The Phenomenon of Arrested Insect Development in the Hawaiian Islands[1]

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Roubaud (1922) grouped the higher Diptera into two broad categories on the basis of their annual development cycles. Those which had a continuous succession of generations throughout the year as long as the climatic conditions permitted were designated as homodynamic species and those which did not do so because of a prolonged period of arrested development were designated as heterodynamic species. Since the appearance of Roubaud's work this concept of developmental cycles has been broadened and extended to other orders besides the Diptera.

There has been disagreement on the question concerning the type of annual development that occurs in Hawaii under tropical conditions where there are relatively small seasonal changes in the environment. Although no critical studies have been made, there seems to be a general agreement that the great majority of insects undergo homodynamic development. However, on the question of the occurrence of a heterodynamic type of development there appears to be a dissension of opinion. Some have speculated that this type of development cannot occur because the equable climatic conditions throughout the year are not conducive to an arrest of development; while others have stated that the available information is inadequate to warrant definite conclusions.

The primary purpose of this paper is to present cases of arrested development, a condition necessary for a heterodynamic type of development, and to discuss some of the biological features of arrested development observed in Hawaii. Included in this paper are information obtained from the literature and from the author's observations. The information presented is fragmentary because it consists of only general observations and those made in connection with other studies.

To date cases of arrested development have been recorded from the Hymenoptera, Coleoptera, and Lepidoptera. These cases are summarized in table 1.

Hymenoptera

For convenience the species to be discussed in this order have been divided into (1) solitary wasps, (2) social wasps, and (3) parasites of fruit flies.

Solitary wasps. Three species of solitary wasps are known to undergo arrested development. These are *Hylocrabro tumidoventris* Perkins, *Sphex harrisi* (Fernald) and *Sceliphron caementarium* (Drury).

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Table 1. A summary of insects reported to undergo arrested development in Hawaii under natural conditions except those noted otherwise.

Order	Species	Stage of arrest	First recorded by
Hymenoptera			
Solitary wasps	*Hylocrabro tumidoventris* (Perkins)	larva	Williams (1927)
	Sphex harrisi (Fernald)	larva	Suehiro (1937)
	Sceliphron caementarium (Drury)	larva	Swezey (1906)
Social wasps	*Polistes fuscatus aurifer* Saussure	adult	Swezey (1929), Williams (1939)
	P. macaensis (Fabricius)	adult	Williams (1931)
	P. olivaceus (DeGeer)	adult	Williams (1931, 1939)
	Vespa pensylvanica (Saussure)	adult	Williams (1927)
Parasites of fruit flies	*Opius fullawayi* (Silvestri)	larva	Pemberton and Willard (1918), Back and Pemberton (1918)
	O. tryoni Cameron	larva	Pemberton and Willard (1918), Back and Pemberton (1918)
	O. compensans (Silvestri)	larva*	Christenson (1953)
	O. formosanus Fullaway	larva*	Christenson (1953)
	O. watersi Fullaway	larva*	Marucci (1952)
Coleoptera	*Cryptorhynchus mangiferae* Fabricius	adult	Fullaway and Krauss (1945)
Lepidoptera	*Depressaria umbellana* Stephens	adult†	Chock (1954)

* Observations made in the laboratory under conditions of artificially reduced temperatures.
† Observations made in quarantine room under uncontrolled temperature conditions.

Williams (1927) reported that *H. tumidoventris* makes its nest in fallen logs and that it hibernates in the same manner as other related solitary wasps of the temperate regions. According to Williams the duration of the larval period is exceedingly long during which time the larva remains in an inactive state. The dorsal vessel of the larva in this condition has been observed to pulsate far more slowly than the vessel of a larva in an active condition.

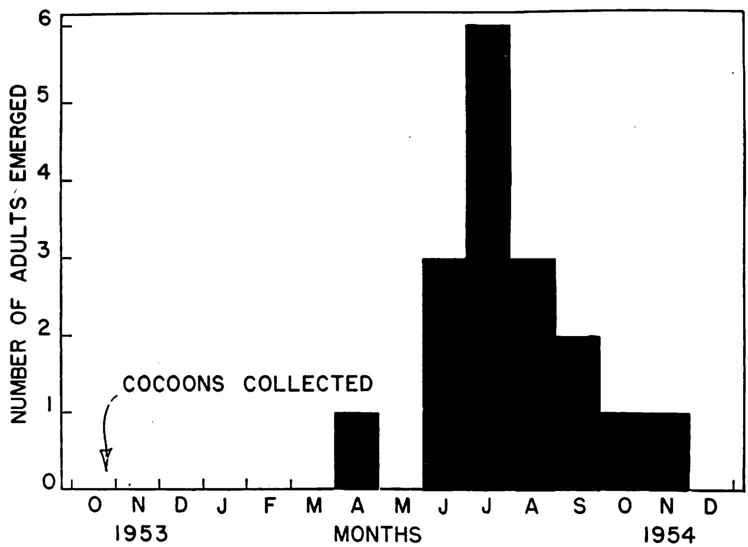

Figure 1. Graph showing the prolonged state of arrested larval development of *Sphex harrisi* (Fernald). The cocoons were collected on October 26, 1954.

Sphex harrisi has been observed to undergo arrested development and apparently has one generation per year in Hawaii. This wasp constructs its nest in small cavities such as those found in the cut end of the petiole of the papaya plant, *Carica papaya* L.; in burrows of abandoned nests of the carpenter bee, *Xylocopa varipuncta* Patton; and in cavities found in dried leaves of the hala (*Pandanus odoratissimus*). The nest, which is lined with small, dry, shreds of grass, is first filled with paralyzed grasshoppers, *Conocephalus saltator* (Saussure). The female of this mass-provisioning wasp then lays an egg on the pleural region of one of the grasshoppers and then the cavity containing the nest is plugged with additional shreds of dried grass. The egg hatches in about 3 days and the larva immediately begins to feed voraciously on the grasshoppers. After 4 to 6 days the fully grown larva, which has a fat engorged appearance, spins a cocoon covered with silken threads and then goes into diapause. Records on the duration of diapause obtained by collecting cocoons on October 26, 1953 are shown in figure 1. It may be noted that adult emergence began in April of the following year and continued until November. The duration of the larval point, therefore, ranged from 6 to 13 months.

The largest number of individuals emerged 9 months after the cocoons were collected. Suehiro (1937) reported that the larva remained in the cocoon for as long as one and one-half years.

That the wasp did not enter diapause in the pupal stage was indicated by opening periodically a few cocoons. Cocoons opened 6 months after collection still contained larvae in an inactive state; those opened 2 months later still contained inactive larvae, but at this time the larvae were found to be wrinkled and flaccid and did not have that engorged appearance which is characteristic of larvae soon after entering diapause. In nearly all cases the larvae in the opened cocoons died and hence were not included in the emergence data.

On the basis of these data and on observations made in different localities and at different times by Swezey (1933, 1947), Williams (1935), Ehrhorn (1937) and Suehiro (1937) it is possible to reconstruct the seasonal life history of *S. harrisi*. The building of the nest, provisioning of the nest with food, and egg laying take place during the fall months. The larvae are fully grown in about 7 to 9 days. These fully grown larvae enter diapause for periods of 7 to 12 months or longer. Adult emergence commences during the spring months and extends into the winter months of the following year.

Sceliphron caementarium, the mud dauber, is another solitary wasp that hibernates in Hawaii. It builds mud nests under the eaves of buildings, wooden flumes, and wooden or concrete bridges. Swezey (1906) reported that in Hawaii this species hibernates in much the same way as it does in the mainland United States. Hibernating larvae have been found in the cells of the mud nest.

Social wasps. The social wasps which undergo arrested development are *Polistes fuscatus aurifer* Saussure, *P. macaensis* (Fabricius), *P. olivaceus* (De Geer), and *Vespa pensylvanica* (Saussure).

The *Polistes* wasps have similar biologies. The adults are predaceous on various caterpillars and may be seen among herbaceous weeds and leafy vegetable crops hunting for food. The young larvae of the wasps are fed periodically with nectar and honey dew, but the older ones are fed masticated caterpillars.

The paper nests are attached under the eaves and rafters of buildings, under bridges, flumes, and on the lower surface of dried leaves of plants such as banana, *Musa paradisiaca* L.; sugar cane, *Saccharum officinarum* L.; and hala, *Pandanus odoratissimus* L. f. The twigs of the lantana, *Lantana camara* L., and the kiawe, *Prosopis chilensis* (Mol.) Stuntz are also favorite nesting sites of these wasps. During the spring months the nests are very small consisting of only one or two cells. On such nests only one or two females may be seen. Later in the season after the emergence of several broods both the nest and the colony attain considerable size. When fall comes they cease to reproduce and hibernate. They often form aggregations in large numbers under the eaves of houses, barns, garages and other suitable places. The wasps in aggregation are sluggish and are not vicious as when they are perched on their nests tending to their young. When disturbed they disperse, but they soon return to the same site where they aggregate again. Apparently not all individuals are involved in this aggregating habit because some individuals may be seen among various plants during the winter months. Williams (1931) observed that in a few instances *P. macaensis* and *P. olivaceus* form aggregations also during mid summer. Evidently there are forms which aggregate during summer and also those which aggregate in winter.

Vespa pensylvanica, the yellow jacket, is another social wasp that apparently hibernates in Hawaii. This is a ground nesting wasp which constructs paper nests in cavities in the ground. Williams (1927) reported that this species occurs at elevations ranging from 3,500 to 4,000 feet. On the island of Kauai, he found on January 1919 a queen of this wasp under a log apparently in hibernation.

Parasites of fruit flies. Included in this group are five species of Opiinae, *Opius fullawayi* (Silvestri), *O. tryoni* (Cameron), *Opius compensans* (Silvestri), *O. formosanus* Fullaway, and *O. watersi* Fullaway. All of these are beneficial insects which were introduced purposely for the control of the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann; the oriental fruit fly, *Dacus dorsalis* Hendel; and the melon fly, *D. cucurbitae* Coquillett.

Opius fullawayi and *O. tryoni* were introduced to control the Mediterranean fruit fly. The females of these two species oviposit in the larvae of this fruit fly. The development of the larvae hatching from these eggs takes place within the host larvae and the adult parasites emerge after the pupation of the host. During the course of their investigations on the evaluation of the effectiveness of these two parasites, Pemberton, Willard, and Back (1918) found that the period between oviposition and emergence of the adult parasites was highly variable because a certain proportion of the parasites hibernated.

Opius tryoni normally pupated 8-9 days after the host pupated and the adult emerged 5-8 days later. However, because a certain proportion of the larvae hibernated within the host puparia some did not emerge for as long as a year. Although hibernation occurred throughout the year, the greatest proportion went into hibernation during the winter months and the least during the summer. Adult emergence from those hibernating larvae was greatest during the spring and early summer months.

The hibernating behavior of *O. fullawayi* was reported to be similar to that of *O. tryoni*. However, in the case of *O. fullawayi* the proportion of hibernating larvae was less than that of *O. tryoni* and the period of hibernation was also of shorter duration. As in the case of *O. tryoni* the proportion entering hibernation was highest during the winter and least during the summer months. Adult emergence was highest during the spring months.

Although this paper is not concerned with the factors inducing arrested development it might be of interest to cite the observations of Pemberton and Willard. They reported that the hibernation of *O. tryoni* and *O. fullawayi* was induced by (1) low temperature and (2) an unknown factor. When parasitized Mediterranean fruit fly larvae were subjected to temperatures of 74-78° F., the proportion going into hibernation was less than 1.4 percent. However, when exposed to temperatures of 60-64° F., the percentage was 67.7. These figures indicate the association between hibernation and low temperature. That another unknown factor existed was indicated by observations made on host larvae pupating in sand or soil and in dry glass vials. The percent of parasites undergoing hibernation in the host which pupated in sand or soil was greater than that in the host which pupated in glass vials.

In addition to the two species of *Opius* already discussed, three other species have been observed to undergo arrested development. *Opius compensans* and *O. formosanus,* imported parasites of the oriental fruit fly, were reported by Christenson (1953) to undergo diapause when subjected to reduced temperatures in the laboratory. Marucci (1952) observed that *O. watersi,* a parasite of the melon fly, entered diapause when released on the University of Hawaii campus. During November and December of 1950, approximately three months after release, Marucci found 50 percent of the parasite larvae in diapause. The insect remained in diapause for over three months. For reasons not known at present this parasite failed to become established in Hawaii.

Coleoptera

The mango seed weevil, *Cryptorhynchus mangiferae* (Fab.) is a common insect in Hawaii. During the spring and summer months the females lay eggs in young mango fruits, *Mangifera indica.* The larvae develop and pupate within the seed, and the adults emerge after the fruit ripens and falls to the ground. During the winter months after the mango season is over it has been reported that the adults become inactive and hibernate in crevices of boards, fences, and stone walls (Fullaway and Krauss, 1945).

Lepidoptera

The Board of Agriculture and Forestry, Territory of Hawaii, imported a moth, *Depressaria umbellana* Stephens, from England to control gorse, *Ulex europaeus,* which is a pest of rangelands. In the quarantine room, this moth remained on the host plant clustered in an inactive state along the main axis of the inflorescence during the winter months, apparently in diapause. When disturbed the moths flew against the walls of the cages but soon returned to their original resting sites (Chock, 1954).

Discussion

Although the information presented is fragmentary and incomplete, there is evidence which shows that there are insects that do not reproduce continuously throughout the year in Hawaii because they undergo a prolonged state of arrested development during certain times of the year. These insects appear to have annual developmental cycles characteristic of heterodynamic species.

The type of arrested development with which we are concerned in Hawaii needs elucidation. Some authors have used the term hibernation while others have used diapause in reference to the arrested development that they observed. In the preceding pages the present writer used, where possible, the same term as that used by the authors cited which no doubt created some confusion. Another confusing aspect is the synonymous use of the terms diapause and hibernation by certain authors. Again, hibernation has been used by others to denote any state of inactivity during winter. It is, therefore, difficult to be certain as to the specific type of arrest when the term hibernation is used.[2] A study of the cases of arrested development reported from Hawaii yields the following information: (1) arrest of development generally begins during the fall and winter and ends during the spring, summer or fall of the following year, (2) there is relatively small seasonal fluctuations in environmental conditions associated with arrested development, (3) the species involved are all immigrant insects from a more temperate area than Hawaii, (4) arrest of development occurs during immature and adult stages. These findings, when considered in the light of the known features of the phenomenon of diapause, indicate that all cases of arrested development reported from Hawaii represent diapause.

In agreement with the findings of other workers elsewhere, the current observations made in Hawaii indicate the variability among insects in their responses toward stimuli which induce diapause. In Hawaii there are immigrant insects which undergo diapause and those which do not even though the latter are known to do so in temperate areas. According to Dickson (1949) it is possible to divide insects inherently capable of undergoing diapause into two groups on the basis of whether or not a specific stimulus or combination of stimuli is required for the induction of diapause: (1) species that enter diapause each generation. Diapause in these insects may be induced apparently by any condition which permits the survival of the species, and (2) insects that undergo diapause only under the stimulus of certain factors or combination of factors in the environment such as temperature, moisture, food, and photoperiod. The insects which enter diapause in Hawaii under natural conditions cannot be placed with certainty in any one of these categories on the basis of the available information. However, if we consider the relatively stable conditions of the environment as compared to temperate regions, it seems that they may be logically placed in the first category. These species, displaced from their native habitats, are undoubtedly undergoing diapause in response to one or more stimuli provided by the Hawaiian environment, although teleologically speaking, there seems to be no necessity for it. Whether or not they are responding to the same stimuli as those of their original habitat is unknown. On the other hand, those immigrant insects which undergo diapause elsewhere but do not do so in Hawaii evidently belong in the second category. Obviously, there is no stimulus in Hawaii to induce them to undergo diapause.

The food habits of insects undergoing diapause in Hawaii might be worthy of comment. Among the 16 species listed, 14 are predaceous and two phytophagous. This preponderance of insects with predaceous food habit seems to be more than a fortuitous occurrence.

Further studies on this subject might reveal other interesting information. They might reveal that the general phenomenon of arrested development might be more prevalent than it appears from this preliminary treatment of the subject. Furthermore, such studies might show the

[2] Shelford (1929) pointed out that the terms depicting arrested development have been loosely used in the literature and made suggestions in terminology.

occurrence of other types of arrested development. At the present time there is little or no information on arrested development from areas of extreme environmental changes such as from the tops of high mountains under nearly temperate conditions and from the low, dry leeward areas which receive but small quantities of seasonal rainfall. Such studies might also bring to light the reason for the periodic outbreaks of certain insects which appear to occur without apparent reason. Further knowledge of the phenomenon of arrested development might conceivably be of value in biological control projects which involve the importation of beneficial insects from various parts of the world to control weed as well as insect pests.

Summary

The known cases of arrested development in Hawaii are recorded in this paper. The insects concerned are represented in the Hymenoptera, Coleoptera, and Lepidoptera. There are 14 species in the Hymenoptera and one each in the Coleoptera and Lepidoptera. The available information indicates that these insects do not reproduce continuously throughout the year because of a prolonged period of arrested development even though climatic conditions appear to be favorable throughout the year. Hence, they possess annual developmental cycles characteristic of the heterodynamic type of Roubaud (1922). On the basis of the biologic information of the species concerned and on the known characteristics of the phenomenon of diapause it appears that all cases of arrested development recorded to date represent diapause. Some of the features of diapause which might be of biological interest are discussed.

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