

**SPIDERS OF THE CARIBBEAN: PATTERNS AND PROCESSES OF
DIVERSIFICATION IN THE SPIDER GENUS *SELENOPS* (ARANEAE;
SELENOPIDAE)**

The islands of the Caribbean have a complex history, some being formed by volcanic activity, others by movement of continental fragments, with the creation and break-up of land bridges, superimposed on the geological tapestry. Not surprisingly, studies of the biota of these islands have generated some of the most interesting questions in biogeography. Questions remain, however, concerning the role of dispersal versus vicariance in shaping the patterns of species diversity and the timing of these events (e.g.- Savage 1982; Pregill and Crother 1999; Iturralde-Vinent and MacPhee 1999; Williams 1989). Perhaps the disagreement is best exemplified in one well-studied taxon of the Caribbean, the lizards of the genus *Anolis*. Etheridge (1959) suggested two separate colonizations to explain the distribution of *Anolis* lizards, while Guyer and Savage (1986) propose one colonization from which a second major group has arisen, while Williams (1989) disagreed with both parties, suggesting the data available were inadequate. Recently, Schneider et al. (2001) and Creer et al. (2001) have used modern techniques and more rigorous analyses and have elucidated some patterns present in two *Anolis* species groups of the Lesser Antilles. The difficulty in reaching any general conclusions regarding the biogeography of the region may be because most of the data available are based almost entirely on vertebrates (e.g.- Creer et al. 2001, Schneider et al. 2001, Malone et al. 2001; Woods 1989; White and MacPhee 2001). In order to acquire a clear picture of the evolution of fauna in the Caribbean, it is important to examine many specimens of many different taxa to corroborate or contradict known patterns, providing a degree confidence in particular events or elucidating new biogeographic scenarios (Liebherr 1988).

In the Caribbean, the relatively few biogeographic studies conducted on arthropods are based on morphology alone (e.g. – carabids, Liebherr 1988), or else have focused on taxa that are not dispersal limited or (e.g.- butterflies, Davies and Bermingham 2002). The use of arthropods is important, as sample sizes can generally be much larger than those found in vertebrates. Also, if disparate taxa display similar patterns, this provides evidence for common processes underlying these patterns. I have chosen to focus on the spider genus *Selenops*. These relatively large spiders were last revised by Muma (1953) on the basis of genitalic characteristics which have recently been demonstrated to be highly variable making them potentially unreliable for species determination (Crews 2003). Many species have been described from only a single male or female specimen or are undescribed (Hounscome 1994). I have selected *Selenops* as a focus group because over 40% of the described species in this tropical / subtropical genus occur in the Caribbean region, with many species being single-island endemics. These spiders are habitat-restricted, occurring only in heavily forested areas. To date, there have been no biogeographic studies of spiders in the Caribbean region, although other studies of the biogeography of spiders on islands are available as a basis for comparison (Gillespie 1999 - Hawaii; Arnedo et al. 2001 – Canary Islands; Oxford and Gillespie 2001 - Hawaii; Hormiga et al. 2003 – Hawaii).

The questions this research will address are listed below:

I.) Did lineages comprising the genus *Selenops* arise through dispersal or vicariance? When examining taxa on islands it is important to consider how the islands formed as this provides information about the processes responsible for the formation of species. Endemic taxa on fragment islands are generally comprised of paleo-endemics (species which formed through relictualization and persistent isolation) while those on *de novo* islands are typically neo-endemics (species which formed through differentiation after initial colonization and persistent isolation) (Gillespie & Roderick 2002). In many Caribbean taxa, it seems both vicariance and dispersal have played a role in diversification. This has interesting implications for comparing evolutionary processes in closely related taxa as some species of the genus *Selenops* may be neo-endemics and some paleo-endemics. Also, controversy exists concerning the origin of some Caribbean islands. These factors make it difficult to distinguish explicit patterns of origination and diversification present in many taxa.

II) Do the patterns of divergence in *Selenops* indicate the presence of ecotypes?

In many island taxa whose primary mode of speciation has been through an evolutionary radiation, the existence of ecotypes is prominent. The most famous example of this in the Caribbean occurs in *Anolis* lizards (Losos 1992, 1994). In the same geographic locality, certain species live on the ground, others on the tree trunks and yet others on the branches of trees. The utilization of these specific microhabitats by this genus allows for more species diversity per unit area. Similar patterns of ecotype diversity appear to allow several species of Hawaiian *Tetragnatha* spiders to exist in sympatry (Gillespie et al. 1997; Gillespie 2004). It is known that several *Selenops* species on islands are found in sympatry, making it likely that multiple ecotypes also exist in this genus. The presence of ecotypes opens many doors concerning diversification and formation of communities on islands.

III.) Do *Selenops* found in the Caribbean, Central America & Mexico and the Galápagos Islands demonstrate the same biogeographic patterns as that found in Darwin's finches? Upon examining Darwin's finches and their relatives, Burns et al. (2002) found a unique biogeographic pattern—that species from the Galápagos Islands are more closely related to species in the Caribbean than to those in Central America. They hypothesized that this is due to the submergence of the Isthmus of Panama during the time that the birds were undergoing diversification. To date, other animals with the same distribution have not been explicitly examined, although a study of the relationships of iguanas (Wiens and Hollingsworth 2000) does not support this biogeographic pattern, but it is likely that the major groups of iguanids in this study diversified long before Darwin's finches and their relatives.

IV.) Why are some species widespread while other *Selenops* are restricted?

The majority of the species in the Caribbean consist of single-island endemics, although some of the larger islands, such as Cuba and Hispaniola contain multiple species. However, there are two species *S. insularis* and *S. galapagoensis* which are found in several localities and are sometimes very common, particularly in disturbed habitats

(pers. obs.). These species could be widespread for several reasons. First, perhaps they are better dispersers than any of the other species. If this is the case, it will be interesting to try to elucidate the reasons for this as there are no apparent differences in the means of dispersal between these two species and any of the others. Second, perhaps they are not actually one species. It is possible that their morphology is conserved, but they could be highly molecularly divergent, as has been found in many other spider groups (Crews 2003; Hedin 1997, 2001; Bond et al. 2001). This has interesting implications for the evolution of genitalia in this group. For instance, why would the genitalia of these two species remain the same over time when the genitalia of other lineages evolved rapidly and divergently? Third, the species could be recently introduced to many islands due to humans. If so, it is important to assess whether or not they are competing with and displacing native *Selenops*.

Methods

To accomplish the above, I will need to collect as many lineages as possible and comprehensive morphological and molecular data. If lineages are left out of the analyses, diversity may be underestimated and biogeographic relationships can potentially be misleading. I will collect spiders on all islands possible including several different habitats on these islands. Because little is known about the basic biology and natural history of these spiders, I will be paying particular attention to their habits and microhabitats, particularly in areas where known species distributions overlap. I am also borrowing specimens from several museums to increase sample sizes.

Like many arthropod groups, spider species are delimited by genitalic differences as it is thought that the evolution of genitalia is rapid and divergent due to strong sexual selection (Eberhard 1985). I will quantify the morphology of genitalic structures using geometric morphometric analyses employing landmark data. This process uses multivariate statistical approaches to test for shape differences (Bookstein 1991; Adams et al. 2002). It has benefits over linear measurements such as controlling for size, rotation and reflection. This approach has been demonstrated to be able to detect very small differences otherwise unnoticed (Adams and Funk 1997; Crews 2003). Petrunkevitch (1925, 1930) determined eye size and position and relative leg lengths were of specific importance. I will examine both lines of evidence and use statistical techniques such as CVA (canonical variates analysis) or cluster analyses to determine the utility of these characters.

With the advent of molecular techniques, morphologically homogenous groups have been found to comprise many evolutionary lineages (Kambhampati et al. 1995; Wilcox et al. 1997; Bond and Sierwald 2003). These are known as cryptic species complexes or cryptic lineages. I will use mitochondrial and nuclear DNA to examine the relationships between and among proposed species, species groups and populations. I will sequence portions of the mitochondrial genome (16S, ND1, CO1, Cyt b) and nuclear genome (28S, 18S, Efl- α). The utility of these particular genes in resolving both deep and shallow

divergence has been demonstrated in several other spider studies (Hedin and Maddison 2001; Bond et al. 2001; Hedin 2001).

After I have generated DNA sequence data as mentioned above, I will use phylogenetic programs such as PAUP* (Swofford 2002) to generate phylogenies which will allow me to create area cladograms to test biogeographic hypotheses. I will be able to examine shallow and deep splitting events to elucidate whether current distributions and patterns are due to *de novo* speciation or dispersal events. Also, I can use these programs to generate pairwise distances between samples to determine levels of genetic diversity. Based on results of other studies of spiders I expect genetic diversity to be high as spiders that are dispersal limited are often surprisingly deeply divergent, even within putative species (Bond et al. 2001; Hedin 1997; Crews 2003). I will also use programs such as MDIV (Nielsen and Wakely 2001) and Mesquite (Maddison and Maddison 2003) to perform simulations on my data to learn more about historical population structure. In some cases, if radiations of taxa are very fast, there can be incomplete lineage sorting and resolution of how the organisms are related may not be clear only using phylogenies, which could also occur within populations on islands. In such cases, I will use TCS networking (Templeton et al. 1992) which uses statistical parsimony to build haplotype (unique DNA sequence) networks and will provide more resolution than tree-building. These haplotype networks can also be used to test the relationship of geographic distances to genetic distances (Posada et al. 2000).

Conclusions

Despite the many biogeographical studies in the Caribbean, questions about dispersal versus vicariance and the timing of particular events remain. "It is clear that if we are to make advances in understanding Caribbean biogeography, we must refine our techniques of analyses and obtain more data from previously unused taxa" (Liebherr 1988). Also, this region is suited to be a model for biogeographic studies due to its geological and biological complexity, so approaches that succeed here will have utility in other systems (Connor 1988), and conversely these approaches can be applied to other islands or even continental systems as patches of habitat utilized by organisms are much like islands. The study of *Selenops* in the Antilles will address questions important to conservation biologists, island biogeographers and evolutionary biologists. The answers to these questions may allow predictions of the effects of habitat loss and will provide insights into the conservation and major evolutionary processes of the arthropod fauna of islands.

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