LEK BEHAVIOR AND ECOLOGY OF TWO HOMOSEQUENTIAL SYMPATRIC HAWAIIAN DROSOPHILA: DROSOPHILA HETERONEURA AND DROSOPHILA SILVESTRIS

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According to Loiselle and Barlow (1978), "Lekking is the temporary synchronus aggregation of sexually active males for reproduction." It is a type of communal display. Theoretically, males displaying communally are more conspicuous and have a better chance of encountering females. Until recently, most of the research on lek behavior has been done on birds, especially grouse (Tetraonidae) and mannikins (Pipridae). Lekking in fish has only begun to be investigated (Loiselle & Barlow 1978) and reports of work on insect lek behavior are not numerous (Wilson 1975).

Spieth (1968) was the first to describe lek behavior in Hawaiian Drosophila. Two species of Hawaiian Drosophila that Spieth found to engage in lek behavior are Drosophila heteroneura and D. silvestris. Carson and Stalker (1968) found these two species to be homosequential, that is, the banding patterns on the polytene chromosomes are identical, indicating they are very closely related. They also found that heteroneura and silvestris share a polymorphic inversion, although silvestris has six other paracentric inversions.

Ahearn et al. (1974) found that in the laboratory, ethological isolation between heteroneura and silvestris was strong although incomplete. Unfortunately, quantitative comparisons of the action patterns observed in the courtships of these two species have not been made. Spieth (pers. comm.) has, however, found some qualitative differences.

Hybrid progeny of successful pairings in the laboratory are vigorous and fertile (Carson & Kaneshiro 1976). Recently, Kaneshiro has even collected hybrids in the wild at Kahuku Ranch on the island of Hawai'i (Kaneshiro & Val 1977).

The two flies belong to the Planitibia complex of picture wing Drosophila and are widely sympatric on the island of Hawai'i. The other two species that belong to this complex are differens found on Moloka'i and planitibia on Maui. Morphological, ethological, and chromosomal data indicate that these two flies are ancestral to heteroneura and silvestris (Kaneshiro 1976). It is most likely that planitibia is ancestral to silvestris. D. heteroneura may be derived from planitibia but differens is the more probable ancestor.

My objectives in this study were to observe and describe the lek behavior and ecology of these two species, and to determine if there were differences in these aspects of their systematics that would explain their reproductive isolation in the wild.

Two primary study areas were established on Kealakekua Ranch in Kona to study differences in habitat preference. The lower of the two sites (1067 m/3500 ft) was called Hapu'u. It is in an 'ohi'a (Metrosideros sp.) forest with a dense tree fern (Cibotium sp.) understory. The higher study site (1304 m/4280 ft), called Oiki, was in a remnant 'ohi'a forest with scattered Acacia koa and diverse tree strata interspersed with open pasture.

Two other sites where observations were made were on Keauhou Ranch at 1432 m (4700 ft) near Hawaii Volcanoes National Park and Kahuku Ranch near South Point. The habitats where the flies occur on these two ranches are similar. Both sites are open pasture with small clumps of dense remnant 'ohi'a-tree fern forest. Observations were made at two separate elevations on Kahuku Ranch, 1058 m (3800 ft) and 1235 m (4050 ft).

Observations were also made in 'Ola'a forest at 1237 m (4060 ft) adjacent to the University of Hawaii Volcano Experiment Station. This forest is similar to the hapu'u study area; it is an 'ohi'a forest with a dense understory of tree ferns.

My observations of the behavior of heteroneura on food supported Spieth's contention that predation by birds acts as a selection pressure favoring the evolution of lek behavior in Hawaiian Drosophila. That is, courtship is not on the food as with most Drosophila, but on branch-territories nearby.

Mark-release experiments showed that marked flies often occupied the same branch when consecutive sightings of them were made. At morning and afternoon sightings, and at afternoon and the following morning sightings, marked flies had moved only small distances (about 0.5 m).

Field observations suggested that the morning temperature threshold for feeding behavior for both species is about 10°C (50°F). Males of both species alight on their branch-territories presumably after feeding. Males of both species were active at the lek if weather conditions remained optimal. Conditions outside these limits caused flies to remain inactive or to leave their branch-territories. Males of both species leave their territories near sunset. Temperature decrease below a threshold probably stimulates this behavior if decreasing sunlight does not do so first. No temporal differences in attendencies of the two species at their respective leks were evident.

The initial response of a heteroneura male to the approach of another arthropod moving on its territory is usually an approach, and is often followed by patrolling behavior, the repeated walking of a distance of 10 to 80 cm over a section of vegetation. Patrolling behavior is most often observed (in

either species) after an encounter with another arthropod; however, the frequency and duration of walks appears to decay with time. While on their territories male heteroneura frequently make short flights in an erratic path away from and back to their territory.

Patrolling behavior may perform three different functions. The visual stimuli of a patrolling male may serve to keep the males together, interacting and competing for territories. It may also attract females. Finally, patrolling may be a means by which the most fit males may defend territories and insure that they inseminate the females that alight there.

Female heteroneura (and presumably silvestris) are usually found at about the same height as the males (about 2 m) resting on the undersides of branches. Many hours of observations of male heteroneura on their territories revealed that females alighted on the territories infrequently.

Premating isolation can be maintained through two different means. Behavioral isolation between two species prevents them from exchanging genetic material. Through ecological isolation species are kept separate by the influence of environmental factors.

Differences in body color between the two species suggested they might be adapted to different levels of incident light under the forest canopy. However, the analysis of incident light level data measured on flies suggested that flies do not seek different light levels in their habitat. Instead the results lend support to the hypothesis that differences in body color (particularly abdomen color) may be most important as stimuli in mate recognition.

Observations on Kealakekua Ranch, Kahuku Ranch, and 'Ola'a forest did not reveal any differences between leks of the two species. Heights of male silvestris in vegetation at the different sites were all found to be about 2 m off the ground.

Observations at "shared lek sites" (leks under the same continuous canopy in close enough proximity that interspecific interactions were possible) did not reveal any differences in the leks of the two species at these shared sites. There was no species-specific preference for plants on which territories were defended. In fact, where branches or fern stipes were long enough, I occasionally saw males of both species "on station" (Spieth 1966) on the same branch or stipe. At certain of these shared lek sites some spatial separation of the two leks was evident. One possible explanation at certain sites might be that behavioral interactions might cause the flies to congregate where they only infrequently encounter the other species on the territories. Species-specific pheromones released into the air might also serve to keep both sexes of both species together at the lek but no evidence of this has been reported. Another resource, besides leks, these species shared was food. Often, both species were seen interacting on the same food.

Further evidence for resource sharing was found when both species were reared from the same decaying Clermontia branches collected on Kahuku Ranch.

The only ecological variables to which the two flies appeared to respond to differently were changes in moisture and pressure (that is, lapse rate) associated with elevation. Results of past collections of these species from different elevations on Kahuku and Keauhou ranches, Kilauea Forest Reserve, 'Ola'a forest, and kipukas on the Saddle Road, suggest that silvestris is more common at higher elevations. It is possible, however, that silvestris may just have a wider range of elevational distribution since it is always found where heteroneura occurs.

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