DROSOPHILA

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The genus Drosophila provides excellent opportunities to study evolution on island systems. The endemic Hawaiian Drosophila are a classic example of adaptive radiation and rapid speciation in nature evolving in situ over the course of the past 25 million years. Other groups of Drosophila, found on true islands or in island-like systems (e.g., the Madrean Archipelago), are invaluable tools to understanding evolutionary biology and have served as theoretical and empirical model systems for over 50 years.

HAWAIIAN DROSOPHILA

The endemic Hawaiian Drosophilidae, with an estimated 1000 species, consists of two major lineages, the Hawaiian Drosophila and the genus Scaptomyza. The high degree of species diversity in Hawai‘i is extraordinary, with about one-sixth of the world’s known Drosophilidae being endemic to this small archipelago. Phylogenetic analyses indicate that the family colonized the Hawaiian Islands only once, roughly 25 million years ago. The genus Scaptomyza, which also contains a large number of mainland taxa, seems to have escaped from Hawai‘i and undergone subsequent diversification on the mainland (see below).

There are currently 411 described species of Hawaiian Drosophila, with an additional ~150 awaiting description. These species have been divided into eight species groups (picture wing, nudidrosophila, ateledrosophila, antopocerus, modified tarsus, modified mouthpart, haleakalae, rustica) based largely upon sexually dimorphic characters possessed by males and thought to be used mainly in courtship and mating. These characters range from elaborately pigmented wings to elongate setae, cilia, and bristles on the forelegs to unique structures on the mouthparts and forelegs (Fig. 1). The wide variety of secondary sexual characters possessed by males of the various species groups suggests that sexual selection may have played an important role in the diversification of this group.

Approximately 85% of Hawaiian Drosophila are single-island endemics, possibly owing to their relatively poor flight abilities and low tolerance for desiccation. These physiological constraints, coupled with the unique geological history of the Hawaiian Islands, have led to a spatially distributed pattern of diversification referred to as the progression rule, where older species are found on older islands, and younger species are found on younger islands (Fig. 1).

One explanation for the large numbers of drosophilid species in the Hawaiian Islands involves adaptation to so-called empty niches. This atmosphere of reduced competition allowed these species to experiment with novel life history strategies, and thus to diversify. Several adaptations unique to the Hawaiian Drosophilidae seem to bear out. For example, the small group of ~15 species placed in the Scaptomyza subgenus Titanochaeta have specialized to oviposit in spider egg sacs. Larvae develop and parasitize the spider eggs while they are being guarded by adult spiders. Sixty-seven percent of Hawaiian Drosophila for which data is available breed on only a single host plant family, whereas 79% are specific to a single host substrate, such as leaves, bark, or sap flux (Magnacca et al., 2008).

Hawaiian Drosophila have served as a model system to address a number of evolutionary phenomena, including how founder events and mating asymmetries can drive species formation (Fig. 2). Throughout their evolutionary history, Hawaiian Drosophila have repeatedly undergone founder events, either as they colonize new islands or when populations are subdivided (e.g., by lava flows or erosional processes). Hampton Carson utilized Hawaiian Drosophila to illustrate his founder flush theory, a type of founder effect speciation that proposes a reduction in intraspecific competition and an increase in population size following a colonizing event. Once the population size becomes large again, selection is reasserted, and the population may constitute a new species (Fig. 2).

Alan Templeton also used Hawaiian Drosophila to explain his transilience founder effect theory. Templeton
discussed how, after a bottleneck derived from a founder event, a highly outbred colonizing population would experience a shuffling between epistatic loci that were adapted to work best in certain combinations (Fig. 2). This would cause an instant shift in adaptive peaks to ones optimal for these randomly recombined loci. Although he concludes that this is likely a rare event, the ecological and genetic nature of the Hawaiian Drosophila lend them to this sort of speciation.

Kaneshiro extended founder effect theories to include the complex mating behaviors and secondary sexual characteristics exhibited by Hawaiian Drosophila. In most populations, females are very choosy in selecting males with which to mate. However, small, colonizing populations are initially subject to founder effects, in which the scarcity of males forces females to be less selective when choosing a mate: If they are too choosy, they will not find a mate. Additionally, males from this small population display highly variable mating behaviors because of reduced intraspecific competition and relaxed selection in what are normally highly selected behaviors (Fig. 2). Choosy females from the larger source population will not mate with the males of the founder population, although females of this founder population will accept males from the larger source population.

CARIBBEAN DROSOPHILA
Patterns of in situ species formation are not as clear in the Caribbean islands because many widely distributed species are also found in mainland North and South America. Historically, this has led to a situation in which gene flow from closely related mainland populations can act to homogenize any unique genetic differences that may accumulate in island populations. In spite of the close proximity of mainland ancestors, some Caribbean Drosophila have become genetically distinct from these widespread ancestral species. The repleta and cardini groups highlight two factors, ecological specialization and morphological adaptation, that may act to drive the formation of new species in the presence of gene flow from the mainland.
Ecological adaptation may be an important component of species formation. The *Drosophila repleta* group contains about 100 described species, the majority of which are endemic to the New World and have diversified on various species of necrotic cacti. One group, the *mayaguana* triad, is restricted to the Caribbean and includes the widespread species *D. mayaguana*, and the more narrowly restricted taxa *D. straubae* and *D. parisiena*. Although few morphological differences distinguish these species, they do have unique polytene chromosome inversions and ecological associations (different host cacti) that may have acted as a reproductive barrier to generate distinct species.

Caribbean island *Drosophila* have also been used as models to understand morphological variation and phenotypic plasticity. The *Drosophila cardini* group consists of 16 neotropical species in two subgroups, *cardini* and *dunni*. The *dunni* subgroup is entirely Caribbean in distribution; each species is endemic to a specific island in the Greater and Lesser Antilles. These species display a cline of abdominal pigmentation, with more lightly pigmented species being found in the northwest, and darker species in the southeast (Fig. 3). This pattern may be due to island endemics being more geographically isolated and having smaller population sizes, which can cause traits (e.g., color patterns) to become rapidly fixed in the population. However, studies on the genetic basis of this color variation suggest that genetic control of abdominal pigmentation is highly malleable, with similarities in coloration not necessarily reflecting relatedness.

**SCAPTOMYZA AND ISLAND COLONIZATION**

The cosmopolitan genus *Scaptomyza* (Diptera: Drosophilidae), with nearly 300 described species placed in 20 subgenera constitutes a major radiation within the family Drosophilidae. About 140 described species are endemic to Hawai‘i, and an additional ~250 from this archipelago await description. Phylogenetic analyses strongly support the monophyly of *Scaptomyza* and its placement as the sister group to the endemic Hawaiian *Drosophila*. Unlike the Hawaiian *Drosophila*, however, *Scaptomyza* males generally lack secondary sexual characteristics and do not perform elaborate courtship displays. Instead, they have complex genitalia that can be quite different, even between closely related taxa, and may act to reinforce a “lock and key” form of species recognition.

Biogeographic analyses suggest that the genus *Scaptomyza* originated in the Hawaiian Archipelago and has subsequently “escaped” from the islands and diversified on the continent. This is a particularly interesting biogeographic pattern, because no other known group of organisms has colonized a continent from Hawai‘i. The genus *Scaptomyza*, perhaps because of its history of radiation on and migration from Hawai‘i, is extremely successful as a colonist of remote island archipelagos. Of the 20 currently recognized subgenera, over half possess successful island radiations: Seven (*Alloscaptomyza, Elmomyza, Engiscaptomyza, Exalloscaptomyza, Grimshawomyia, Tantalia, Titanochaeta*) are endemic to Hawai‘i, two (*Bunostoma, Rosenwaldia*) are known from the Pacific including Hawai‘i, one (*Boninoscaptomyza*) is endemic to the Ogasawara Islands south of Japan, and three (*Lauxanomyza, Macroscaptomyza, Trogloscaptomyza*) are endemic to the South Atlantic islands of St. Helena and Tristan da Cunha. The South Atlantic islands Tristan da Cunha and St. Helena also host representatives of two widespread subgenera, *Scaptomyza* (2 spp.) and *Parascaptomyza* (6 spp.), for a total of eight endemic species. Other species in the subgenus *Parascaptomyza* are island endemics from such disjunct islands as the Azores, Canaries, Marquesas, Cape Verde, and Java.

Many insect species lose the ability to fly when they become fully adapted to island life. One species of brachypterous *Scaptomyza, S. altissima*, is known from Tristan da Cunha and Gough Islands in the South Atlantic. Outside of this example, the loss of flight in this family is rare, although the endemic Hawaiian *Drosophila* are significantly less mobile than their mainland counterparts.
ISLAND-LIKE SYSTEMS
The Madrean Archipelago is a system of mountain islands distributed across the southwestern United States and northern Mexico. During the middle Pliocene, this area was characterized by a mild, warm, semiarid climate. Rapid desertification as a result of the uplift of the Sierra Nevada and the coincident elevation in temperature over the past ∼2.5 million years have led to the break-up of these plant and animal communities and their restriction to higher elevations. Present-day mountaintops in this region are characterized by cooler, more mesic habitats than are the surrounding arid deserts. Several groups of mycophagous species in the macroptera, rubrifrons, quinaria, and testacea species groups have formed in association with these island systems because of their dependence on the fungi that are geographically restricted to these areas.

In Drosophila innubila, paleoclimatic data suggest that populations may have been panmictic until 18,000 years ago, when they became fractured into their present-day distributions. Significant genetic differentiation between populations suggests that gene flow is restricted among these sky islands, and the high geographic variation in mitochondrial DNA may be due to an association with the male-killing Wolbachia endosymbiont, which tends to accentuate the effects of genetic drift.

PARALLEL EVOLUTION IN ISLAND DROSOPHILA
Island endemic species often evolve unique morphological structures, behaviors, or ecological associations. Some adaptations may generate large radiations, such as the Hawaiian Drosophila, whereas others, like the spider predators in Scaptomyza (Titanochalea), are represented by only a few species. An association between drosophilids and land crabs, one of the most interesting ecological adaptations in this family, has occurred independently on three different island systems. Although the majority of species in the repleta group are cactophilic, the West Indies endemic D. carcinophila has been reared from the crab species Gecarcinus ruricola. Likewise, although the entire quinaria group is mycophagous, one representative, D. endobranchia, has also been recorded from G. ruricola in the Cayman Islands and Cuba. Similarly, within the predominantly mycophagous Lisocephala, L. powelli from Christmas Island has been recorded from several crab genera, including Gecarcoidea, Birgus, Geograpsus, and Cardisoma. All three crab fly species have independently evolved the ability to utilize the external nephric groove or branchial chamber of these land crabs. These structures are involved in the excretion of nitrogenous and food wastes, respectively. The nephric groove and its associated green gland host a unique assemblage of microorganisms that are sufficient to support the complete development of D. carcinophila and at least one instar of D. endobranchia and L. powelli. Adaptation to this lifestyle from either a cactus or fungal ancestor most likely involves a suite of changes in oviposition preference, olfactory and gustatory receptors, and larval behavior. Recent genome sequencing has facilitated the understanding the genetics of host-plant association in the genus Drosophila, and similar studies will shed light on this fascinating ecological adaptation.

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DWARFISM

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Insular dwarfism is a tendency of many island animals to evolve a smaller size than their ancestors on the near mainland. Dwarfism may be relatively minor but can