

Behavioral Characteristics of Hawaiian *Drosophila*¹

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ABSTRACT

Hawaiian endemic *Drosophila* exhibit a suite of unique behaviors which differentiate them sharply from continental species. These behaviors appear to have evolved as responses to predation pressures. The native avian honeycreepers and the Elepaio appear to have been the prime predators but hunting spiders, Araneida, and predatory flies, *Lispocephala* spp., are active predators on the drosophilids and probably also have influenced the evolution of the flies.

The species-rich endemic Hawaiian *Drosophila* fauna constitutes a monophyletic lineage of the *Hirtodrosophila* radiation (Throckmorton, 1975). With rare exceptions, all of the species are denizens of the native forests. If exposed to temperatures that exceed 20°C, the adults are rendered sterile. As a result the flies are absent from the warm lowland areas of the islands. The majority of the species live in the wet rain forests, located at elevations of 1500–5000 ft on the windward portions of the volcanoes that form the islands. A minority dwell in the cool portions of the “dry forests” found on the leeward flanks of the volcanoes. None inhabits the high arid regions above 7000 ft which do not receive tradewind-created precipitation.

Of the numerous islands that constitute the 1600 mile long Hawaiian archipelago (Stearns, 1966) only six — Kauai, Oahu, Molokai, Lanai, Maui and Hawaii — are currently known to be inhabited by endemic species. With rare exceptions (e.g., *Drosophila adiaestola*, *D. crucigera*, *D. grimshawi*) each of the species is restricted to a single island.

Taxonomically the fauna is divided into ten species groups: anomalipes, antopocerus, bristle tarsi, ciliated tarsi, fungus feeders, modified mouthparts, picture-winged, primaeva, split tarsi and spoon tarsi. The groups range in size from the 2 species of the anomalipes and primaeva groups to the more than 100 species of picture-winged flies.

Species of all the groups exhibit and share a congeries of behavioral traits that differentiate them from *Drosophila* living in other parts of the world. The following considerations are directed to the elucidation of these unique traits and the probable selection pressures that were responsible for their evolution.

METHODS

The data upon which this paper is based were acquired by field observations made during the years 1964 through 1978 at 21 collecting sites on the six Hawaiian Islands. Two of the sites were visited only a single time, each for two days. Three sites — Kokee, Kauai; Waikamoi, Maui; Volcano, Hawaii — were repeatedly visited; at each of these one of the observational periods was of three to four weeks duration.

Unlike continental species, the Hawaiian *Drosophila* exhibit little diurnality in their behavior. They are active throughout the day and thus can be observed and collected from dawn to dusk. If an observer moves deliberately or remains motionless, the flies will ignore intrusion and their activities can be observed. Field glasses and a Questar telescope were also used, especially to observe flies that were on fungi and slime fluxes

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located on the higher branches and trunks of trees. My records indicate that from 1964 to 1978 I devoted more than 3000 hours observing and collecting Hawaiian drosophilids.

Feeding — Ovipositional Behaviors

Fermenting portions of a number of native trees and shrubs plus fungi serve as ovipositional sites. Most species have monophagic larvae, a small number are oligophagic and a few, such as *D. crucigera*, are polyphagic (Heed, 1968; Montgomery, 1975). The adults depend primarily upon their larval substrates for their food. The leaf breeders (species of the antopocerus, bristle tarsi, split tarsi and bristle tarsi species groups) oviposit into fallen fermenting leaves of broad leaved evergreen trees lying on the forest floors and also use these leaves for food; the fungus feeders feed on fungi into which they oviposit; the picture-winged species primarily use fermenting bark, slime fluxes and sap exudates for both food and larval substrates. Fermenting substances such as the various baits which are effective for collecting mainland species are essentially useless for collecting the Hawaiian species. Most picture-wings and the fungus feeder species are attracted to rotting commercial mushrooms. Commercial "baby banana" food which, when inoculated with yeasts isolated from the rotting bark of the native lobeliad *Clermontia*, is moderately attractive to a number of species. "Baby banana" inoculated with ordinary baker's yeast (Fleischmann's) also works well. As yet, however, no effective baits have been found for the leaf breeders and most of the modified mouthpart species.

The number and volume of suitable feeding-ovipositional sites are usually small in any area of the forest. They also tend to be evanescent in character. These characteristics dictate that the flies must constantly move through the forest seeking ovipositional-feeding resources. Collectors can take advantage of this behavior by breaking off branches and making brush piles of appropriate trees or shrubs such as the lobeliad *Clermontia* and the araliads *Cheirodendron*, *Tetraplasandra* and *Reynoldsia*, which are used by many species as ovipositional substrates (Heed, 1968; Montgomery, 1975). After allowing the branches to decompose on the wet forest floor for a month or more, a moderate to large population of adults of numerous species will be found congregated in the area surrounding the brush pile. A slowly dying *Clermontia* or *Cheirodendron* tree will create a similar condition which may last for 2-3 years or more.

When approaching a feeding site the individuals make short, quick flights or walk slowly for a short distance, then pause for a time before repeating their movements. They avoid prolonged flights and never engage in hovering flights which are exhibited by mainland species. When feeding they are alert to any disturbance and flee by a darting type lateral or downward flight. If undisturbed they will feed until satiated, then slowly walk off the food substrate and dart into the surrounding vegetation. While on the food source the flies move deliberately, often walking over or pushing against another individual but never engaging in antagonistic behavior.

Another unique behavioral characteristic which sharply differentiates the Hawaiian flies from mainland species is the fact that they do not engage in courtship while on the food substrates. Rather, courtship and copulation are divorced from the feeding and ovipositional sites and occur at various places in the forest (see below), usually at some distance from the feeding-ovipositional sites.

Distribution of Adults in the Forest

Except when visiting a feeding or ovipositional site, the adults are secretive and solitary during the hours of daylight. Some species such as *D. mimica* (3.7 mm body length) congregate in the leaf litter on the forest floor. Most small bodied species, 2.0–3.5 mm body length, prefer the dense understory vegetation of bracken ferns which typically reaches a height of 2–4 ft. Larger bodied species tend to scatter farther and can be found at various heights on the under surfaces of leaves, ventral surfaces of slanting or horizontal tree limbs, and trunks of trees. Often individuals will remain on the same leaf or limb for several hours.

The flies ignore light to moderate precipitation but during intense rainfall they disappear, apparently seeking refuge in as yet undetermined sites. In their movement through the forests, if two individuals come into close proximity antagonistic behavior occurs and one or both of the individuals flee by flying laterally or diving downward.

With the onset of darkness, the adults ascend into the canopy of the forests; during daylight *D. engyochracea* adults, except the mature males that lek on smooth tree trunks, typically immerse themselves in moss growing on tree trunks, but with the onset of darkness they leave the mossy areas, ascend into the canopy to spend the hours of darkness on the undersides of leaves 10–20 ft above the forest floor, each individual on a single leaf. Likewise *D. mimica* leaves the forest floor litter and ascends high into the canopy.

Lek Behavior

When they leave the food sites, females and immature males scatter into the surrounding dense vegetation. In contrast, mature males of most species upon leaving the feeding site select, occupy and defend individual courtship territories. Small bodied males prefer territories in relatively dense vegetation, typically in relatively close proximity to the food sites. Medium to large bodied males prefer sites in more open areas and above the dense understory vegetation. Branches of tree ferns, trunks of shrubs and trees, the undersurfaces of slanting or horizontal branches and the undersides of broad leafed evergreens are favored. Most species select sites 2–8 ft above the substrate but *D. crucigera* males have been observed on horizontal limbs 10–20 ft above the ground and *D. mimica* males use fallen leaves lying on the forest floor. Each male (1) responds antagonistically toward any individual that attempts to enter his territory, and (2) engages in ritualized species specific movements that can best be designated as advertizing actions. Such behavior has been repeatedly observed both in the field and in the laboratory and I believe can be correctly categorized as lek behavior.

Two types of leks can be identified: solitary and assembled. An assembled lek is created by a number of males selecting a particular tree fern, shrub, or tree branch and establishing their individual territories in close proximity to each other while at the same time other nearby tree ferns, shrubs, and tree branches are totally ignored and have no occupants. In comparison, solitary leks are established by individual males without regard to the presence or absence of other males.

The males of most Hawaiian species possess a pair of intra-anal lobes which are located between the anal plates, and also a slender anal sclerite. The anal sclerite articulates with the genital arch and lies between the lobes (Throckmorton, 1966). On the lek the male raises and extends the tip of his abdomen until the entire abdomen is parallel to or directed upward from the substrate. He then pusates a droplet of clear liquid. Such males may remain immobile for hours except for the constant anal

pulsation. A number of picture-wing species also frequently curl the abdominal tip against the substrate and deposit a droplet onto the substrate. Some such as *D. crucigera* and *grimshawi* also move about, dragging the tip of the abdomen against the substrate, brushing a film of liquid onto the surface. Volatile, pheromonal type materials are present in the deposited liquid and, although they have not been chemically analyzed, human olfaction can readily differentiate species by means of these substances. Species which appear not to produce anal pheromones engage in complex species specific, ritualized advertizing movements when on their leks.

Males of three species groups lack the anal pheromonal structures: the anomalipenes, primaeva and fungus feeders. The anomalipenes species group consists of only two species, *D. anomalipenes* and *quasianomalipenes*. After feeding, the males move a few inches away from the feeding site and then turn and face it. When a female walks away from feeding, a waiting male intercepts her and attempts to court. Rarely a male will assume the courting posture at the rear of a feeding female but he never attempts to display until she has walked off the food mass (Spieth, 1975).

D. primaeva and *attigua*, the two species that constitute the primaeva subgroup, have not been observed courting in the field. In the laboratory they show no indications of lek behavior and the male courtship is an "assault type," suggesting that in their native habitat the males actively search for the females (Spieth, 1981).

The fungus feeder species group males engage in solitary lek behavior. After feeding, the male flies into the surrounding vegetation and lands on the upper surface of a leaf, then turns and faces the food mass. He then fully extends his legs, thus elevating the body. This appears to make the males visible to the females as they leave the food source. The males may remain immobile for prolonged periods but often they fly to another leaf that is already occupied by another male and a fight then ensues. One fly eventually is defeated and flees; thus any given leaf is not occupied by more than one male. The fungus feeder males appear to depend at least primarily on visual rather than pheromonal stimuli for attracting the females to their leks. The fungus feeders are close relatives to the primaeva flies (Spieth, 1981) and it is possible that the latter may also use the same type of display in the field.

A majority of the bristle tarsi, split tarsi, spoon tarsi, ciliated tarsi and antopocerus species use solitary leks. A few species are known to have assembled leks. Males of *D. imparisetae*, a ciliated tarsi species, establish leks on the undersurfaces of leaves. Typically, 10 or more males will use the leaves on the distal end of a particular branch of a tree, each occupying the undersurface of a leaf. Occasionally a male will attempt and often succeed in displacing another individual on a nearby leaf. The males remain on the leaves throughout both day and night and apparently leave only for short periods to feed.

D. percnosoma, a spoon tarsi species, uses the individual pinnae of a single fern frond as a lek site. A number of males will select a single fern frond, where each male occupies and defends the distal tip portion of a single pinnae.

D. petalopeza, a bristle tarsi species, parallels *D. imparisetae* in its lek behavior but does not remain on the lek during darkness.

Most modified mouthpart species establish solitary leks, but one species, *D. comatifemora*, has males that gather in groups of 3-5 individuals which establish their leks close together on tree fern stems or small tree trunks. The male spreads his wings outward and upward 45°, curls his abdomen upward circa 45° and pulsates an anal droplet.

The picture-wing species group has been intensively investigated (Carson and Kaneshiro, 1976; Spieth, 1982). The group is subdivided into 11 subgroups. The

males of the primitive *adiastola* subgroups have solitary leks and the males advertize by pulsating an anal droplet. The *planitibia* subgroup, also primitive, exhibits great diversity (Spieth, 1982). *D. picticornis*, the most primitive member of the subgroup with a body size of 3.20–3.65 mm, uses solitary leks and pulsates an anal droplet. The other 16 species of the subgroup are the largest known drosophilids, most having body lengths that exceed 6 mm. The males prefer leks that are 4–10 ft above the substrate, typically on branches of large tree ferns, shrubs or trees. Males have not been observed to pulsate anal droplets; rather, they walk about on the lek and engage in wing movements. They display high levels of ritualized antagonistic behavior which they direct not only towards other drosophilids but also toward other insects that inadvertently enter their leks (Spieth, 1968). Of the 16 species 9 use solitary leks, two (*D. neopicta* and *substenopiera*) have abandoned lek behavior and search for females, while the remaining five species have assembled leks. Conant (1978) intensively studied the behavior of two of these species: *D. silvestris* and *heteroneura*. Both use assembled leks and he found that the males appeared on their leks in the early morning when the temperature had risen to 10°C and remained until about a half four before sunset or until the temperature dropped below 10°C.

A majority of the males of the remaining 9 picture-winged subgroups have been observed, and excepting *D. grimshawi* they engage in solitary lek behavior and deposit anal liquid on the substrate (Spieth, 1982). *D. grimshawi* males display a unique communal behavior termed "jousting." Prolonged bouts do not result in injury to the individuals involved (Ringo, 1974).

With the approach of darkness males of all species, except *D. imparisetae*, abandon their leks and move into the forest canopy. When on their leks they will, as noted above, tolerate light to moderate precipitation. Intense rainfall, however, causes them to seek shelter in secluded sites.

Pupation

Mature larvae of mainland species pupate in, on or in close proximity to the larval food mass in which they have developed. In comparison, the mature Hawaiian larvae leave the food mass and drop onto the forest floor, then burrow downwards and pupate in the soil. Many food masses such as fungi and slime fluxes are often several to many feet above the substrate.

D. fungiperda, a fungus feeder that uses *Polyporus* sp. mature fungal bodies, has skipping larvae; when mature the larva crawls onto the surface of the fungus, curls its body and grasps the posterior tip with its mouthparts, then vigorously straightens its body which results in breaking the "mouth grasp." This action flings the larva outward and onto the forest floor. It then burrows into the soil and wanders about for 24–78 hrs. before pupating.

When adults emerge from their pupal cases they wriggle to the surface keeping their legs and wings closely appressed to their bodies.

DISCUSSION

The Hawaiian *Drosophila* exhibit several major behavioral characteristics that distinguish them from the majority of *Drosophila* species. These are: (1) The high level of antagonistic behavior that they direct toward other individuals. This aggressiveness attains its apex with males when on their leks but also pertains, albeit at a lower level for all individuals, except when they are on the feeding-ovipositional sites. (2) The total absence of antagonistic behavior when on the feeding ovipositing sites. (3) The

lack of any courtship activity on the food-ovipositional sites. (4) The lek type courtship behavior. (5) The burrowing of the mature larvae into the substrate and pupation in the soil.

Throckmorton (1966, 1975) and Okada (1967) suggest that the migrant ancestral species that colonized Hawaii came from East Asia. Utilizing immunological comparisons of a hemolymph protein, Beverley and Wilson (1984, in press) concluded that the colonization occurred circa 40 million years ago. Their data also indicate that the picture-winged and modified mouthpart species groups, which are closely related and represent the two most derived species groups of the Hawaiian flies, arose from a common ancestor about 22 million years ago. Courtship behavioral data for the picture-winged species are in agreement with their estimates (Spieth, 1982). The character and species composition of the stochastically derived flora and fauna that dwelled on the then existing Hawaiian islands when the Asian migrant arrived can never be fully determined. Clearly the fauna and flora consisted of fewer and different species from those of the Asian mainland from which the ancestral drosophilid had originated.

It is known that when the Polynesians reached Hawaii, circa 500 A.D., a large and diverse avian fauna existed, consisting primarily of honeycreepers, plus an owl, a crow, several species of geese, two ibises and a flycatcher (Diamond, 1982; Olson, and James, 1982). Mammals were represented by a single species, the Hawaiian bat. Reptiles and amphibians were absent as well as many common invertebrates, such as ants and mosquitoes.

When Captain Cook arrived in 1778 the honeycreeper fauna consisted of 37 species or subspecies (Ralph, 1982). Vast flocks existed in all the forests in which the native *Drosophila* dwelled. In addition to feeding on nectar, most if not all of the species avidly feed on insects. Warner (1967) found that the liwi, *Vestiaria coccinea*, a medium sized honeycreeper, when given an opportunity to feed upon live Hawaiian drosophilids immediately pursued and captured the insects, then used its beak to compress each insect into a small mass and swallowed it. With large bodied *Drosophila* the bird had difficulty compressing the insects and often released them. Berger (personal communication) presented a laboratory reared native honeycreeper with live *Drosophila* and the bird immediately pursued, captured and ate the insects. Some species of honeycreepers such as the akiapolaau, *Hemignathus lucidus wilsoni*, have evolved woodpecker habits. These birds diligently search through the forest for slime fluxes and rotting sections of bark. Upon finding such sites they vigorously use their sturdy beaks to uncover and avidly feed upon any insect larvae or pupae that they find.

In addition to the honeycreepers, a native species of flycatcher, the Elepaio, *Chasiempis sandwichensis*, is also found on Hawaii. It is an avid insect feeder and captures its food from leaves and branches of trees, shrubs and ferns.

In searching for productive collecting sites I found that areas of the forests where the honeycreepers were absent or few in number contained few or no native *Drosophila*, whereas the presence of numerous birds invariably indicated the presence of moderate to large populations of drosophilids. Furthermore, when collecting for several successive days in such an area honeycreepers invariably found some of the *Drosophila* baits that had been smeared on tree trunks and left numerous beak marks indicating that they were capturing the flies. Such baits quickly became nonproductive.

The native *Drosophila* and the honeycreepers (Munro, 1964) are monophyletic, each having descended from a single migrant ancestor. The descendants of these two founders have lived and evolved in the same areas of the native forest for millions of years and during this long period of time the birds have steadily preyed on the *Droso-*

phila. At a later date (Munro, 1964) the Elepaio arrived and joined the honeycreepers as *Drosophila* predators.

In addition to the native birds, two other groups of organisms are known to be consistent predators on the Hawaiian drosophilids: spiders (Araneida) and flies (*Lispocephala*, family Muscidae).

The *Lispocephala* are small to medium sized (3.0–9.0 mm) and numerous species dwell in the habitats in which *Drosophila* are found. The adults have been observed capturing and feeding on small bodies, 2–3 mm drosophilids, but never on the larger bodied species. Their larvae are also carnivorous and feed avidly on drosophilid larvae. Field collected samples of drosophilid larval substrates are often infested with the larvae.

A species rich araneid fauna also exists in Hawaii. Spiders have been observed feeding on native *Drosophila* and, although no definitive proof exists at present, it is reasonable to assume that the movement of the drosophilid adults into the forest canopy during darkness is an adaptive response to the predatory behavior of night feeding hunting spiders. It is known that the six species of the endemic Hawaiian drosophilid genus *Exalloscaptopomyza* do not ascend into the canopy. These species breed exclusively in the flowers of native morning glories. With the approach of darkness, the adults secrete themselves inside the corolla of the morning glory flowers whose petals "close" at the onset of darkness. They are thus protected against predators such as spiders. If a number of these flies are collected and placed in a glass vial, during darkness all of the individuals huddle into a compact group, on the wall of glass containers, a trait not displayed by any of the *Drosophila* species.

REFERENCES CITED

- Beverley, S.M. and A.C. Wilson. 1984. Ancient origin for Hawaiian Drosophilinae Inferred from Protein Comparisons. In press.
- Carson, H.L. and K.Y. Kaneshiro. 1976. *Drosophila* of Hawaii: Systematics and Ecological Genetics. Ann. Rev. Ecol. Syst. 7:311–345.
- Conant, P. 1978. Lek behavior and ecology of two sympatric homosequential Hawaiian *Drosophila*: *Drosophila heteroneura* and *Drosophila silvestris*. M.S. Thesis in Entomology, Univ. Hawaii, Honolulu, 191 pp.
- Diamond, J.M. 1982. Man the exterminator. Nature 298:787–789.
- Heed, W.B. 1968. Ecology of the Hawaiian Drosophilidae. Univ. Texas Publ. 6818:387–420.
- Montgomery, S.L. 1975. Comparative breeding site ecology and the adaptive radiation of picture-winged *Drosophila*. Proc. Haw. Ent. Soc. 22:65–102.
- Munro, G.C. 1964. Birds of Hawaii. Charles E. Tuttle Co., Inc., Rutland, Vermont and Tokyo, Japan.
- Okada, T. 1967. A revision of the subgenus *Hirtodrosophila* of the old world, with descriptions of some new species and subspecies (Diptera, Drosophilidae, Drosophila). Mushi 41:1–36.
- Olson, S.L. and H.F. James. 1982. Fossil birds from the Hawaiian Islands: Evidence for wholesale extinction by man before western contact. Science 217:833–835.
- Ralph, C.J. 1982. Birds of the forest. Nat. Hist., N.Y. 91:40–44.
- Ringo, J.M. 1974. Behavioral characters distinguishing two species of Hawaiian *Drosophila*, *Drosophila grimshawi* and *Drosophila pullipes* (Diptera-Drosophilidae). Ann. Ent. Soc. Am. 67:823.
- Spieth, H.T. 1968. Evolutionary implications of sexual behavior in *Drosophila*. In: Evolutionary Biology, Vol. 2, eds. M.K. Hecht, W.E. Steers and B. Wallace. Appleton-Century, N.Y., pp. 157–510.
- . 1975. The behavior and biology of the Hawaiian *Drosophila anomalipes* species group. Ann. Ent. Soc. Am. 68:506–510.
- . 1981. Courtship and evolutionary status of the Hawaiian *Drosophila primaeva*, Hardy and Kaneshiro. Evolution 35:815–817.
- . 1982. Behavioral biology and evolution of the Hawaiian picture-winged species group of Hawaiian *Drosophila*. In: Evolutionary Biology, Vol. 14, eds. M.K. Hecht, B. Wallace, G.T. Prance. Plenum Press, pp. 351–437.
- Stearns, H.T. 1966. Geology of the State of Hawaii. Pacific Books, Palo Alto, CA.

- Throckmorton, L. 1966. The relationships of the endemic Hawaiian Drosophilidae. Univ. Texas Publ. 6615:335-396.
- Throckmorton, L.H. 1975. The phylogeny, ecology and geography of *Drosophila*. In: Handbook of Genetics, R.C. King, ed. Plenum Press, N.Y., pp. 421-426.
- Warner, R.E. 1967. Some observations on the birds of Kipahulu Valley. Scientific Report of the Kipahulu Valley Expedition. The Nature Conservancy, pp. 133-144.