

*Reprinted from the*  
ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

# The Behavior and Biology of the Hawaiian *Drosophila anomalipes* Species Group<sup>1,2</sup>

HERMAN T. SPIETH

Department of Zoology, University of California, Davis 95616

## ABSTRACT

Two species, *Drosophila anomalipes* and *D. quasianomalipes*, comprise the *anomalipes* species group of Hawaiian *Drosophila*. The *anomalipes* group is restricted to Kauai and has not colonized the younger islands.

Behaviorally and structurally the species of the group display archaic characteristics that indicate their relationship to continental species.

Congeries of closely related *Drosophila* species are characterized as species groups. Diverse evidences indicate that each species group consists of the evolutionary descendants of a single ancestral species (Bock and Wheeler 1972). A number of species groups has been identified in the endemic Hawaiian drosophiloid fauna (Throckmorton 1966, Carson et al. 1970). Most Hawaiian species groups are composed of numerous species, and are represented by one or more species on each of the Hawaiian islands that is inhabited by the endemic fauna.

The *anomalipes* species group, however, is exceptional in that it consists of only 2 species, *Drosophila anomalipes* Grimshaw and *D. quasianomalipes* Hardy, which are not only sympatric in distribution but are also restricted solely to Kauai, the oldest and westernmost Hawaiian island that currently possesses a drosophiloid fauna. Individuals of the 2 species are large (4.5–6.0 mm), sturdy flies that move freely about in their habitat and are easily collected. Despite intensive collecting no other Hawaiian species showing close relationships to *anomalipes* or *quasianomalipes* has been found on any of the other islands. As shown below, the 2 species have unique behavioral and morphological characteristics that (1) set them apart from all other Hawaiian species, and (2) provide indications that the 2 species are archaic remnants of an earlier Hawaiian fauna.

## MORPHOLOGY

Both species are predominantly yellowish, tinged with rufous. Differences in brown pigmentary markings on the antennae, wing membranes, and the abdominal tergites readily separate the species.

The sexually dimorphic male forelegs and the male genitalia are similar but species specific. The female ovipositors are long, tubular in shape and mostly membranous with narrow latero-ventral sclerotized valves (Fig. 1–5). Normally the ovipositors are completely withdrawn and hidden in the abdomen. Both species possess an exceedingly long vagina. Massive musculature envelops the vagina whose inner sheath can move freely within the muscular coat. The inner surface of the distal half of the vaginal sheath is supplied with numerous short spines. The female is able not only to extrude her ovipositor fully but also to

evert the spiny portion of the vaginal sheath as a tubular extension beyond the tip of the ovipositor. The tubular extension is about as long as the ovipositor and the combined structure equals the length of the female's abdomen, i.e., 2.5–3.0 mm for *anomalipes* and ca. 2.5 mm for *quasianomalipes*.

The dorsal spermathecae of each species (Fig. 6–8) are subspherical to quadrate capsules with the introvert extending inward ca.  $\frac{1}{2}$  to  $\frac{3}{4}$  of the diameter of the capsule. This is in sharp contrast to other Hawaiian drosophiloids, which have essentially spherical capsules with short introverts (Throckmorton 1966).

The ventral receptacle of the female *quasianomalipes* (Fig. 8) is similar to that of other Hawaiian drosophiloid species but *anomalipes* (Fig. 6) is exceptional in that it lacks the folded section and instead is coiled, thus being comparable to non-Hawaiian members of the subgenus *Drosophila*.

## COURTSHIP BEHAVIOR

*Drosophila anomalipes*.—The male orients upon a female, faces her body, approaches and taps her with one or both foretarsi. He usually then circles in front of her and extends both wings outward and upward 80°. With wings held extended he sways his body, moving ca. 1 mm from side to side. After a short display he circles quickly to her rear, positions himself directly behind her, depresses his body, curls the tip of his abdomen under and forward and thrusts his head under her wing tips. Quickly then he lunges forward onto the female, extending his forelegs which encircle her 3rd and 4th abdominal segments. The distal knobs of his foretibiae (Fig. 5) are applied to her venter. Simultaneously he extends both of his wings laterally ca. 90°, usually vibrating them to and fro, and also curls his abdominal tip still farther forward and seeks intromission. Once sexually excited the male typically omits tapping and frontal display and goes directly to the head-under-wing posture at the female's rear.

A nonreceptive female can usually prevent the male from lunging onto her by depressing her body and wing tips. If, however, the male succeeds in his lunge, the nonreceptive female kicks backwards with her hind legs, extends and rapidly vibrates both wings and extrudes her long ovipositor parallel to the substrate. A male infrequently achieves partial intromission with a nonreceptive female, but within 30–45 s

<sup>1</sup> Diptera: Drosophilidae.

<sup>2</sup> This study was supported in part by NIH Grant No. GM-10640 and by NSF Grant No. GB-711. Received for publication Oct. 7, 1974.

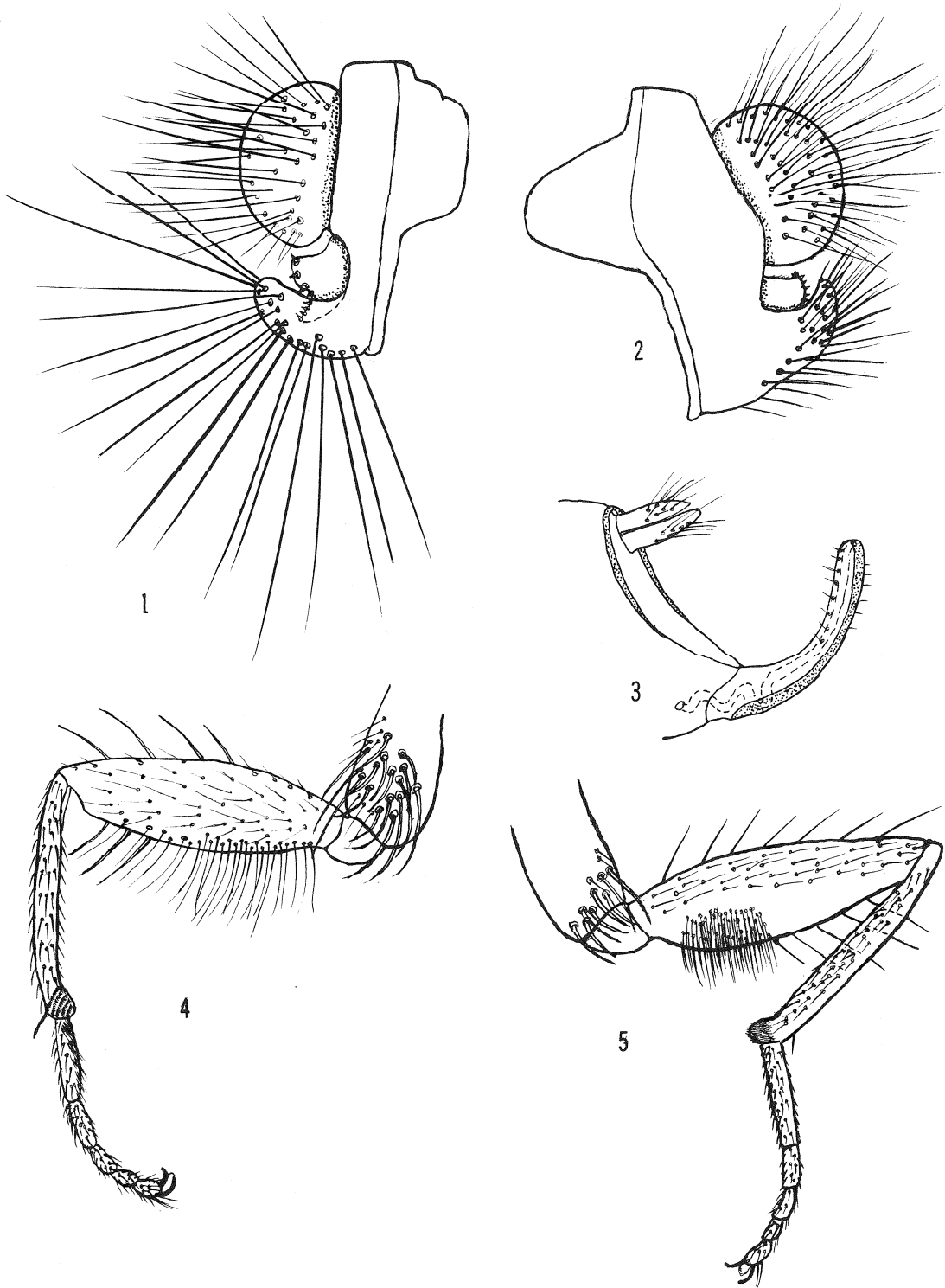
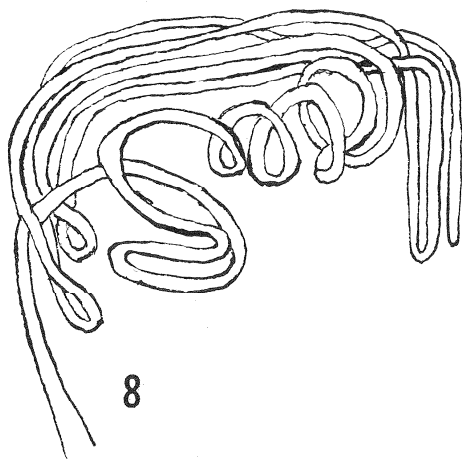
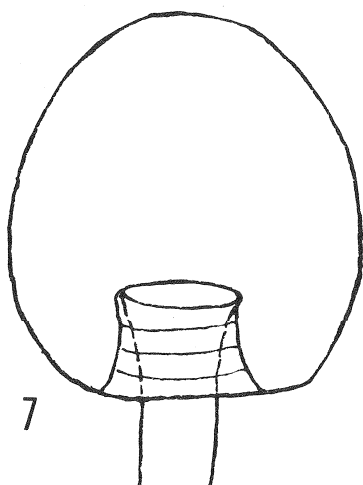
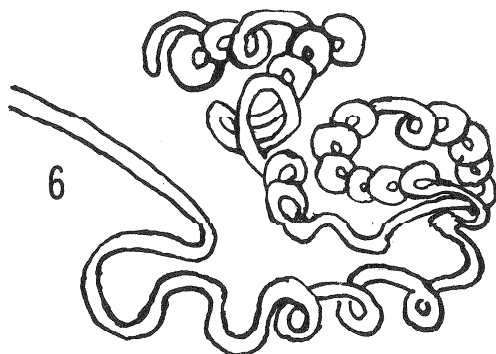


FIG. 1-5.—1-2, Male genitalia, *D. quasianomalipes* (left), *D. anomalipes* (right); 3, Extruded ovipositor, *D. quasianomalipes*; 4-5, Male foreleg, *D. quasianomalipes* (left), *D. anomalipes* (right).

FIG. 6.—Female ventral receptacle, *D. anomalipes*.FIG. 7.—Female spermatheca, *D. quasianomalipes*.FIG. 8.—Female ventral receptacle, *D. quasianomalipes*.

is dislodged. Dissections of the females confirm that no sperm transfer occurs in such instances.

In laboratory observations where the female cannot escape by flying away as she does in the field (see below), the nonreceptive female after several male assaults keeps her ovipositor fully extended which quickly causes the male to cease courting.

*Drosophila quasianomalipes*.—The courtship is similar to that of *anomalipes* except that (1) when posturing in front of the female, the male spreads both wings horizontally to 35–45°, holds them extended for a brief period and then circles to rear; (2) when at head-under-wing posture at rear, the male extends both wings horizontally 10–15° and before lunging vibrates them up and down with small amplitude movements. These vibrations occur in pulses and a pulse always occurs immediately preceding the male's forward lunge; (3) in addition to kicking and wing vibration, the nonreceptive female also extrudes her ovipositor but it is extended upward at an angle of 45° rather than parallel to the substrate. Further, she directs the tip of her abdomen away from the face of the male.

#### FIELD BEHAVIOR

Restricted to Kauai, the 2 species are most abundant in the western highlands (elevation 1000–1250 m), specifically in the Kokee region at the head of Waimea Canyon and west of the Alakai Swamp. The drosophiloid fauna of Kauai is sparser than that of the other major islands but a number of native species, especially of the picture-winged, bristle tarsi, and modified mouthparts species groups, dwell in the Kokee area. Introduced species such as *D. sulfuri-gaster* and especially *D. immigrans* which have successfully colonized the forest are also present.

Most Hawaiian species are extremely wary, especially when approaching a food source or a bait (Spieth 1966). Instead of flying directly to the site they alight several inches to several feet away, then approach by short quick flights or bouts of walking, interrupted by periods of sitting immobile. Upon reaching the food, they ignore other drosophiloids, feed quickly, never engage in courtship and eventually slowly walk away. If startled they fly with a diving movement. Baits placed in open containers are essentially useless since sweeping a net over the container results in the flies diving into the wet food on the bottom. Baiting is therefore accomplished by smearing bait on selected small areas of the trunk or branches of trees or shrubs, 3–6 ft. above the ground.

The Hawaiian species exhibit some diurnality in visiting the bait sites and usually few or no individuals are found feeding during the middle of the day. At Kokee the species show considerable variation in feeding behavior resulting apparently from the complex interactions of daily variations in temperature, humidity and light intensity. Banana baits attract picture-winged and modified mouthpart species plus *anomalipes*, *quasianomalipes* and the introduced species, especially the ubiquitous *immigrans*. Others such as the bristle tarsi species never come to the

bait even though they are readily collected by netting over ferns located only a few feet from the baits.

The field behavior of *anomalipes* and *quasianomalipes* differs strikingly from that of the other endemic species. The males of *anomalipes* are the first natives to arrive at the baits, both in the morning and in the afternoon. They are accompanied by *immigrans*. Males of *quasianomalipes* follow 10–15 min later and the females of both species arrive a short time after the males. Neither species displays the caution shown by other endemics. The males come briskly to the baits, and feed for a short time. After feeding they walk 1–4 in. from the edge of the bait, face outward, assume an alertly watchful stance and await the arrival of females. *D. immigrans* exhibits the same behavior. At a number of my bait sites these three species have been numerous and often a mixed group of 5–15 males will be awaiting the females. *D. immigrans* females are colored quite similarly to those of *anomalipes* and *quasianomalipes* and a large female of *immigrans* is only slightly smaller than a *quasianomalipes*. At a distance of 2–6 in., none of the males of the 3 species can visually distinguish the females from each other. As a result, when a female approaches the bait, a number of males, often involving all 3 species, rush at her and attempt to court. This results in the males jostling each other, vibrating their wings and striking each other with their forelegs. Almost invariably the female flees, and then the males may briefly court each other before returning to their watchful stances.

If a single *anomalipes* or *quasianomalipes* male approaches an incoming female, he typically engages in frontal display. If an *immigrans* female is courted, the male may continue his frontal display for 1–2 min before one of the pair breaks off the encounter. A male *immigrans* does not engage in frontal display and further, as soon as any male makes physical contact with a female, he can distinguish his conspecific from a foreign female.

Infrequently an *anomalipes* or *quasianomalipes* male may be feeding when his conspecific female arrives on the bait. Typically he will then immediately initiate courtship and proceed to the point of assuming the head-under-wing stance at her rear. She will then extrude her ovipositor and continue to feed. He may maintain his stance for up to 30 minutes, following her if she moves but never attempting to mount.

One such pair was observed in which the female finished feeding and walked off the bait. The male followed at head-under-wing posture and as soon as the pair was off the bait and on “uncontaminated” bark of the tree he immediately lunged onto her. Thus while males of the two species will initiate courtship when on a food source, they apparently will not complete the act.

Other Hawaiian species, especially *D. picticornis* and *D. villosipedis*, regularly visit the food masses while *anomalipes* and *quasianomalipes* are present. They behave in typical “Hawaiian” fashion as described above. *D. picticornis* is exceedingly sensitive to disturbances and often the vigorous activity of the

*immigrans*, *anomalipes* and *quasianomalipes* resulting from their pursuit of females is sufficient to cause the *picticornis* individuals to flee.

Search of the areas surrounding bait sites has resulted in finding (1) no other situations where *anomalipes* and *quasianomalipes* court, and (2) the location of lek sites of all the other species that come to the bait except *picticornis*, plus the leks of several other species that do not come to the bait.

During several hundred hours of observation, at all times of day from daybreak to dark, I have observed many scores of courtships by the males of *anomalipes*, *quasianomalipes* and especially *immigrans* but saw only one copulation—a pair of *immigrans*. I also observed a considerable number of other Hawaiian species on their courting leks without seeing a courtship.

#### DISCUSSION

The external morphology of both *anomalipes* and *quasianomalipes*, as Throckmorton (1966) noted, clearly indicates an Hawaiian origin for the 2 species. Likewise the morphology of the male vasa deferentia, paragonia, ejaculatory bulb and ejaculatory apodeme and the female ovipositor, egg filaments and vagina is Hawaiian in type and also indicates close relationship to the “picture-winged” and “modified mouthparts” species groups—2 groups which various data indicate are closely related to each other (Throckmorton 1966). The exceptional features of *anomalipes* and *quasianomalipes* are the dorsal spermathecae of both and the ventral receptacle of *anomalipes* but not of *quasianomalipes*, which has a typical Hawaiian ventral receptacle. No other Hawaiian drosophiloid species is known to have the “continental type” spermathecae that these 2 females possess, and the *anomalipes* ventral receptacle is similar to that of *D. immigrans* and other members of the subgenus *Drosophila*.

The male courtship displays involving the use of both wings, the frontal displays, and the posture at the head-under-wings stance, are characteristic of other Hawaiian males. The female nonreceptive response of extruding the ovipositor is non-Hawaiian and is similar to that of many continental species.

It is the behavior of the 2 species, especially the males at their feeding sites, that is so distinctly non-Hawaiian in character. Thus the males behave in all respects similarly to drosophiloid males in other parts of the world except that while they will initiate a courtship while on the food substance they will not attempt to achieve copula unless the female removes herself from the surface of the food. No other Hawaiian drosophiloid species has ever been observed engaging in any sexual activity on a feeding site; courtship and copulation occur at some distance from any food site and typically involve lek behavior on the part of the male (Spieth 1966, 1970). An enigma is the fact that, so far as is known, neither species has been able successfully to colonize any other of the Hawaiian islands. The adults of *anomalipes* and *quasianomalipes* are large, sturdy, and possess excel-

lent flying ability. *A priori* one would select them as likely candidates for withstanding the rigors involved in colonizing other islands.

In sum, although *anomalipes* and *quasianomalipes* evolved from the same ancestral stock as the other Hawaiian drosophiloid species, they still retain morphological and especially behavioral characteristics that must have been derived from the ancestral population that originally colonized Hawaii, possibly one of the islands westward of Kauai, which, due to erosion, is no longer capable of supporting a native drosophiloid fauna.

The most parsimonious interpretation of the evolutionary position of the 2 species is that they are archaic remnants of an original evolutionary radiation of *Drosophila* in the Hawaiian islands. Restricted today to Kauai, the oldest and westernmost island, for reasons still unclear they have not been able during the past 3 million years successfully to compete with more derived endemic species in colonizing the eastern, younger islands of the Hawaiian chain.

## REFERENCES CITED

- Bock, I. R., and M. R. Wheeler. 1972. The *Drosophila melanogaster* species group. Univ. Texas Publ. 7213: 1-102.
- Carson, H. L., D. E. Hardy, H. T. Spieth, and W. S. Stone. 1970. The evolutionary biology of the Hawaiian Drosophilidae. Pages 437-543 in M. K. Hecht and W. C. Steere, eds. Essays in evolution and genetics in honor of Theodosius Dobzhansky. New York: Appleton-Century-Crofts.
- Clayton, F. E., H. L. Carson, and J. E. Sato. 1972. Polytene chromosome relationships in Hawaiian species of *Drosophila*. VI. Supplementary data on metaphases and gene sequences. Univ. Texas Publ. 7213: 155-62.
- Spieth, H. T. 1966. Courtship behavior of endemic Hawaiian *Drosophila*. Ibid., 6615: 245-313.
1970. The evolutionary biology of the Hawaiian Drosophilidae. Pages 469-91 in M. K. Hecht and W. C. Steere, eds. Essays in evolution and genetics in honor of Theodosius Dobzhansky. New York: Appleton-Century-Crofts.
- Throckmorton, L. H. 1966. The relationships of the endemic Hawaiian Drosophilidae. Univ. Texas Publ. 6615: 335-96.