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DROSOPHILA HETERONEURA AND *DROSOPHILA SILVESTRIS*: HEAD SHAPES, BEHAVIOR AND EVOLUTION

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The *planitibia* subgroup of the picture-winged *Drosophila* is represented on Hawaii, the easternmost island of the chain, by two closely related species, *D. heteroneura* and *D. silvestris* (Carson, 1979). Hawaii consists of seven sequentially aged volcanoes that are fused into a single large land mass (Fig. 1, Table 1). The flies dwell in the rain forests on the slopes of these volcanoes at elevations of circa 900–1,500 m. *Drosophila heteroneura* essentially is restricted to the 900–1,200 m range and thus is fully sympatric with *silvestris* but populations of the latter extend above the areas occupied by *heteroneura*. Further, *silvestris* is present on the northernmost volcano Kohala where *heteroneura* is lacking.

Drosophila heteroneura prefers areas of the forest where the density of the vegetation, especially the trees that form the forest canopy, is lower than that preferred by *silvestris*. As a result the light intensity in the understory portions of the forests where *heteroneura* lives is higher than in the areas typically selected by *silvestris*. Thus, although the species broadly overlap in their distributions, there is partial geographical and ecological isolation between them.

The prime larval substrates of both species are the fermenting parts of plants, especially the bark of *Clermontia* spp (Montgomery, 1975). *Clermontia* is an understory shrub widely but not uniformly scattered throughout the forests. In areas where a number of individuals of *Clermontia* are present, both species of flies can be found in close association and both species have been reared from the same fermenting mass of *Clermontia* (Kaneshiro and Val, 1977).

Morphologically the two species are distinctly different and readily separable (Hardy, 1965; Carson, 1979). Sexual isolation under laboratory conditions is strong but not complete (Kaneshiro, 1976). However, when heterogamic mating does occur the F_1 hybrids produced are viable and fertile (Carson, 1979). Further, fertile hybrids have been recovered in the field (Kaneshiro and Val, 1977; Carson, 1979).

The following discussion is concerned with the probable roles that behavior and the geological history of the island of Hawaii have served in the evolution of these two species and is based on behavioral data from laboratory and field studies conducted during the past decade. The laboratory studies used both field captured and laboratory reared individuals. Conant (1978) conducted intensive field studies on both species in the Pauahi area, which is located in the Kona district 8.6 km east of Captain Cook, where the two species live in sympatry. His findings parallel my field data.

Basic Courtship Patterns

The observable pattern of the courtships of the two species is complex but essentially similar. The male visually orients upon a female and approaches her head on. Both males and females exhibit a high level of agonistic behavior; as soon as a female becomes alert to an approaching male she assumes an agonistic posture. The faces of the males, especially the prefrons area enclosed by the ptilinal suture, exhibit crisply delineated pigmentary patterns that are species specific. In addition, the male engages in species specific body and/or wing movements as he approaches the female (Spieth, 1978; Watson, 1979). The pigmentary patterns plus the male's

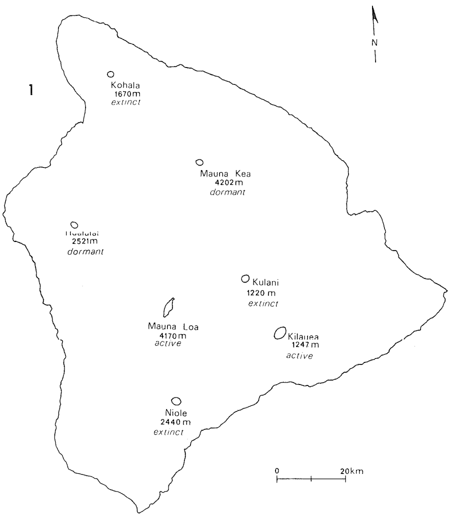

FIG. 1. Island of Hawaii.

TABLE 1. *Volcanoes of Hawaii.*

	Age	Elevation	Status
Kohala	0.6–0.8 my	1,670 m	Extinct
Mauna Kea	0.35–0.6 my	4,202 m	Dormant
Hualalai	0.25–0.4 my	2,521 m	Dormant
Mauna Loa	0.1–0.5 my	4,170 m	Active
Kilauea	<0.1 my	1,247 m	Active
Kulani*	?	circa 1,220 m	Extinct
Niole*	circa 0.7 my	circa 2,440 m	Extinct

* Kulani is located 29 km northeast of the cone of Mauna Loa and Niole is south of the Mauna Loa cone. Both are covered by Mauna Loa lavas.

body movements visually inform the female of his species identity and his motivation to court rather than to engage in agonistic behavior. If the female does not flee or respond agonistically he then circles to her rear, and places himself directly behind her with his head under the distal ends of her wings. He begins to semaphore his wing vanes slowly at first, with small amplitude and with the vanes horizontal. The movements increase in amplitude and speed and, also, the vanes are rotated. When the amplitude of the movements reaches 90° the vanes are vertical. As the wing sweep increases still farther and beyond 90° the vanes begin to supinate. When they reach a forward extension of about 150° the vanes are then fully supinated. Suddenly the male ceases semaphoring and holds his supinated wings at the fully extended forward position, vibrating both wings with rapid small amplitude movements. Simultaneously with the initiation of the wing vibration the male lifts his forelegs, extends his femora upward and forward, folds his tibiae and tarsi backward against the femora and lunges upward and forward over the female's abdomen. The dorsal surface of the antennal segments slide against and push upward the female's wing vanes until they are elevated about 45°. He then vibrates his forelegs at high speed in small amplitudes causing the sexual setae of the tibiae and tarsi to strike the dorsum of the female's abdomen and drops backward, slowly sliding the vibrating tibiae and tarsi over her abdomen, and finally he curls the distal segments of the tarsi under the tip of her abdomen. He then curls the tip of his abdomen forward and attempts to achieve intromission.

Drosophila silvestris and *heteroneura* are members of a closely related complex of five species. The other three species dwell on older islands that are located west of Hawaii: *planitibia* of Maui, *differens* of Molokai, and *hemipeza* of Oahu. A closely related group of species, the hanaulae complex, has four species on Maui, one on Molokai and two on Oahu, but none on Hawaii. All males of both species complexes exhibit the same basic courtship pattern. The displays in front of the females, especially of those species which are sympatric, exhibit species specific differences which are both quantitative and qualitative. The male displays at the rear of the female appear to exhibit only quantitative species specific differences: speed and magnitude of the wing movements and possibly speed of foreleg vibration.

Secondary Sexual Modifications

The species of both complexes exhibit unique modification of their head configuration. The postfrons, the area between the first ocellus and the ptilinal suture, is elongated and protruded forward result-

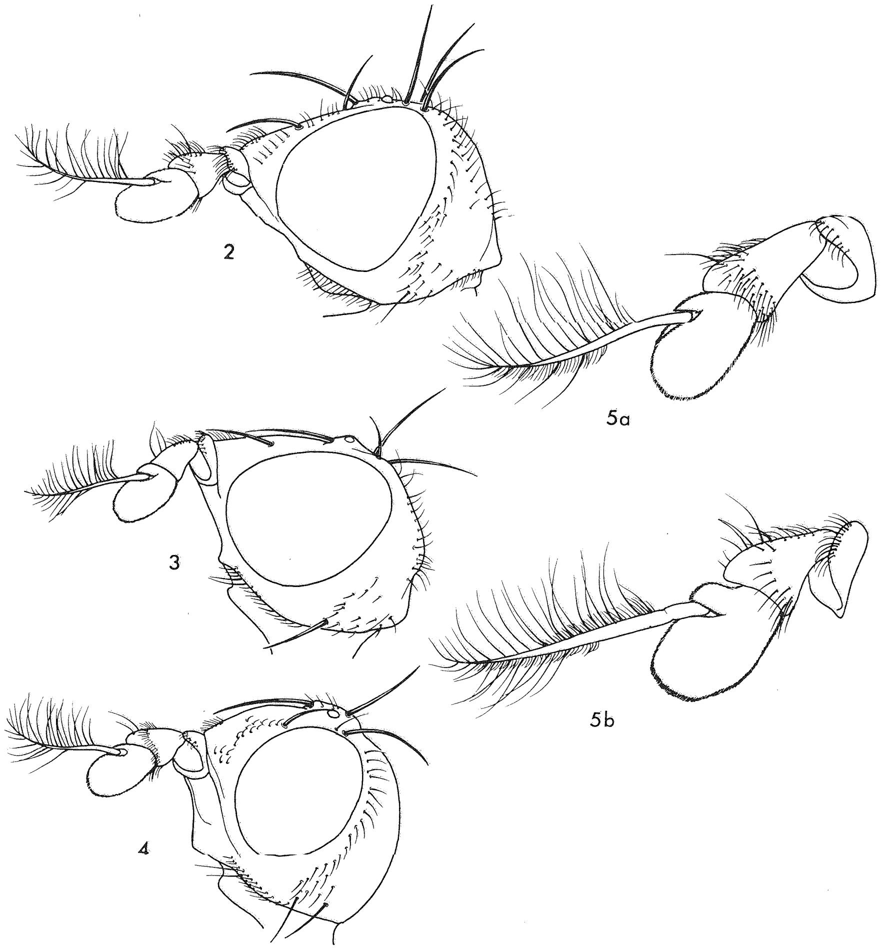

FIG. 2. Side view of head of *D. differens* ♂.
FIG. 3. Side view of head of *D. silvestris* ♂.
FIG. 4. Side view of head of *D. heteroneura* ♂.
FIG. 5a. Antennae of *D. heteroneura* ♂.
FIG. 5b. Antennae of *D. silvestris* ♂.

ing in the antennae being positioned at the antero-dorsal margin of the face (Figs. 2, 3 and 4). The pedicel and scape of the male antennae are enlarged and the setae of the scape hypertrophied (Figs. 5a, 5b). The aristae, in addition to the typical elongated setae (branches), bear numerous short setae (Figs. 5a, 5b). When the courting male lunges forward and upward over the female's abdomen and pushes the female's wing vanes upward, the scape and pedicel of the male's antennae slide and thrust against the ventral surface of her wings. At the same time the short numerous setae on the aristae serve as a cushion and allow the aristae to slip under the surface of her vanes without abrading against the dense microtrichae of the vanes.

Such unique modifications of the male's anatomy (the positioning of the antennae, the hypertrophied pedicel, scape, and its setae, and the short setae on the arista) are all functionally involved in the courtship sequence. I suggest that the most parsi-

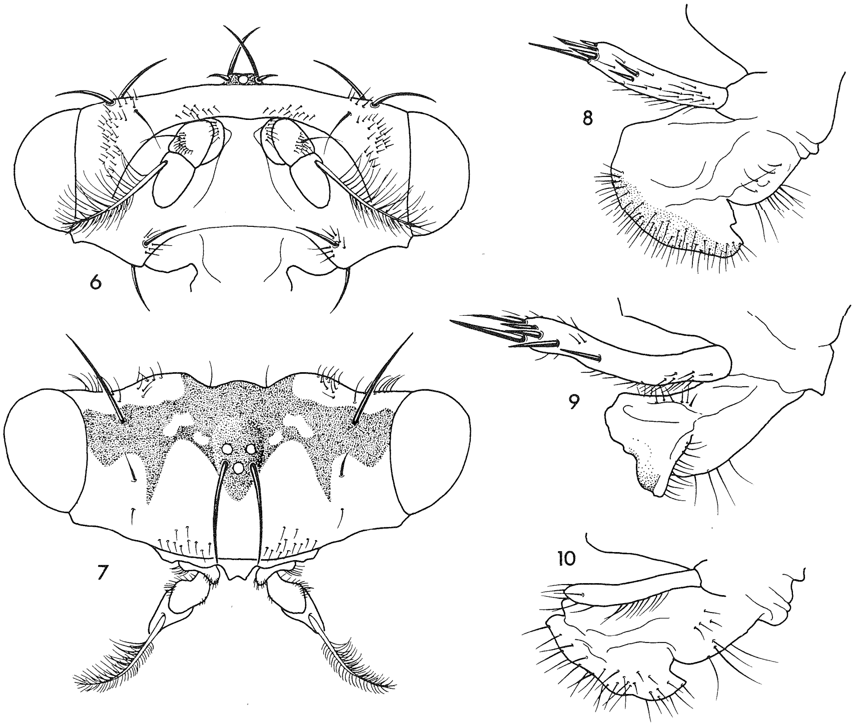

FIG. 6. Face of *D. heteroneura* ♂.
FIG. 7. Dorsal view of head of *D. heteroneura* ♂.
FIG. 8. Maxillary palp of *D. heteroneura* ♂.
FIG. 9. Maxillary palp of *D. silvestris* ♂.
FIG. 10. Maxillary palp of *D. differens* ♂.

monious explanation of the evolution of these functionally important structural modifications is that the behavioral elements of the courtship antedated the modifications and thus provided the selection pressures which resulted in the subsequent morphological modifications. Numerous similar examples involving various parts of the male's anatomy exist in other Hawaiian *Drosophila*; invariably when a species possesses such a character it serves an important role in the behavior of the individual.

As a result of the forward protrusion of the postfrons, the faces of the males of most species of both complexes slant backward (Fig. 2). *Drosophila heteroneura* is an exception. It has undergone a further and unique modification of its head shape. The face of *heteroneura* resulting from a shortening of the postfrons is vertical rather than backward slanting and the lateral portions of its head are hypertrophied outward. When viewed from the front (Fig. 6) it appears stalkeyed and from above mallet-shaped (Fig. 7). The antennae of *heteroneura,* however, retain the same shape and placement as do those of its relatives (Fig. 4), and the *heteroneura* antennae serve the same function in the male's courtship at the rear of the female as do the antennae of the other 11 species of the two species complexes.

Drosophila silvestris also has a moderately shortened postfrons and the degree of facial slant is intermediate between that of *heteroneura* and *differens* (compare Figs. 2, 3 and 4).

Drosophila heteroneura and *silvestris* also differ from their relatives in that both have sturdy maxillary palps that are hypertrophied in length and diameter and bear 4–6 heavy setae (Figs. 8 and 9), whereas all the species of the two complexes on other islands have short slender palps that bear only slender terminal setae (Fig. 10).

Lek Behavior

In common with many other Hawaiian *Drosophila* species, males of *heteroneura, silvestris* and their close relatives mate at leks or mating arenas (Spieth, 1966, 1968, 1974). The majority of the Hawaiian species choose secluded lek sites in dense vegetation. *Drosophila heteroneura, silvestris* and their relatives are atypical, selecting lek sites that are easily visible, 1–3 m above the substrate. Their leks are not randomly distributed; rather, the males select individual shrubs and tree ferns whose surroundings meet rather precise environmental conditions of light intensity, canopy cover, air movements and the absence of immediately surrounding vegetation. One to 10 males may assemble on such a shrub or tree fern, each occupying the surface of a branch or fern rachis. The male advertises his sexual readiness by patrolling back and forth on his lek, waving his wings as he moves. The advertising male apparently does not produce any pheromones but individuals of both sexes have acute vision and the females are attracted visually. Males frequently enter each other's leks and this invariably results in aggressive behavior which frequently results in ritualized fighting (Spieth, 1974). The two males slowly approach each other head on, bobbing their heads upward by extending the forelegs but keeping the abdominal tip depressed. Eventually the longitudinal axis of their bodies forms an angle of about 70°–80° with the substrate and their heads are about 0.5 cm apart. Each then raises and places its midlegs in front of the forelegs, turns its head slightly sidewise, and then raises its forelegs and wraps them around the body of the opponent. Simultaneously they thrust the sides of their heads and the venters of their thoraces against each other. They then struggle to depress the body of the opponent downward. The lowering of the body of an individual is the signal of submission and defeat, and terminates the fight. The flies may struggle for five or more minutes before one is defeated and flees. If one of the two contestants is smaller than the other and is thus unable to raise his head as high as that of his opponent as they approach each other, then the smaller one "admits defeat" just *before* physical contact is made.

The 12 species of the two complexes have the largest body sizes of any known *Drosophila*. It is suggested that the combination of the male fighting behavior and the visual advertising pattern on the leks has provided the selection pressures that led to the evolution of large size.

Aggressive Behavior of D. heteroneura

Drosophila heteroneura displays an exceptional fighting pattern that is strikingly different from that of *planitibia* and *differens*. The *heteroneura* males do not elevate their heads as they approach head on but rather keep their bodies horizontal and depressed to the substrate. When they meet, physical contact is made by thrusting their hypertrophied maxillary palps and flattened faces against each other and then they push vigorously against each other, attempting to force the other backwards. These fights may last for several minutes. During these intense pushing contests the interlocked maxillary palps prevent sidewise and up-and-down slippage of the facial surfaces that are in contact, and both wings are usually extended 90° (Fig. 11). When an individual succeeds in pushing his opponent backward he is the victor and the defeated fly turns and flees. Thus, the fighting behavior on the lek (rather than the courtship behavior) has provided the selection pressure that caused the evolution of the unique secondary modifications of the *heteroneura* male's head shape. The question thus exists, why did *heteroneura* evolve a unique fighting pattern?

Adequate data exist to prove that species of endemic birds, the honey creepers and the fly catcher (*Chasiempsis sand-*

wichensis), which dwell in the same forests as do the *Drosophila,* feed avidly on the flies (Warner, 1967; Spieth, 1974). Before the birds were decimated by the impact of Western culture they existed in vast numbers (Perkins, 1903, 1913). On the average *Drosophila heteroneura* selects areas in the forests which have a relatively high light intensity while *silvestris* and the other relatives of *heteroneura* on Molokai, Maui and Oahu prefer conditions where the light intensity is much lower. *Drosophila heteroneura* lacks the intense melanistic body patterns that characterize its relatives; rather its body color is paler and tinged with yellow. Under the relatively high light intensity of the forests in which it dwells, the horizontal fighting stance with the body depressed close to the substrate plus the paler body color cause the fighting males to be much less visible on the leks than they would be if they were darkly colored and assumed the upright stance of their relatives. The fighting stance and body coloration of *heteroneura* can be best considered as antipredator adaptations.

Viable and fertile F_1 and F_2 hybrids can be procured from *heteroneura-silvestris* crosses. Val (1976, 1977) and Templeton (1977) have studied the genetics of the inheritance of a number of the differences of the two species with emphasis on the head shapes. Templeton found that the head shape of *heteroneura* males is virtually invariant despite considerable variation in head size. Templeton (1979) suggests that the invariant head shape of *heteroneura* provides a clue to factors that did or did not contribute to the explosive speciation that has occurred in the Hawaiian *Drosophila*. The females of the Hawaiian species, in common with *Drosophila* in other parts of the world, control the choice of a mate. Since numerous species live in sympatry Templeton assumes that this sympatry creates "intense selection upon the female to make the right choice." The female makes her choice upon the basis of the recognition signals provided by the male. He assumes further that the females have a choice "norm" and that any male that deviates his signals from the female's norm will be discriminated against during courtship. Templeton's scheme is characterized by self-perpetuating feedback between the sexes and strong stabilizing selection upon the male's recognition signals presented to the female. Templeton further assumes that the unique head shape of *heteroneura* serves as a male recognition signal to the courted female and that its invariant nature is a prime support for his thesis.

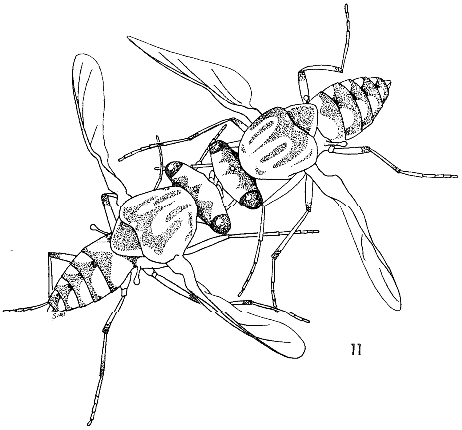

FIG. 11. Fighting stance of *D. heteroneura* ♂♂.

Alternative interpretations of the data are available and seem appropriate. The unique head shape of the *heteroneura* male evolved apparently as a result of predation by birds and not as a male courtship signal. It is therefore not surprising that the shape of the head is invariant. Due to the nature of the contact between the two fighting males, any deviant shape would be selected against. Further abundant behavioral data exist that females do not have a "norm" of response to secondary sexual characteristics such as those that serve as male signaling structures. Rather the female preferentially responds positively to supernormal stimuli but discriminates against subnormal stimuli (Eibl-Eibesfeldt, 1970; Hinde, 1970). As Selander (1972) has pointed out, such secondary male sexual characters are "highly adaptive in attracting and stimulating females, but they render the individual more vulnerable to predators or otherwise reduce the probability of survival. Thus, such characters develop only to the point where increasing mortality leads to a lessening of competition among males." Endler (1978) in studying guppies noted that the brighter color pattern types are sexually advantageous but become disadvantageous in the presence of visual predators. He found that in areas where predation was low the fish were conspicuous and colorful but that in areas where predation was high the color patterns were much reduced. A stabilized equilibrium thus occurs, not because the females have a "norm" but because of a balance between sexual selection and selection for male survival. Previous to reaching the point of equilibrium sexual selection pressure will operate to favor those deviant males that produce a supernormal signal. Ringo (1977) has suggested that the lek behavior of the Hawaiian *Drosophila* has resulted in the rapid evolution of secondary sexual characters which in turn has led to rapid speciation.

History of Hawaii

The island of Hawaii consists of seven individual shield volcanoes that arose sequentially and fused with others as they matured (Table 1 and Fig. 1). Two of these, Niole and Kulani, are today extinct and except for a few remnants each is completely covered by the younger lavas of Mauna Loa (Macdonald and Abbott, 1970). Kohala, the oldest, was formed about 700,000 years ago (Table 1). At approximately the same time the now extinct Niole, which reached a height of circa 2,440 m, arose from the ocean about 112 km south of Kohala (Macdonald and Abbott, 1970). Subsequently the younger Mauna Kea and Hualalai shields appeared above the ocean's surfaces. The age of Kulani is unknown, but since it is extinct and covered by Mauna Loa lavas it must be more than 500,000 years old. Kilauea, the youngest volcano, arose recently on the flank of Kulani (Macdonald and Abbott, 1970). Excepting Kilauea, as each of the younger volcanoes arose from the sea and matured, their lavas obliterated the oceanic channels that separated them from their older neighbors and eventually their lava flowed against the flanks of their neighbors and fused with them.

The tradewinds, which strike the northeast slopes of the volcanoes, are the prime source of precipitation on the islands. The winds are known to have maintained their same direction for at least the last million years but are shallow in character, extending upward only 1,500–1,800 m. As a result the tradewind-created precipitation ends at about 1,800 m. This results in the upper areas of the higher volcanoes being essentially deserts. Further, the tradewinds deposit their heaviest precipitation on the windward slopes of a volcano and the lee sides of the volcano approach desert conditions. Thus, at the 1,200 m level on the windward side of Mauna Kea the annual rainfall averages between 380–500 cm, whereas at 1,200 m on the leeward side the annual precipitation is 40 cm. The smaller and younger Hualalai volcano lies southwest of Mauna Kea (Table 1 and Fig. 1). Since the time when it emerged from the sea it has been in the rain shadow of Mauna Kea and today has an annual precipitation of 130–190 cm at the 1,220 m level, with still lower amounts at the 1,000 m level.

It is suggested therefore that the Hualalai forests in the 900–1,200 m range have always been, as they are today, less dense and more open than are forests on other volcanoes where the rainfall is much higher.

Origins of heteroneura *and* silvestris

It is conceivable that *heteroneura* and *silvestris* are the descendants of a single ancestral migrant that colonized Hawaii or alternatively that they are descendants of two separate migrants. For either of these possibilities *D. differens* of Molokai and *D. planitibia* of Maui are the putative ancestral species. Craddock (1974) and Kaneshiro (1976) have investigated this question by studying the hybrid viability and sexual isolation that exist among the four species. Their findings show that *planitibia* is a descendant of *differens* but give equivocal answers as to the ancestry of *heteroneura* and *silvestris*. The history and structure of the island of Hawaii provide clues which can supplement their findings.

All migration of *Drosophila* founders from one island to another has been accomplished by airborne individuals. The distribution of the species on Hawaii suggests that successful migrants from Oahu and Molokai typically were carried eastward and southward, landing not on Kohala but rather farther south on Hualalai or Mauna Loa. As an example, Carson and Johnson (1975) intensively studied *D. setosimentum* and their data indicate that the original founder landed on either Hualalai or Mauna Loa. The morphology and polytene chromosomes suggest that *setosimentum* is a descendant of *D. cilifera* of Molokai.

The various factors suggest that a migrant from the *differens* population of Molokai colonized the Hualalai volcano when it was relatively young and probably not yet fused to Mauna Loa. This population, the ancestor of both *heteroneura* and *silvestris,* was "trapped" in a sparse forest with relatively high light intensity. Bird predation created a selection pressure which resulted in the males abandoning upright combat on their leks. At first they kept their bodies parallel to the substrate and ceased to engage in the up and down bobbing action. Instead they rushed at each other head on and butted as well as slashed with their forelegs. This type of combat provided the selection pressure that eventually resulted in the hypertrophied maxillary palpi and unique male head shape. The courtship of the male at the rear of the female did not change and consequently the male antennae retained the ancestral form and function.

I have observed many fights between *silvestris* males but only twice did the individuals engage in the upright fighting. In all the other combats the males faced each other, kept their bodies horizontal to the substrate, extended their wings laterally and rushed at each other, vigorously butting their heads together. The only major differences between their fighting behavior and that of *heteroneura* are that the facial contacts between the males of *silvestris* are of short duration and they also slash vigorously with their forelegs as they make contact. The tips of the elongated armored palps extend well beyond the face of both *silvestris* and *heteroneura* and when the flies rush at each other the tips are directed forward so that the terminal spines strike the face or mouthparts of the opponent.

It can be reasonably assumed that the evolution of the fighting pattern involved three stages which followed each other sequentially in time. Stage one involved abandonment of upright fighting which was replaced by the flies retaining the horizontal position and rushing at each other. During stage two the hypertrophy of the maxillary palps occurred and during stage three the postfrons was shortened and the face flattened. The present day *silvestris* males exhibit a fighting behavior comparable to that which the ancestors of *heteroneura* would have exhibited during stage two. It is therefore suggested that *silvestris* is the descendant of a migrant from such an ancestral *heteroneura* population. This migrant successfully colonized one of the volcanoes eastward of Hualalai.

Further evidence that both *heteroneura* and *silvestris* arose from the same ancestral population is indicated by their sharing of the unique chromosomal inversion (3M/+) which neither *planitibia* nor *differens* exhibits. This inversion presumably appeared in the original founder population on Hualalai.

A hundred thousand years ago Mauna Kea and especially Mauna Loa were active but smaller and lower than they are today. Kilauea was not in existence but Kulani and Niole were mature volcanoes (Fig. 1 and Table 1).

The cauldera of Niole is located about 55 km southeast of Hualalai, and its slopes were exposed to the trade winds, and at that time the volcano must have had forests which were similar in density and wetness to those of the present-day forests of the Kohalas, Molokai and Maui. A population established in these forests would have faced selection pressures different from those found on Hualalai but similar to those which *differens* experienced on Molokai. Furthermore, colonizers from the Niole population could have easily moved north to Kulani whose forests were probably then contiguous with those of Niole. As the rapidly growing Mauna Loa engulfed Niole, other avenues for colonization were probably developed southward and westward.

The males of the five species of the planitibia complex bear two rows of elongated sexual setae on their tibiae which correspond to rows 5 and 6 of *D. melanogaster.* Carson and Bryant (1979) have investigated these setal rows of *silvestris* and find that the *silvestris* populations that today dwell north and east of Niole have an extra intermediate row located between rows 5 and 6 while the populations that dwell in the area where Niole existed and south and west of Niole have the ancestral pattern, which suggests but does not confirm that *silvestris* evolved on Niole.

At the same period of time when the lava of Mauna Loa engulfed Niole its westerly flowing lava piled high upon the southern flanks of Hualalai and eventually reached an altitude of over 1,600 m. This enabled the rain forests of the two volcanoes to fuse and provided a southward "escape route" for *heteroneura* along the Kona Coast. From Kona *heteroneura* spread east, then northward to Kilauea and Mauna Kea but it still has not been able to colonize the Kohala volcano.

By now the two species have evolved behavioral patterns that prevent introgression of the species in their normal habitats. A male *heteroneura* has a yellow face and *silvestris* a black face with a lighter, narrow ventral margin. As the male approaches the female his facial pattern is presented to her. It should be noted that such pigmentary patterns of the species of the complex are labile. Thus, *differens* has a yellow face with slight melanistic infusions in the antennal fossae while *planitibia* of Maui, which unquestionably is a descendant of *differens,* has a black face that is similar to that of *silvestris.* The courting *heteroneura* male holds both of his wings extended to about 70° with the vanes rotated to a vertical position, whereas the *silvestris* male as he approaches a female extends both wings outward and upward about 90° with the vanes rotated to vertical and he then arcs back and forth laterally, moving through an arc of about 30°. During the display at the rear of the female the *silvestris* male extends his supinated wings farther forward than does *heteroneura.* There also appear to be quantitative differences in the amount and speed of wing and leg vibrations but these have not been fully quantified.

SUMMARY

It is postulated that *D. heteroneura* and *D. silvestris* are the descendants of a migrant from the *D. differens* population of Molokai which colonized the young Hualalai volcano. The character of the Hualalai forest was such that the males of the colonizing population were subjected to intense predation when occupying their courtship arenas (leks). This resulted in the males abandoning their ancestral upright fighting posture. Instead the male kept his body horizontal with and close to the substrate and then rushed head on against an opponent. This shift in behavior produced the selection pressure that eventually resulted in the evolution of the hypertrophied maxillary palps and the unique head structure which the *heteroneura* male now exhibits. The evolution of the hypertrophied maxillary palps preceded in time that of the head shape. At a point in time when the Hualalai population had evolved the hypertrophied male maxillary palps but had not fully acquired the unique head shape of present day *heteroneura,* a migrant from this population colonized the then mature Niole volcano. The Niole forests at that time possessed a character similar to that of Molokai and

thus the selection pressure that was operating on the Hualalai population was eliminated. Evolution of the head shape ceased but the hypertrophied maxillary palps were retained. Subsequent growth of Mauna Kea and especially Mauna Loa resulted in the fusions of the seven volcanoes that comprise the present-day island of Hawaii and allowed the two species to expand their areas and become sympatric.

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