphology (J. E. Garb, work in progress).

Among the Hawaiian Philodromidae, nine endemic species have been described in two endemic genera, *Papioglossus* and *Proernus* (Simon, 1900; Suman, 1970). There have been no studies of Hawaiian philodromids subsequent to Suman's revision and it is almost certain that many more undescribed species exist.

5. Lycosidae: Original work on Hawaiian spiders by Simon (1900) (also Koch, 1883; Keyserling, 1890), resulted in ten newly described wolf spiders endemic to the islands, placed in the genera *Aricosa* (one species), *Lycosa* (five species), *Lycosella* (two species), and *Syroloma* (two species). *Aricosa*, *Lycosa*, and *Lycosella* are cosmopolitan genera, while *Syroloma* is endemic to Hawaii. More recently,

a study of the cavernicolous fauna of the Hawaiian Islands, largely by Frank Howarth (1981, 1993) resulted in a new species of *Lycosa*, *L. howarthi* (the small-eyed-big-eyed spider), and an endemic genus, *Adelocosa*, with one species, *A. anops* (the no-eyed-big-eyed spider), (Gertsch, 1973).

Factors involved in species proliferation

Factors implicated in speciation events associated with radiations of Hawaiian arthropods include one or more of the following: repeated founder events and isolation, sexual selection, adaptive shifts, hybridization, and (in some cases) cospeciation (Roderick & Gillespie, 1998). Each of these have probably played some role in different radiations of Hawaii's spiders. For some radiations, speculation on mechanisms would be premature. Here we will consider groups for which patterns are beginning to emerge:

Founder events and vicariant isolation

Many arthropod lineages in the archipelago have progressed down the island chain, forming distinct species on each volcano or island on the way. Among spiders in the genus *Argyrodes*, there are two endemic lineages that appear to be independent colonizations: the short-bodied forms that are kleptoparasitic on the webs of *Labulla*, and the long-bodied, free-living species. The short-bodied species, because of their kleptoparasitic behaviour, might be expected to have highly structured populations. We have hypothesized that such structure may be reflected in the level of molecular resolution, while at the same time the kleptoparasitic lifestyle may have constrained the morphology of these species of *Argyrodes*. Results to date support these findings (M. A. J. Rivera, work in progress): DNA sequence data from a 473 bp region of the mitochondrial protein coding gene Cytochrome Oxidase I has been obtained for all the putative species in this group. Genetic distances range from 0.2–2.1% within island species and a remarkable 5.2–9.1% between island species. Despite these large genetic distances, the gross morphology of taxa in this lineage is very similar. The phylogeny suggests a general pattern of colonization by progression

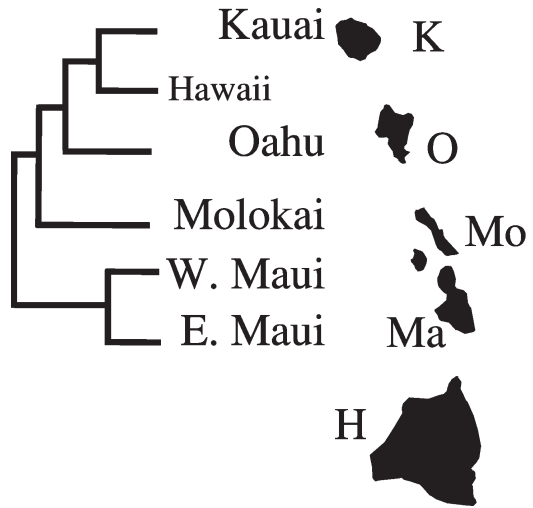


Fig. 1: Preliminary phylogeny of a kleptoparasitic lineage of endemic Hawaiian *Argyrodes* (Theridiidae) based on mitochondrial cytochrome oxidase DNA sequences. K = Kauai, O = Oahu, Mo = Molokai, Ma = Maui, H = Hawaii.

down the island chain, with the exception of one migration event directly from the island of Kauai to the island of Hawaii (Fig. 1).

In contrast to the short-bodied *Argyrodes*, the closely related “*Ariamnes*” group has many more species and representatives exhibit marked ecological and morphological diversity. However, preliminary sequence data indicates that genetic distances are much shorter than in the short-bodied species group (distances between putative species range from approximately 1%–6%). The Oahu group forms a distinct clade that appears to be ancestral to Maui and Hawaii species; however, due to the short distances between representatives, there is little phylogenetic resolution for the rest of the group at this point. More sequence data and more species are necessary to determine the true phylogenetic pattern for the long-bodied *Argyrodes*.

Adaptive shifts

Howarth (1981, 1993) was the first to document the importance of adaptive shifts in species formation in the Hawaiian biota. He showed that many of the cave endemics in the different Hawaiian Islands had their closest relatives on

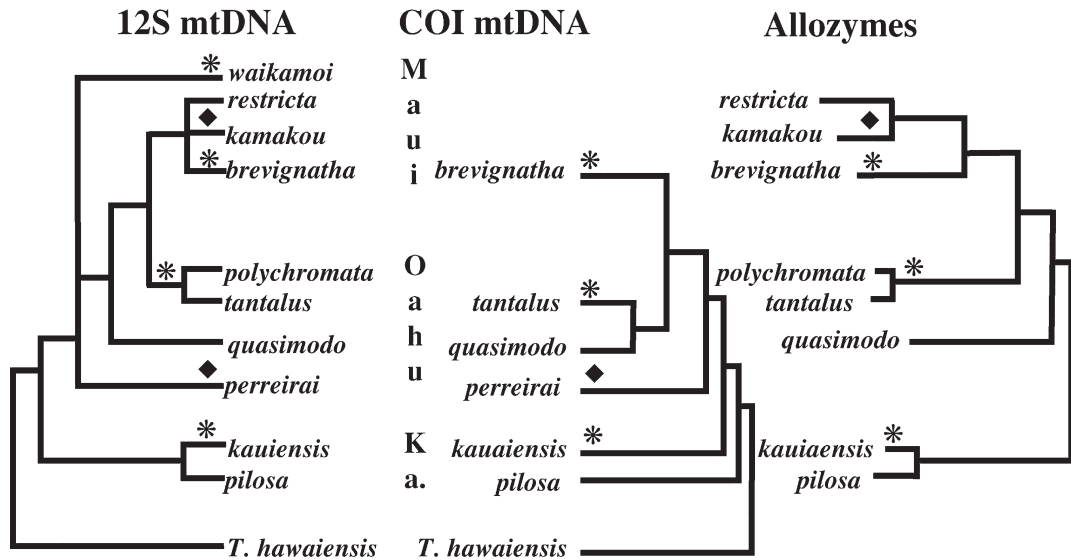


Fig. 2: Phylogeny of the "spiny leg" clade of Hawaiian *Tetragnatha* based on molecular data from ribosomal 12S and cytochrome oxidase mitochondrial DNA, and allozymes. Under the assumption that the ancestral species was "brown": * = evolution of green coloration and associated characteristics, ◆ = evolution of maroon coloration and associated characteristics. Island associations are indicated (Ka. = Kauai). Some species are found on more than one island: in particular, *T. quasimodo* occurs on all of the high islands except Kauai; *T. restricta* and *T. brevignatha* occur on Hawaii as well as Maui. From Roderick & Gillespie (1998).

the surface. Prior to this work, it had been thought that cave species evolved through a process of relictualization, with species being isolated in caves subsequent to major climatic changes (Barr & Holsinger, 1985). However, cave species on Hawaii's youngest island cannot be more than 1 million years old and have never experienced conditions such as glaciation that might cause relictualization. Accordingly, Howarth (1981) argued, these species must have evolved from the epigeal fauna as a result of adaptive shifts. One striking example that appears to illustrate this phenomenon is in the Lycosidae. Although there has been little systematic work on this group, it does appear that the closest relatives to the cave species *Adelocosa anops* on Kauai, and *Lycosa howarthi* on Hawaii, are surface species, like *L. kalukanai* or *L. likelikeae* on Kauai, *L. hawaiiensis* on Hawaii. More research is required to prove this hypothesis, and to determine relationships among other Hawaiian lycosids.

Recently, Gillespie and colleagues (Gillespie *et al.*, 1997, in progress) have examined the role of adaptive shifts in the radiation of spiders in the genus *Tetragnatha* in order to determine the extent to which species splitting is associated with shifts in ecological affinity. A preliminary phylogenetic analysis based on morphological characters (Gillespie, 1993) indicated that the "spiny leg" clade of Hawaiian *Tetragnatha* grouped according to ecological affinity, with many characters supporting distinct "green", "brown" and "maroon" ecomorphs. A phylogeny was then generated based on molecular data from mitochondrial ribosomal 12S and cytochrome oxidase DNA, and multiple nuclear loci (allozymes). Ecological associations were considered in the context of the phylogeny (Gillespie *et al.*, 1997). The results of the molecular analysis suggest that species on any one island are generally most closely related to each other, and each of the different ecomorphs appear to have evolved independently on the different Hawaiian islands (Fig. 2). This result prompts the intriguing possibility that there has

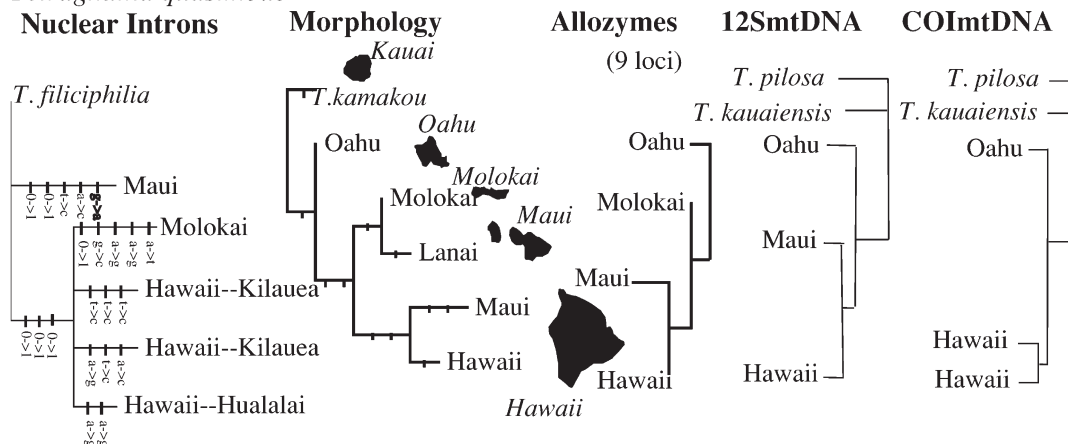
Tetragnatha quasimodo

Fig. 3: Relationships among populations of *Tetragnatha quasimodo* based on morphological and different molecular characters. Islands in plain type indicate the source of populations of *T. quasimodo*.

been convergence of the same set of “ecomorph” types on each island in a manner similar to that in lizards of the Caribbean (Losos, 1992; Losos *et al.*, 1994).

Single widespread species within radiations

Most species that belong to large Hawaiian radiations occupy rather small ranges, with many species being endemic to single mountains. However, many radiations also contain one or a few species that are widespread. Among Hawaiian *Tetragnatha* spiders, *T. quasimodo* is widespread, while the remaining species in this “spiny leg” clade are confined to much smaller areas. We have conducted a preliminary examination of population structure in *T. quasimodo* based primarily on electrophoretic, and mitochondrial and nuclear intron DNA sequence information of populations (Fig. 3). *T. quasimodo* is found on all islands except Kauai (Gillespie, 1991a). Using populations from Oahu, East Maui and Hawaii (two populations) we estimated average heterozygosity based on allozyme frequencies (Gillespie & Roderick, unpubl.). To measure genetic differentiation and gene flow among populations we used Wright’s (1951) F_{ST} , and hence $N_e m$. We also used an intron within nuclear DNA intron polypeptide chain elongation factor-1a F2 (Roderick *et al.*,

submitted) to examine population subdivision in this widespread species. The results all suggested sequential colonization of volcanoes from the oldest to the youngest, and also showed that populations were highly structured between islands, with little gene flow.

Another species of spider that is widespread through the islands, but appears to be part of a large radiation of taxa with smaller ranges, is the Hawaiian happy face spider *Theridion grallator*. *T. grallator*, which is best known for its extraordinary colour polymorphism, is a small spider found on the undersides of leaves in mesic and wet forest in the Hawaiian Islands. Three characteristics of the *T. grallator* system suggest that colonizations of different islands have been rare events and may have been associated with genetic bottlenecks: (1) island-wide genetic differences: a fundamental difference exists in the genetics underlying the colour polymorphism in different populations (Oxford & Gillespie, 1996a,b,c); (2) pattern details of each morph differ between islands (Gillespie & Oxford, unpubl.); and (3) allozyme electrophoresis with 8 polymorphic loci and mitochondrial DNA sequences have suggested that there is very little gene flow between populations on different islands (Gillespie & Oxford submitted; Gillespie & Claridge, unpubl.). As for *T. quasimodo*,

described above, populations of *T. grallator* on different islands are effectively isolated.

Conservation

The loss of arthropods in Hawaii is higher than that in the rest of the United States combined (Dunlop, 1989). The number of species proposed as candidates for listing as endangered (207) is twice that of the highest number suggested for continental USA (Hafernik, 1992); and, if studies of birds and plants are any indication, Hawaii has the greatest number of endangered species in the USA (Dobson *et al.*, 1997). These figures indicate the critical need for protecting Hawaii's native arthropods, yet no Hawaiian arthropod has yet been listed as endangered or threatened under the US Endangered Species Act. The reason for the anomaly is the fragmentary knowledge of Hawaiian arthropods. This is particularly true of spiders. The vulnerability of Hawaii's native species to perturbation and invasion from alien species is largely a consequence of their isolation from competition and predation from continental faunas during their evolutionary history. In addition, the heavily dissected terrain and enormous spatial variability in climate, which may have accelerated speciation considerably, have also resulted in species with very localized distributions (Simon *et al.*, 1984). Many Hawaiian honeycreepers and land snails are going towards extinction or have become extinct, particularly at lower elevations (below 600 m). We have virtually no information on the conservation status of the enormous array of endemic arthropods, which are being increasingly threatened by Hawaii's "Noah's Ark of undesirable biota" (Gagné, 1988). Included among the alien biota are 3055 arthropods, 46 land birds, 19 mammals and 946 plant species (Stone, 1985; Moulton & Pimm, 1986; Wagner *et al.*, 1990; Eldredge & Miller, 1995; Miller & Eldredge, 1996). Some of these alien species feed on the native plants, or interfere with their reproduction; others prey on, parasitize, or compete with native animals (Howarth, 1985; Smith, 1985; Stone, 1985). Of all the alien invertebrate predators, ants are the most notorious in their effect on the native Hawaiian biota (Howarth, 1985; Howarth & Medeiros, 1989; Gillespie & Reimer, 1993). Of the 35 or more

species of ants currently established in Hawaii, the major threats to native fauna are generally considered to be the big-headed ant *Pheidole megacephala*, the long-legged ant, *Anoplolepis longipes*, the Argentine ant, *Iridomyrex humilis*, and the fire ants, *Solenopsis* spp. (Reimer *et al.*, 1990). The possible importance of ants in the extirpation of native arthropods was recognized even early in this century (Perkins, 1913). Since then, additional extinctions of native invertebrates have been attributed to ants, particularly at lower elevations, on all the main Hawaiian islands (Zimmerman, 1948; Gagné, 1979; Hardy, 1981). However, all evidence to date is circumstantial: the only controlled studies on the interaction of the ants with native species have been preliminary assessments (Medeiros *et al.*, 1986).

Conclusions

This paper highlights the value of the spider in the Hawaiian archipelago for elucidating phylogeographic patterns. Recent studies, as described here, are beginning to reveal diverse patterns of species proliferation. A number of trends are beginning to emerge. For example, most of the spiders that have colonized the Hawaiian Islands have been from highly dispersive taxa. Indeed, most groups that have colonized Hawaii once appear to have done so repeatedly (e.g. *Tetragnatha* and *Argyrodes*). Lineages tend to progress down the island chain, with the most ancestral groups (population or species) on the oldest islands. However, patterns of differentiation vary between taxa. Certain groups are represented by single taxa that may be relicts of historical radiations. Among the radiations, some groups have single (or a few) species on each volcano and appear to have differentiated on the basis of founder events and subsequent isolation. Proliferation in some of the larger radiations generally appears to have involved adaptive shifts within islands, superimposed on the pattern of sequential island colonization. What determines whether or not species differentiate within a given land mass? At this point we can only speculate, by comparing species that have speciated only between volcanic land masses with those that have speciated within a given volcanic land mass. Here are some possibilities:

The radiations of *Tetragnatha*, and perhaps also the long-bodied clade of *Argyrodes* and thomisids, show a pattern of differentiation that involves adaptive shifts within islands. When species colonize new land masses (as evidenced currently on the youngest island, Hawaii), they undergo great expansion in geographical and ecological range. It may be that exposure to the greatly expanded ecological conditions allows differential selection, and subsequent speciation within a land mass.

Two radiations show a pattern whereby differentiation occurs almost exclusively between land masses: *Labulla* and the short-bodied clade of *Argyrodes*. *Labulla* is very conservative in its habitat requirements throughout the islands: it builds its large web against trunks or other structures that can serve both as a refuge from the web surface and a support for the web. It may be that these habitat requirements are too stringent for this lineage to expand its ecological range upon colonization of a new land mass, thereby preventing proliferation. Similarly, the short-bodied *Argyrodes*, because of their kleptoparasitic lifestyle, are virtually confined to the *Labulla* webs, and may be constrained in a similar manner.

In terms of conservation, research has identified management priorities for native spiders in Hawaii: (1) prevention (or at least minimization) of invasion of alien arthropods; however, introduction of alien arthropods is almost impossible to control; (2) reforestation of mid-elevation pasture land; (3) possible management of certain alien forest types (such as guava) to maintain structural diversity; and (4) investigation of the role of corridors in maintaining diversity.

While Hawaii is well known for its sun and surf, the extraordinary spider fauna remains largely unknown. In the future, the islands will continue to have sun and surf; however, the destiny of the indigenous spiders is considerably less assured.

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