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Evolutionary Dynamics of Behavioral Divergence among Populations of the Hawaiian Cave-dwelling Planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae)[1]

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ABSTRACT: The cixiid genus *Oliarus* has undergone extensive adaptive radiation on the Hawaiian Islands, with 80 described endemic species descending from an initial successful colonization by a single ancestral species. In Hawaiian *Oliarus*, however, adaptive radiation is not restricted to surface habitats. Several evolutionary lines have invaded lava tubes independently on the islands of Molokai, Maui, and Hawaii. Populations of one of the cave invasions on the island of Hawaii, the blind, flightless, and pigmentless species *Oliarus polyphemus* Fennah, have been found in numerous lava tubes within four of the five volcanoes on the island. Recent investigations on mating behavior, especially the analysis of the substrate-borne courtship signals of several *O. polyphemus* populations, revealed a high degree of divergence: the signals of all seven cave populations studied differ significantly. Because these signals serve for mate recognition within species of planthoppers, we regard the *O. polyphemus* populations studied to be reproductively isolated (i.e., representing separate biological species). Hypotheses to explain this high degree of divergence among *O. polyphemus* populations are discussed.

ONE OF HAWAII'S most intriguing ecosystems is found in lava tubes that have been (and still are being) formed by volcanism. Within these lava tubes a remarkably adapted fauna has been discovered during the last 20 yr, mainly by F. G. Howarth, F. D. Stone, and collaborators (Howarth 1987). Among the important elements of this fauna are the cave-adapted and morphologically highly modified planthoppers of the genus *Oliarus* in the family Cixiidae. *Oliarus polyphemus* Fennah from lava tubes on the island of Hawaii displays the troglomorphies typical for obligately cavernicolous insects, namely reduction of eyes, wings, and pigment (Figure 1*A*).

As is common for Hawaiian cave organisms, close relatives of the cave-adapted *Oliarus* species are still extant on the surface (Howarth 1981*a*). The genus *Oliarus* is represented on the surface on all major islands with about 80 endemic species and subspecies (Giffard 1925, Zimmerman 1948, Nishida 1992). Apparently this species richness is the result of intensive adaptive radiation after the successful colonization of a single ancestral species. Epigean *Oliarus* species are characterized by large compound eyes, long wings, and dark pigmentation (Figure 1*B*).

Howarth (1986) has shown that in Hawaiian *Oliarus* adaptive radiation is not restricted to surface habitats. We now know of six separate evolutionary lines that have invaded caves independently: one on Molokai, three on Maui, and at least two on the island of Hawaii (unpublished data). All of these are

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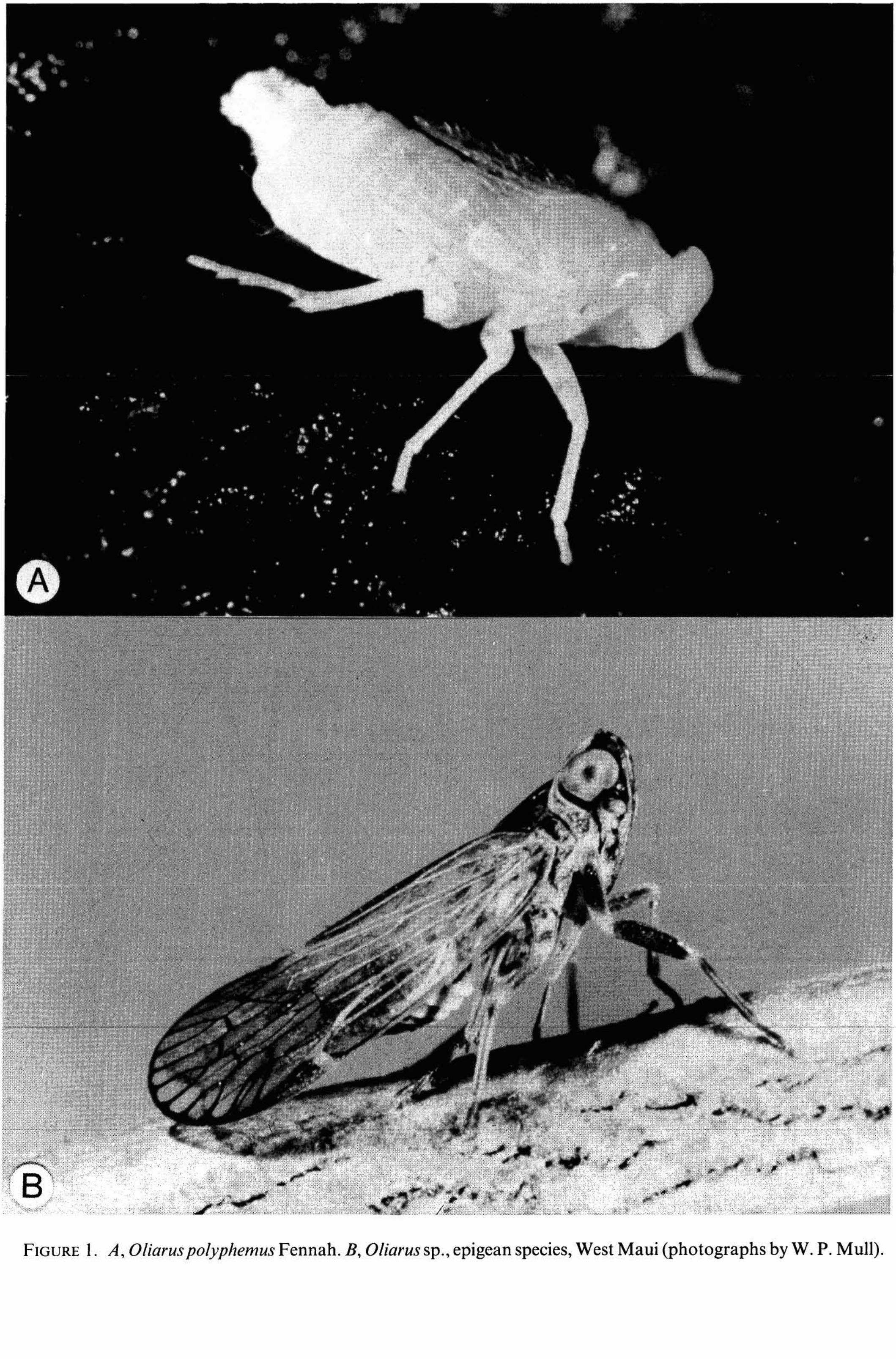

FIGURE 1. *A*, *Oliarus polyphemus* Fennah. *B*, *Oliarus* sp., epigean species, West Maui (photographs by W. P. Mull).

obligate cave dwellers, confined to a life underground.

Our work on cave-dwelling *Oliarus* has focused on the behavioral ecology of one of the evolutionary lines on the island of Hawaii, *O. polyphemus*. Populations of *O. polyphemus* are known to exist in many lava tubes on Hawaii Island, in lava flows of all major volcanoes except Kohala, and from sea level to over 2000 m elevation. It was believed to be the most widespread obligate cave species in Hawaii, with underground dispersal maintaining gene flow via the mesocavernous rock system (Howarth 1983), a labyrinth of voids and cracks that exists in young basalt (*milieu souterrain*: Juberthie et al. 1980). Nymphs and adults of cave-dwelling *Oliarus* feed on roots of native Hawaiian trees, especially *Metrosideros polymorpha* Gaud. (Myrtaceae), which is a very successful pioneer plant on young lava flows (Howarth 1986).

Because of the high evaporation rate, young lava flows are dry on the surface, and pioneering plants experience extreme water stress. To obtain essential amounts of moisture, colonizing plants must send their roots deep into the lava. In fact, a lava flow appearing quite bare on the surface, with only a few tiny shrubs, can have curtains of abundant roots dangling into the caves, 10 m or more beneath the ground. These roots provide an enormous food resource for animals that are able to exploit them. Howarth (1986) considered the exploitation of this food resource to be the driving force for the evolution of cave-adapted planthoppers. However, to be able to utilize these resources, an animal must manage to cope with the ecological conditions within these lava tubes: permanent darkness, constant temperature, and constantly high humidity close to saturation (Howarth 1983).

To meet the challenges of this seemingly hostile environment requires adaptations in physiology and behavior. A substantial body of research has been done concerning physiological adaptations in cave organisms (e.g., Hadley et al. 1981, Ahearn and Howarth 1982, Hüppop 1986), but very few investigations have focused on behavioral changes during cave adaptation, especially of arthropods (e.g., Juberthie-Jupeau 1988).

Intraspecific Communication and Evolutionary Divergence in Oliarus polyphemus *Populations*

Assuming that behavioral adaptations to the underground environment (e.g., for mate location and recognition) may have played an important role in the evolution of cave species, we concentrated on acoustic communication, which is a crucial component of the planthoppers' courtship behavior (Claridge 1985). In epigean leafhoppers and planthoppers, "sounds" are produced by specialized structures located in the first two abdominal segments, the tymbal (Ossiannilsson 1949). In contrast to the well-known songs of cicadas, the sounds produced by leafhoppers and planthoppers are not transmitted via the air, but via the substrate, which is usually the food plant (Ichikawa 1976). These vibrational signals are of low frequency, between 100 and 2000 Hz, with a maximum energy at 100–500 Hz (de Vrijer 1984). The songs serve as species recognition signals (e.g., Claridge 1985). They differ significantly in groups of morphologically similar, but separate species (e.g., Claridge and Reynolds 1973, Booij 1982, Strübing 1983). By this they help to prevent interspecific matings, resulting in species isolation (Claridge 1985).

From previous work we knew that Hawaiian cave planthoppers retain the same communication mechanism (substrate-borne vibrations) as the surface-dwelling Fulgoroidea (Howarth et al. 1990). Field experiments revealed that this communication system is extraordinarily efficient in the natural environment of the cave planthoppers: signals were found to be transmitted along single root strings over distances of a few meters, and even between roots (via rootlets branching off the main root strings and touching each other), apparently without substantial loss of information content (Moore et al., in press).

We also discovered that the calling signals from the *O. polyphemus* population from Kaumana Cave (eastern Mauna Loa) are distinct from those of an *O. polyphemus* population from Pahoa Cave (eastern Kilauea). Preliminary playback experiments provided evidence for the presence of premating isolation barriers, leading to the assumption that the song differences between populations from Pahoa and Kaumana caves are not due to geographical variation, but more likely to divergence processes (i.e., they were regarded as cryptic acoustical species [Howarth et al. 1990]).

To obtain clues for understanding the evolutionary history of cave adaptation as well as of divergence events in *O. polyphemus* populations, our study focused on the analysis of courtship characteristics and on the degree of variation of calling signals both within and among populations. In addition, information on life history and population density was obtained from observations in the field and in the laboratory.

MATERIALS AND METHODS

Sampling and Rearing

Fifth-instar nymphs of *O. polyphemus* were obtained from the caves and transported to the laboratory along with samples of *M. polymorpha* roots under simulated cave conditions (see Howarth 1979). In the laboratory, fresh sprouts of soybeans proved to be a suitable food substitute for *M. polymorpha* roots, which were not readily available. Five to seven immatures were kept in rearing cages lined with moist filter paper and containing a small quantity of sprouts. The insects were kept under conditions similar to those in their natural environment (complete darkness, constant temperature: 18°C) in the facilities of the Hawaiian Drosophila Stock Center, University of Hawaii at Manoa, Honolulu. Freshly molted adults were separated and caged individually to obtain unmated adults for behavioral studies.

Measuring Population Density and Monitoring Population Dynamics

For the *O. polyphemus* population from Pahoa Cave, population density estimates were obtained by correlating the average number of *O. polyphemus* individuals counted (all instars) with the average surface area of available roots of a given part of the cave. A cave passage with abundant *M. polymorpha* roots ("Rich Root Room") known to house an established *O. polyphemus* population was selected as the study area. The passage is ca. 50 m long, ca. 10 m wide, and 1.70–2.50 m high. *Oliarus polyphemus* individuals were categorized either as small nymphs (sn, instars I–III), large nymphs (ln, instars IV–V), or adult males/females. To obtain preliminary data on the dynamics of the population, a total of four counts was made at various intervals over a period of 3 months (November 1989 to January 1990). During the monitoring period, no samples were taken.

Recording

The courtship signals of *O. polyphemus* males and females from the following lava tubes were recorded: Kaumana Cave, Lanikai Cave (Mauna Loa), Pahoa Cave, MacKenzie Park Cave, Doc Bellou Cave, Ainahou Cave (Kilauea). Only male calls were recorded from the *O. polyphemus* population from Pink Pistillaria Cave (Hualalai).

To record the vibrational communication signals, the magneto-dynamic system (Strübing and Rollenhagen 1988) was used, which operates on the principle of electromagnetic induction: with the help of a small magnet, mechanical oscillations (caused by a "singing" insect and transferred to the substrate via its legs) are transformed by an induction coil into electrical oscillations, which are then recorded on tape. Because the natural substrate (living *M. polymorpha* roots) and also the substitute soybean sprouts were unsuited for standardized laboratory experiments, the test insects were placed on a small balsa-wood board (1 by 5 cm by 1 mm) to which the magnet was attached. To obtain recordings of courtship signals, a male and female were placed together in a glass tube (ca. 4 cm by ca. 8 cm high).

To obtain a representative sample size, we attempted to record at least 5–10 individuals of each sex per population (five calls per individual). This was achieved for the *O. polyphemus* populations from Kaumana and Pahoa caves; from other populations the calls of fewer individuals were recorded. The following parameters of the calls were analyzed: general song pattern (time-dependent amplitude modulation), call duration, number of pulses per call, and interpulse interval (=time interval between successive pulses). Recordings and analyses were made at the laboratory facilities of the Hawaiian Evolutionary Biology Program at the University of Hawaii at Manoa, Honolulu. Equipment used for recording and analysis of calling signals was as follows: Philips D 6920 AV MK 2 and Sony TC-D 5 M (stereo-cassette recorders), a Tectronix Digital Oscilloscope, and a Kay Sonagraph.

RESULTS

Life History

Fifth-instar nymphs brought to the laboratory from the field took up to 151 days before the adult molt (Table 1). Some fifth-instar nymphs move away from roots (see below) and make separate wax cocoons in which they remain about 7 days while metamorphosing to the adult stage (Howarth 1981*b*). In the field, these cocoons, each usually with its cast nymphal skin, are commonly seen in small cavities on the cave wall. This behavior was not observed in our laboratory studies. In both males and females, reproductive activity (equals calling activity) started on an average of 7–10 days after the adult molt and persisted up to 51 days (males). Adult males survived up to 122 days, but females generally experienced a shorter life span (up to 70 days). Eggs were deposited 4–14 days after copulation (Kaumana Cave: 4–5 days, $n = 2$; Pahoa Cave: 7–10 days, $n = 2$; MacKenzie Park Cave: 10–14 days, $n = 2$); they were laid in batches of up to 10 in wax "nests" on roots. These nests are formed by wax filaments secreted from wax glands on the female's ninth tergite and wiped off with the hind legs (observed in a female from Kaumana Cave). Another female from Kaumana Cave was observed to insert parts of her ovipositor (gonapophyses VIII and median gonapophyses IX) deep into the substrate.

First-instar nymphs hatched 70–74 days after oviposition and lived up to 30–32 days before they molted to second instar. Field observations revealed that all instars could be found throughout the year: reproduction is apparently asynchronous. Our data provide evidence that generation time in *O. polyphemus* populations is ca. 12 months (Table 1). Because comparable data for epigean cixiid species are scarce (e.g., Müller 1942, Reinert 1980), we cannot yet determine whether *O. polyphemus* populations follow the life history pattern of K-selected organisms (as is characteristic for obligate cave dwellers) (e.g., delayed reproduction, increased longevity, and smaller total number of eggs produced [Culver 1982]).

Population Density

The average number of *O. polyphemus* individuals (comprising all instars) observed in the study area ("Rich Root Room") was 184 (Table 2). This part of the cave passage contained an estimated 1000 *M. polymorpha* roots, each consisting of a main root string and numerous rootlets branching off laterally from the main string. The surface of single roots (main string: ca. 2 m in length and ca. 4 mm in diameter, plus the total surface of ca. 200 rootlets: 0.1 m in length and ca. 1 mm in

TABLE 1

DURATION IN DAYS OF THE LIFE STAGES OF *Oliarus polyphemus*

	NYMPHAL INSTARS							LIFE SPAN	
EGG	I	II	III	IV	V	PREADULT	PREMATING	♂	♀
70–74	30–32	?	?	?	≤151	ca. 7	7–10	122	70

TABLE 2

NUMBER OF *Oliarus polyphemus* INDIVIDUALS OBSERVED IN THE "RICH ROOT ROOM," PAHOA CAVE

		O. polyphemus			
Date	*n*	sn	ln	am	af
7 November 1989	124	63	60	—	1
23 December 1989	221	74	142	3	2
11 January 1990	190	77	110	2	1
26 January 1990	200	72	126	2	—

NOTE: Average number (±1 SD) of individuals observed on each date, 184 (±42). sn, small nymphs (instars I–III); ln, large nymphs (instars IV–V); am, adult males; af, adult females; *n*, total number of individuals.

diameter) averages 0.08792 m^2; thus the total root surface of the study area was 87.92 m^2. The estimated population density is one *O. polyphemus* individual per 0.47 m^2 root surface, or about two *O. polyphemus* individuals per 1 m^2 root surface, respectively.

The population in this room appears high compared with that observed in other passages in Pahoa Cave and in most other caves. It is believed that the major part of the *O. polyphemus* population occurs in the inaccessible cracks and crevices in the lava, as indicated by the relative rarity of small nymphs.

Population Dynamics

Our data show that fourth and fifth nymphal instars represent the highest percentage of the population; adult planthoppers were scarcely observed (Table 2). Even though the nymphs build conspicuous white wax cocoons in which they remain while feeding, larger nymphs with their larger cocoons are easier to see on roots. Nymphs are vulnerable to disturbance and are easily dislodged from their feeding sites, especially by water drops and potential predators. Smaller nymphs are more vulnerable and less dispersive than larger nymphs and probably remain in protected root sites near their place of hatching. Larger nymphs disperse along roots and can colonize more exposed sites. The rarity of adults could be due either to a high nymphal mortality during the last instars or to emigration of adults immediately after the molt. There is evidence for both assumptions: the last (fifth) nymphal instar is indeed a critical phase because of its long duration and the subsequent molt, during which the animals are exposed to a high risk of predation. On the other hand, there is also evidence for the rapid dispersal of *O. polyphemus* individuals (see *Discussion*). The great majority of observed *O. polyphemus* individuals was observed on root substrates. Individuals observed on rocky substrates were mostly fifth-instar nymphs ready to molt. Older fifth-instar nymphs tend to leave the roots and move to a protected area (cavities in the cave walls) to transform into adults, presumably to avoid predation. Observations in the laboratory also revealed that the structured surface of basaltic rock seemed to provide a more suitable substrate to cast the nymphal skin than did the smooth surface of roots.

Reproductive Behavior

When first placed into the recording tube but before the onset of acoustic communication, males and females showed escape reaction on random encounter. This is apparently due to nonrecognition of a conspecific potential mate caused by the absence of visual and chemical recognition clues. Only when one partner was responding to the initial signaling by the other (usually the female, see below) was the escape reaction suppressed and the actual courtship phase commenced. This phase usually lasted for ca. 1 hr and ended with copulation. In the majority of observed courtships, the female initiated calling and throughout the courtship phase remained the more "song-active" partner. During the entire courtship phase, the female remained on one spot and kept calling consistently every few seconds. A male perceiving her calls would start trying to locate the calling female by "trial and error" orientation movements, only occasionally responding to the female's calls. In none of the observed cases was a "song-active" female observed to reject a responding male or to show escape reaction during male mating attempts. Once copulation was initiated, both sexes stopped calling. Observed copulations lasted 36–57 min (Kaumana Cave: 36–38, $n = 2$; Pahoa Cave: 49–57, $n = 2$; MacKenzie Park Cave: 36–41, $n = 2$; Doc Bellou Cave: 40, $n = 1$). In the laboratory we did not observe multiple matings in males or females. We do not know, however, whether or not they occur in the planthoppers' natural environment.

Change of Courtship Pattern: A Behavioral Adaptation?

An important question from the viewpoint of an evolutionary biologist is whether and how patterns of mating behavior change during adaptation to a permanent life underground. All epigean *Oliarus* species display well-developed compound eyes, which makes a visual component during certain phases of courtship at least likely. In contrast, *O. polyphemus* is completely eyeless. Because so far there is no confirmation for chemical communication (e.g., by pheromones) in planthoppers, we can assume that in troglobitic cixiids, substrate vibrations are the most important (if not the only) means by which potential mates can recognize each other.

It is remarkable that in nearly all cases observed the female initiated calling, was the more song-active partner throughout the courtship, and never rejected a responding male that had successfully located her. This behavior strongly differs from observations made in epigean planthoppers (e.g., of the family Delphacidae). There usually the males initiate calling, and in the genus *Javesella* Fennah were observed to emit a few successive calls, then stopped calling for a variable length of time, walked off the grass stem, and produced a new series of calling signals when they were placed back on a grass stem. In the field, this calling strategy is probably used by males to acoustically explore the usually dense vegetation (e.g., grasses) that forms their natural environment to find receptive females (de Vrijer 1986).

To confirm whether the switch to female calling occurred before or during cave adaptation in *O. polyphemus* we need to record the singing behavior of its epigean relatives. In any case, the altered behavior of cave-dwelling *O. polyphemus* could be a strategy to economize mate location. The fact that song-active females, in nearly all cases observed, accepted responding males for copulation indicates that song activity in females is strongly correlated with receptiveness. Consequently, males only (are aware of and) respond to females that are ready to mate, and invest less energy in exploring the environment acoustically, but may instead be able to search a wider area for receptive females. The apparent low motility of the female during courtship makes it easier for the male to locate her. The low motility of females may also minimize predation risk.

Variation of Courtship Signals in and among Populations

In all populations tested, the general call pattern of males and females was similar: calls consisted of more or less homogeneous pulse trains. The structure of calls changed as the individual matured (Figure 2): males from Kaumana Cave were observed to produce their first calls 2 to 3 days after molting. These signals were structurally different from those of mature males. These calls apparently do not indicate courtship behavior; their irregularity is likely to stem from the still insufficiently sclerotized structures of the sound-producing organ. From approximately the seventh day after molting, the calls were fully developed and remained more or less constant throughout the reproductive phase. Within populations, calls of males and females showed a comparatively small range of variation (Figure 3). Variable parameters were call duration and number of pulses per call.

Remarkably, variation was highest among *O. polyphemus* populations from different lava tubes (Figure 4). The parameters concerned were call duration and interpulse interval. The calls of males and females from the *O. polyphemus* populations from Kaumana and Pahoa caves were found to differ significantly in these parameters (Figures 5, 6). Preliminary playback experiments revealed that males from Kaumana and Pahoa caves

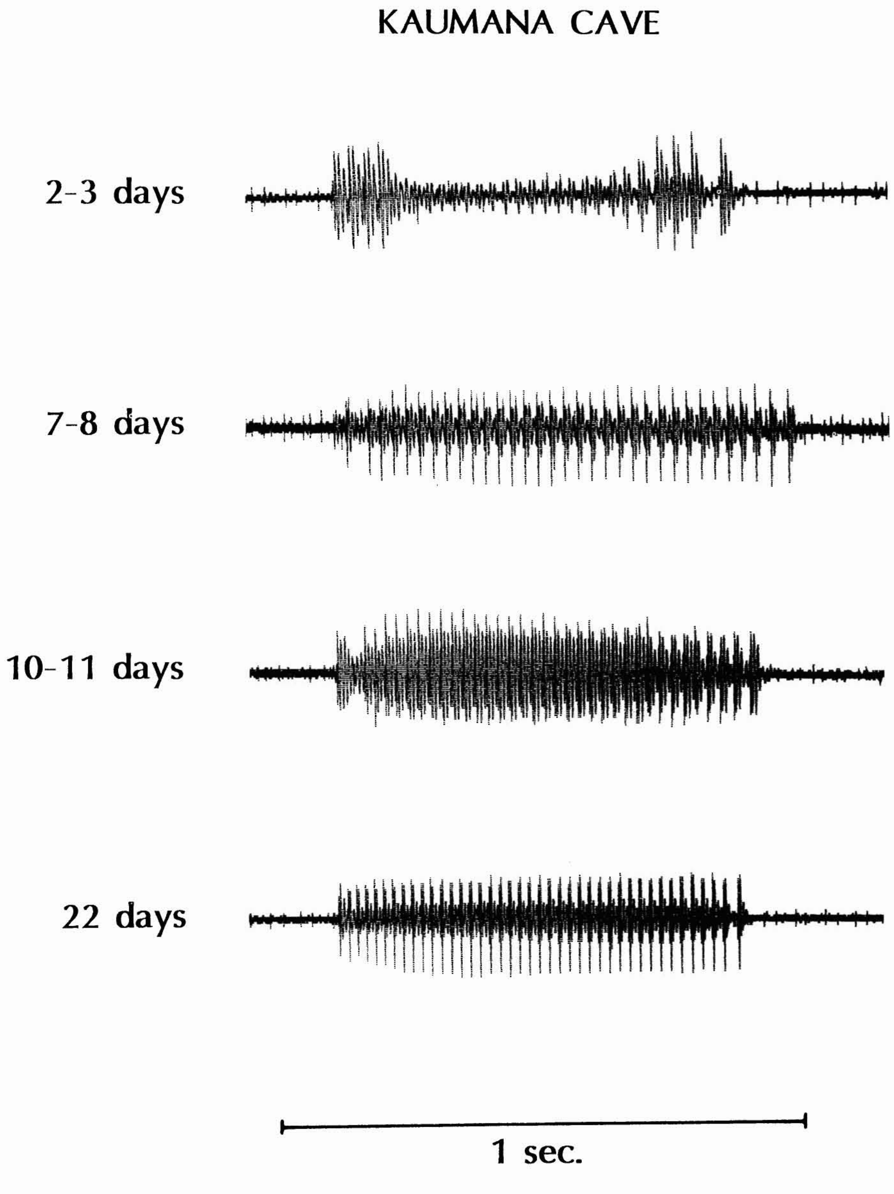

FIGURE 2. Change of call structure of an *Oliarus polyphemus* male from Kaumana Cave, Hawaii Island, in correlation with individual age.

showed high preference in "responding" to calls of females from their own populations.

In one of the caves, Pink Pistillaria Cave (Hualalai Volcano), we found two distinct call patterns (Figure 4). The individuals concerned also differed clearly in morphological traits such as body size and body proportions.

DISCUSSION

The apparent nonrecognition of courtship signals other than of individuals of the same population strongly corroborates the assumption of the existence of an effective premating isolation barrier. There is strong evidence

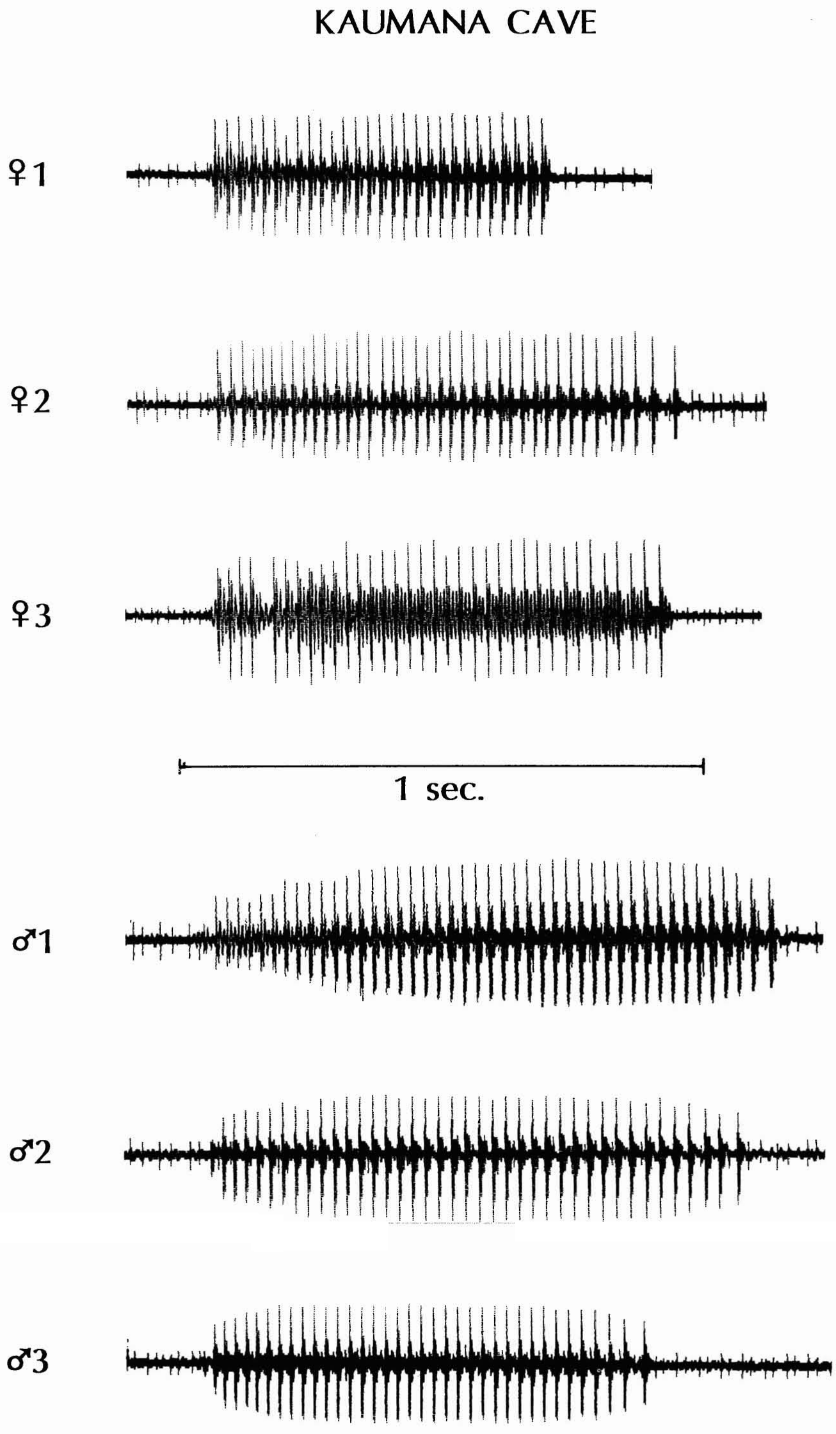

FIGURE 3. Variation of female and male calls within the *Oliarus polyphemus* population from Kaumana Cave, Hawaii Island.

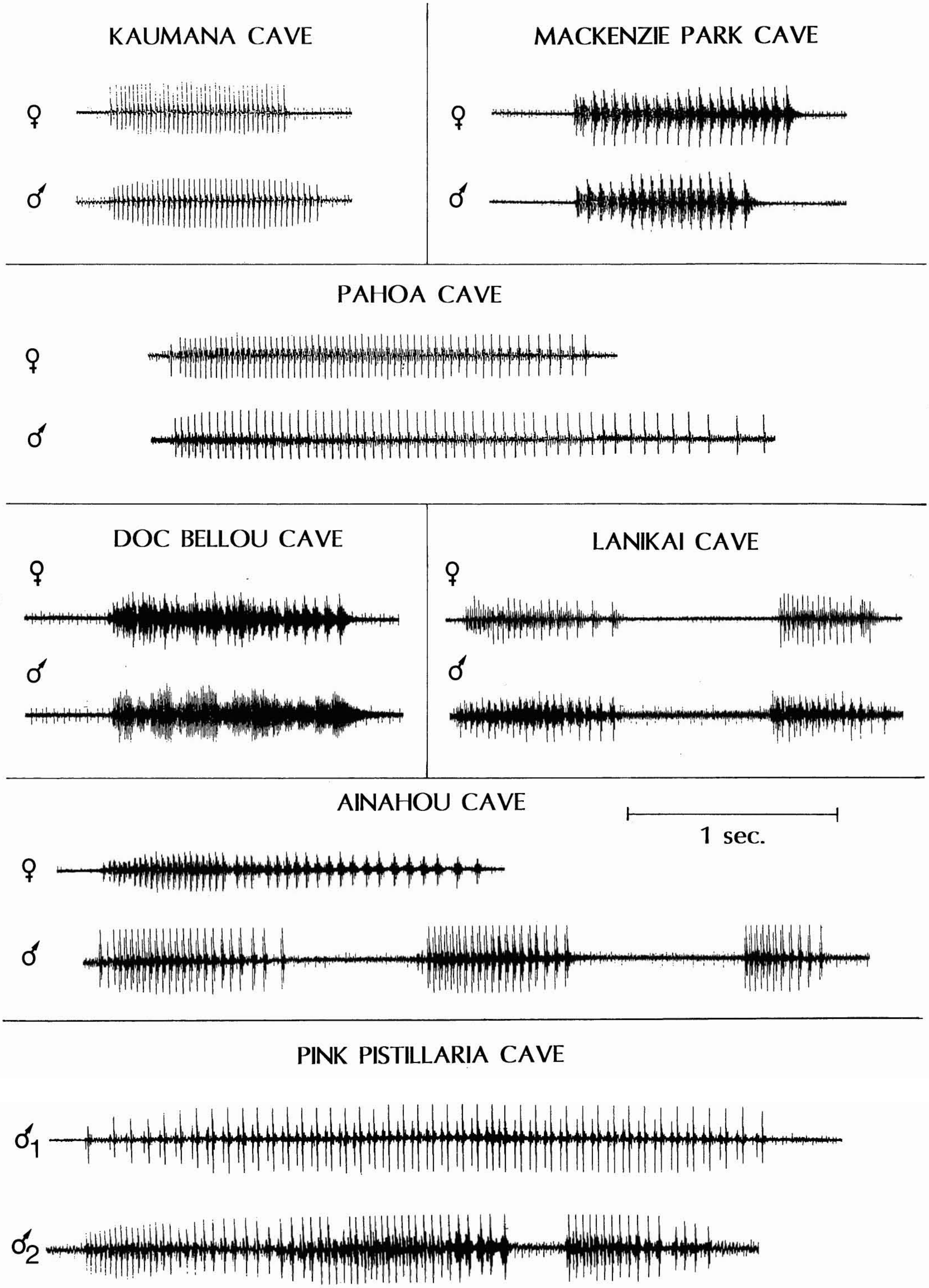

FIGURE 4. Female and male calls from *Oliarus polyphemus* populations from different lava tubes on Hawaii Island.

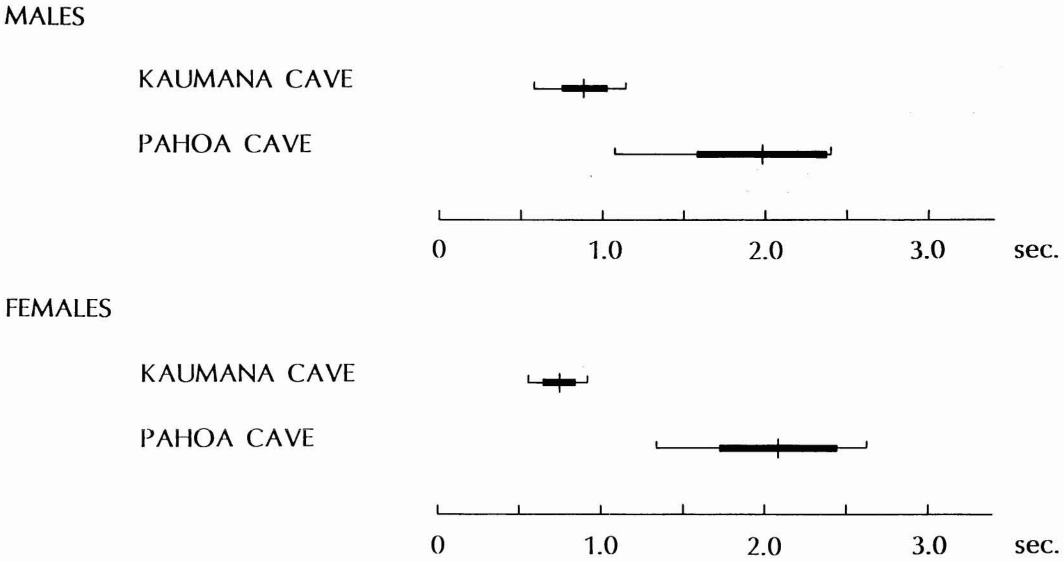

FIGURE 5. Call duration of male and female calls of *Oliarus polyphemus* populations from Kaumana and Pahoa caves, Hawaii Island. Vertical line: mean value; thin horizontal line: range of variation; thick horizontal bar: standard deviation. *N*, number of individuals; *n*, number of measured values. Kaumana males: $N = 10$, $n = 48$; Kaumana females: $N = 6$, $n = 28$; Pahoa males: $N = 6$, $n = 24$; Pahoa females: $N = 6$, $n = 29$.

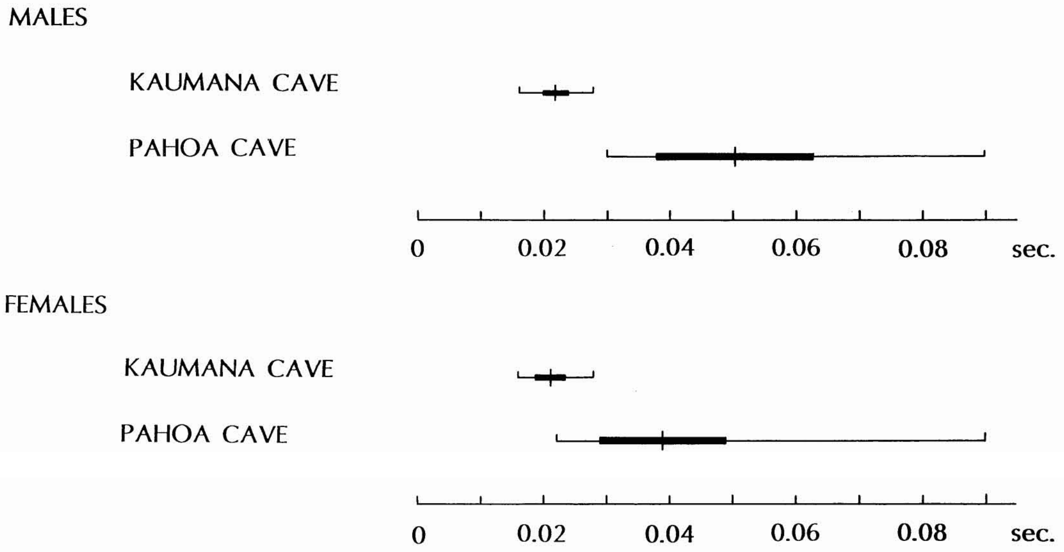

FIGURE 6. Interpulse intervals of male and female calls of *Oliarus polyphemus* populations from Kaumana and Pahoa caves, Hawaii Island. Vertical line: mean value; thin horizontal line: range of variation; thick horizontal bar: standard deviation. *N*, number of individuals; *n*, number of measured values. Kaumana males: $N = 9$, $n = 296$; Kaumana females: $N = 5$, $n = 155$; Pahoa males: $N = 5$, $n = 164$; Pahoa females: $N = 6$, $n = 185$.

that the *O. polyphemus* populations from Kaumana and Pahoa caves represent reproductively isolated units (i.e., separate species).

A similar situation is probable for the populations from the other lava tubes studied: our results provide evidence that the *O. polyphemus* populations from MacKenzie Park Cave, Doc Bellou Cave, Ainahou Cave, and Lanikai Cave each also represent separate species. These results clearly disprove the assumption of a single, widespread species: rather, *O."polyphemus"* must be regarded as a complex of morphologically similar but reproductively isolated species. The situation in Pink Pistillaria Cave (Hualalai Volcano) even supports the inference that two of these species occur sympatrically. We defer naming these as new species until we have more field data on the geographical ranges of these populations and more laboratory data on song variation and degree of isolation between adjacent populations.

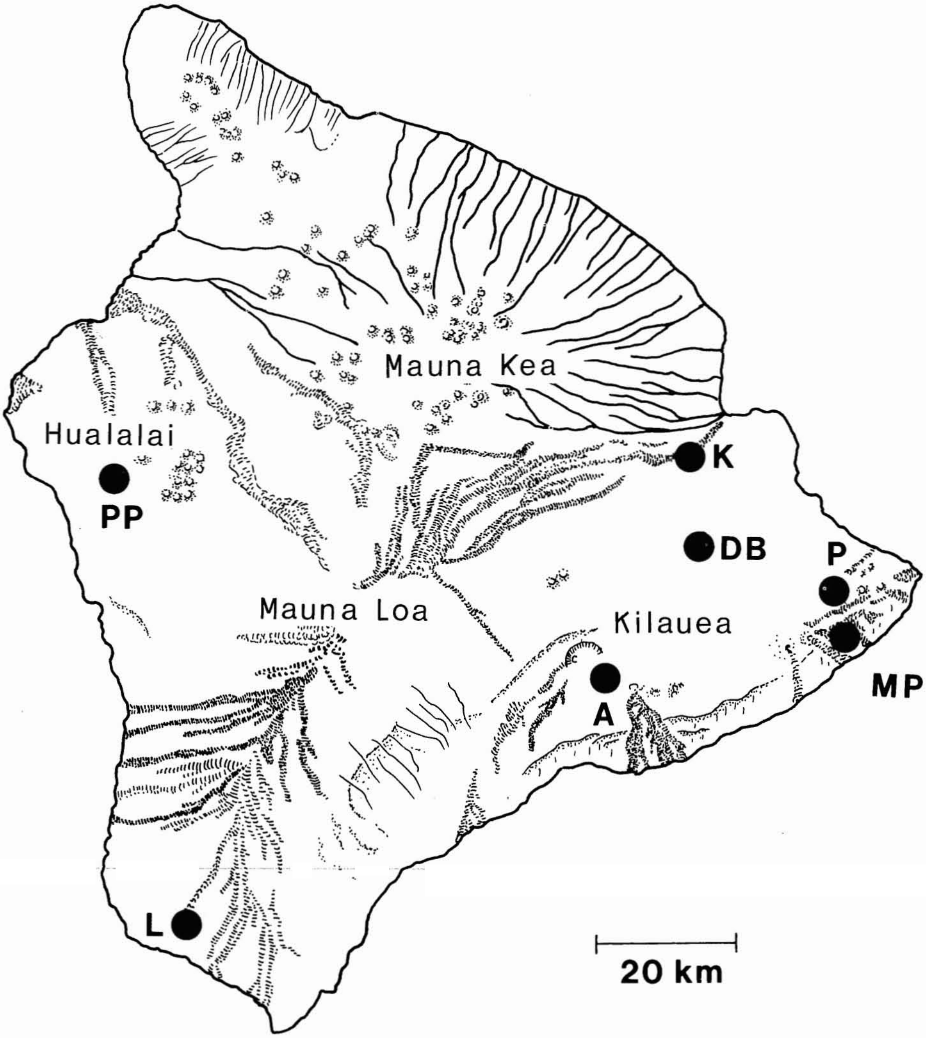

FIGURE 7. Map depicting historic lava flows on Hawaii Island and location of study sites (redrawn from Armstrong [1983]). PP, Pink Pistillaria Cave; L, Lanikai Cave; K, Kaumana Cave; A, Ainahou Cave; DB, Doc Bellou Cave; P, Pahoa Cave; MP, MacKenzie Park Cave.

The song data do not provide evidence of gene flow between caves that are only a few kilometers apart, although underground dispersal is theoretically possible through the mesocavernous rock system (Howarth 1983). For example, Pahoa Cave, Doc Bellou Cave, and MacKenzie Park Cave are located between sea level and 300 m elevation on Kilauea's East Rift and are separated at most by 20 km without obvious dispersal barriers between them (Figure 7); yet the cave planthopper songs are different in each of them.

The comparatively small range of variation of male and female calls within a population may indicate low heterozygosity or strong selection. We cannot determine from our data whether this is caused by the apparently diminished if not interrupted gene exchange between neighboring lava tubes, by the small population size (neutralistic view), by the relative environmental uniformity of the caves ("natural" selectionistic view), or by mate selection ("sexual" selectionistic view).

We do not know whether divergence occurred after a single colonization event or is the result of multiple invasions of caves by one or several epigean ancestral species. The situation in Pink Pistillaria Cave may be a hint at multiple invasions, because the fact of two species feeding on the same host makes sympatric speciation unlikely. However, it is equally conceivable that the sympatric occurrence of two species of the *O. polyphemus* complex in Pink Pistillaria Cave is the result of a secondary area of overlap (see below).

The high level of ecological and morphological conformity (in genital and external, especially troglomorphic, characters) in all *O. polyphemus* populations studied, however, is unlikely to be due to convergent evolution, and it seems plausible to assume that divergence in the *O. polyphemus* species complex may have occurred after the initial adaptive shift to the cave environment by a single ancestral species. The congruence in configuration of male genital characters suggests that the cave species may be of common ancestry with the epigean species *O. inaequalis* Giffard, a rainforest species also living on the island of Hawaii (Fennah 1973, Howarth 1993).

Oliarus polyphemus is most numerous in caves within intermediate-aged pahoehoe lava flows (i.e., from 100 to a few thousand years old [Table 3]). It becomes rare and may disappear from older caves once sufficient soil develops to prevent tree roots from penetrating into the deeper underlying rock strata. *Oliarus polyphemus* is adapted to disperse through and colonize young pahoehoe lava flows and probably colonizes available caves soon after its host, *M. polymorpha*, establishes on the flow. For example, the planthopper dispersed to the 1919 Lava Tube in Kilauea summit caldera sometime before 1980, even though the caldera floor appeared barren, with only a few small plants, mostly *M. polymorpha*, growing in widely separated cracks. Also, it had colonized Kaumana Cave, which is within the 1881 lava flow from Mauna Loa, long before its discovery there in 1972. If the

TABLE 3

Oliarus polyphemus POPULATIONS STUDIED (AGE DATA FROM HOLCOMB [1987], LOCKWOOD AND LIPMAN [1987], MOORE ET AL. [1987])

CAVE	VOLCANO	ELEVATION (IN m)	AGE (IN yr)	SURFACE ENVIRONMENT
Pink Pistillaria	Hualalai	800	Undated: >2,000	Rainforest
Lanikai	Mauna Loa	250	Undated: ca. 1,000	Early successional, dry
Kaumana	Mauna Loa	300	110	Young rainforest
Ainahou	Kilauea	900	350–500	Open mesic forest
Doc Bellou	Kilauea	350	350–450	Open rainforest
Pahoa	Kilauea	150	350–500	Open rainforest
MacKenzie Park	Kilauea	10	1,500–10,000	Coastal mesic forest

cave planthopper disperses so rapidly, why has it also rapidly diverged into separate, distinct, geographically isolated populations?

The geology of the island of Hawaii may have favored subterranean speciation processes after a single colonization event. Recent radiocarbon dating of ash layers and lava flows on Hawaii Island demonstrated that these young, active volcanoes are extremely dynamic environments: the total surface area of Mauna Loa is renewed at a rate of about 40% per 1000 yr, and the recent renewal rate for Kilauea is even faster, at nearly 90% per 1000 yr (Holcomb 1987, Lockwood and Lipman 1987). Lava flows radiate from the summit and rift zones, creating summit-to-sea strips of different-aged substrates, as well as isolating small-to-large islands of older substrates within younger flows (Figure 7). Many of these flows are aa. Because of their dense interior and clinkery surface, aa flows may be a less suitable habitat for cave planthoppers or possibly present a greater barrier to their dispersal than pahoehoe flows do. As long as active volcanism persists, new cave planthopper habitat is continuously being created (i.e., new lava flows are being colonized by *M. polymorpha*, which then provides roots as the essential food resource for cave planthoppers); while on older lava fields soil formation, erosion, and development of a dense vegetation cover progress, resulting in the local disappearance of cave planthopper habitat underground. Ash fallout from explosive eruptions, which occur intermittently (Lockwood and Lipman 1987), can hasten soil formation locally. Conceivably, as the cave planthoppers continually colonized newer flows, some older populations became isolated by these successional processes. Because of founder effects, sexual selection, and small population size, differentiation acquired during separation might have become established quickly, eventually leading to reproductive isolation. If a barrier between two closely related but reproductively isolated species is subsequently breached (e.g., when a lava flow covers the barrier), these populations may expand their ranges and secondarily become sympatric. The two distinct planthopper populations in Pink Pistillaria Cave could have resulted from such an area of secondary overlap.

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