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NEOGEOAEOLIAN HABITATS ON NEW LAVA FLOWS ON HAWAII ISLAND: AN ECOSYSTEM SUPPORTED BY WINDBORNE DEBRIS[1]

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Abstract: Lava flows of pahoehoe basalt on Kilauea Volcano, Hawaii Island, are colonized by arthropods within months after an eruption and 6 months or more before the first macroscopic plants appear. The barren rock surface is xeric, windy, and subject to high insolation and to daily temperature extremes; however, the numerous cracks and surface irregularities offer refuge for the animals. These animals scavenge on allochthonous windborne (aeolian) organic debris. The most abundant scavenger, as determined by baited trapping, is a remarkable, specialized cricket, *Caconemobius fori*, which appears to be restricted to these unvegetated lava flows near Kilauea. A native wolf spider, *Lycosa* sp., also colonizes the very young flows. Few other native or exotic Hawaiian arthropods are able to exploit the rigorous environment. On the nearly continuously active Hawaii volcanoes, new flows cross older flows before the latter can become vegetated. Thus the habitat has been available for colonization possibly as long as Hawaii Island has been subaerial, i.e., approximately 700,000 years.

Aeolian ecosystems were defined by Swan (1963) as those ecosystems in which the major nutrient source is allochthonus windborne material, i.e., imported from outside the ecosystem. A number of highly specialized animals, mostly scavenging arthropods, are now known to be restricted to this rigorous habitat (Mani 1962, Swan 1968). Swan (1968) considered aeolian ecosystems to be only those areas above the limit of vascular plants on high mountains and at high latitudes. He separated the ecosystem into 3 divisions: (1) the aquatic—in melt water pools and torrents; (2) the nival—on snow; and (3) the terrestrial—on exposed rock. He postulated that certain photosynthetic plants which obtain their inorganic nutrients from windborne dust and debris can also be included in the aeolian biome. Such plants include certain algae, mosses, and lichens. He made no mention of new lava substrates or other unvegetated areas.

Recolonization and succession of plants on new substrates have been of great interest to ecologists. Smathers & Mueller-Dombois (1974) made an extensive 9-year quantitative and qualitative study of revegetation of new lava substrates on Hawaii

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Island at Kilauea Iki, a small pit crater adjacent to Kilauea Caldera, beginning just after the eruption ceased. The 1959 eruption had provided a variety of substrates: a deep lava lake with a pahoehoe (see below for description) surface, a spatter cone, a pumice blanket, and a thin ash layer. They found that the first pioneers on the pahoehoe were macroscopic algae which appeared only on the edge in 6 months. After 1 year, algae, mosses, and ferns were still confined to the edge of the flow. Seed plants followed in year 4. By the 9th year, the total percentage of vegetation cover was still very small. The plants were mainly confined to cracks and irregularities in the surface, so that, superficially, the surface still looked practically barren.

The early animal colonization of these habitats has received little attention. In fact, the assumption has usually been made that plants must colonize a substrate first and create favorable microhabitats for subsequent animal colonization (Smathers & Mueller-Dombois 1974, Würmli 1974). Würmli (1974) first noted the existence of an aeolian-based food chain on new lava flows on Mt Etna, Sicily, Italy. He considered the new lava substrates to be the most rigorous and inhospitable of biotopes. However, he did find 2 spiders, a pholcid and a salticid, which fed on allochthonous windborne prey on a'a lava (see below for description) after it had been colonized by a carpet of the lichen *Stereocaulon vesuvianum.* The salticid is known so far only from these a'a flows and may be restricted to them (Würmli, in litt.). Würmli felt that pahoehoe lava was even less amenable than a'a to colonization and found no animals living on barren pahoehoe, but pahoehoe is not as common as a'a on Mt Etna.

The Hawaiian Archipelago is a string of oceanic volcanic islands stretching more than 2500 km across the mid-Pacific. The Island of Hawaii, the youngest island, is at the southeastern end of the archipelago and is less than 1 million years old (Macdonald & Abbott 1970). The archipelago is 4000 km from the nearest continental land area and is one of the most isolated of the oceanic island chains. The native fauna and flora are composed of those groups which dispersed across upwards of 4000 km of open ocean or island hopped and became successfully established. Thus, the Hawaiian Islands provide an extreme example of a disharmonic fauna on an isolated oceanic island chain and some of the clearest examples of adaptive radiation among those groups with early successful colonists. In pointing out the disharmony among the native fauna of oceanic islands, especially Hawaii, most authors (e.g., Zimmerman 1948, MacArthur & Wilson 1967, Gressitt 1971) have stated or alluded to the fact that many potential niches remain unfilled.

Consequently, it was surprising to discover a new species of cricket, *Caconemobius fori* Gurney & Rentz, 1978, which is both restricted to and specialized to exploit unvegetated recent volcanic substrates (neogeoaeolian) on Kilauea Volcano on Hawaii Island. I first collected the cricket, along with a number of obviously windborne animals, more than 1 km from any vegetation and within 100 m of an active volcanic vent in March 1973, while on a geology field trip to study newly forming lava tubes. Since the completely apterous lava cricket (FIG. 1) is a close surface relative of the Hawaii I cave nemobiine, *C. varius* Gurney & Rentz, 1978, I undertook this study to survey the cricket and other arthropod fauna of new lava flows and to study the distribution and ecology of the cricket.

DESCRIPTION OF THE ENVIRONMENT

Würmli (1974) considered unvegetated lava flows to be the most rigorous of all biogeocoenoses. Indeed, the barren black substrate, especially if associated with a sulfurous fume cloud, presents one of the most desolate environments on the earth's surface. The habitat is extremely xeric, not so much from low rainfall as from the high evaporation from the black surface, the poor water holding capacity of lava, and the rapid percolation of water into the porous rock. Water loss is further aggravated by the drying power and stress of almost constant wind. The temperature fluctuations on the surface are extreme. At Kilauea Iki, adjacent to my study area, insolation can raise the surface temperature to a maximum of 60°C (Smathers & Mueller-Dombois 1974); Würmli (1974) recorded temperatures well over 60°C on Mt Etna. The surface temperature plummets at night due to radiational cooling. At the latitude and altitude of Kilauea, there is a 25°–50°C difference between the daily maximum and minimum surface temperatures. Because of the lack of shade, the insolation itself can be harsh. The lack of obvious food adds to the appearance of desolation. Additionally, the youth of the substrate implies that no specialized animals would be restricted to this habitat. That some animals are restricted to recent lava substrates suggests that volcanism must be continuous over long geologic periods and that the animals are able to migrate to new substrates as these become available. The geological evidence (Macdonald & Abbott 1970) supports this hypothesis.

Geology

This discrete ecosystem is clearly defined by the geological setting. Excellent general accounts of the geology of Hawaii Island and Kilauea Volcano are given in Macdonald & Abbott (1970) and in Stearns (1966). Kilauea, rising over 1200 m above sea level, is a young shield volcano on the southeastern portion of the Island of Hawaii. It is among the most active volcanoes in the world and has averaged an eruption once every 3–4 years during its 200 years of recorded history. See Armstrong (1973) for a map of historic lava flows. Eighty percent of the surface of Kilauea Volcano is estimated to be less than 6000 years old (Holcomb, pers. commun.). The area of unvegetated flows is extensive, although, due to moisture or other substrate conditions, not all of it may be colonized by the specialized organisms reported here. The summit caldera is 4 km long and 3.2 km wide. The main vent of Kilauea is a collapsed crater, called Halemaumau, in the floor of the summit caldera. Other eruptions have occurred on either the southwest or east rift zones, which extend many km in those directions from the summit caldera. The floor of the caldera is veneered mostly with recent pahoehoe lava which is not vegetated.

The Kilauea flows interdigitate with those of the much larger Mauna Loa Volcano. Mauna Loa has been as active as, and its eruptions even more voluminous than those

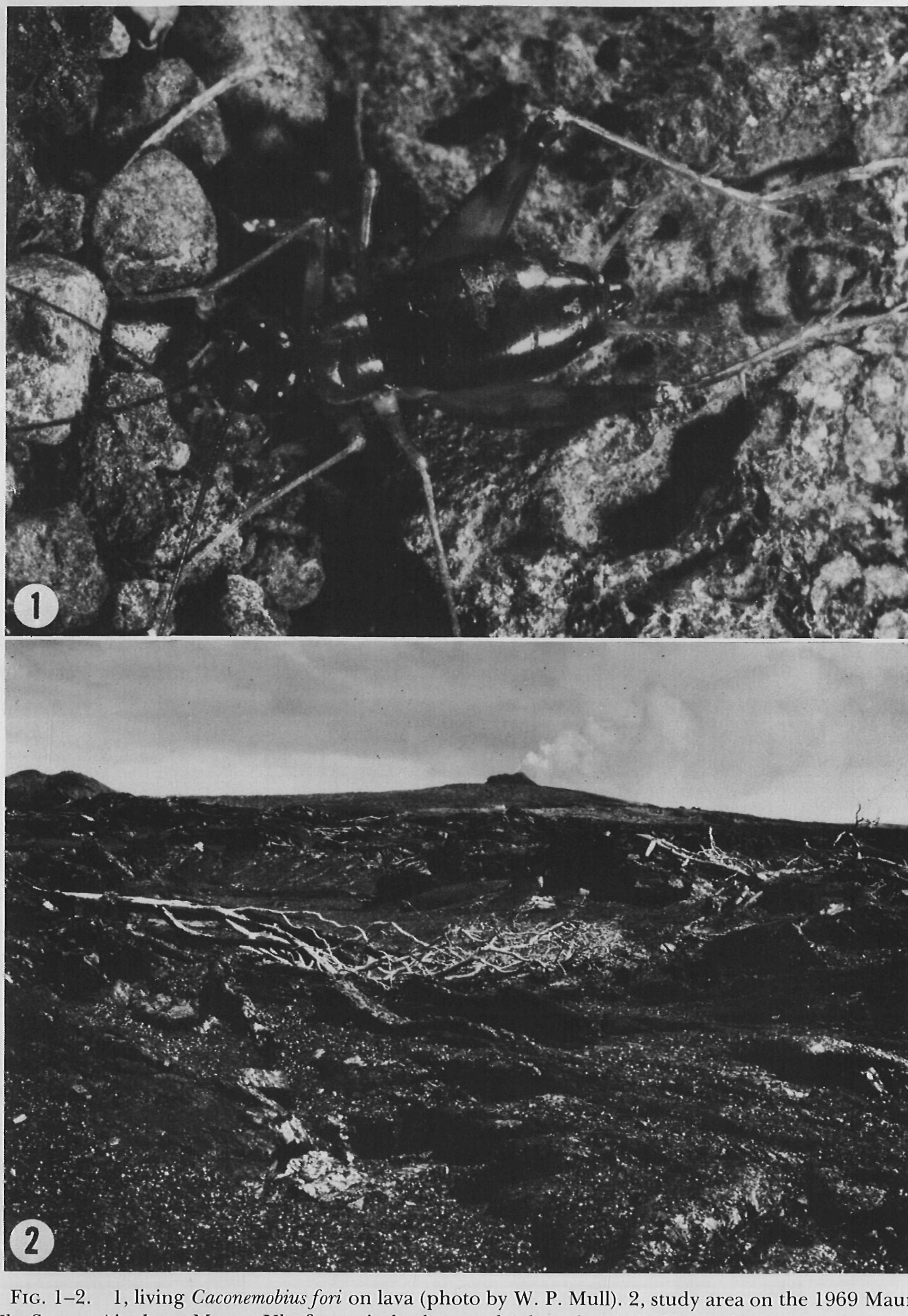

FIG. 1–2. 1, living *Caconemobius fori* on lava (photo by W. P. Mull). 2, study area on the 1969 Mauna Ulu flow at Ainahou; Mauna Ulu fumes in background (photo by N. C. Howarth).

of Kilauea. Its summit is over 4000 m above sea level and most of its unvegetated lavas are well into the aeolian zone sensu Swan (1968). Doty & Mueller-Dombois (1966) noted the occurrence of scattered xerophytic mosses and lichens there. However, except for the edge of one sparsely vegetated prehistoric flow crossing Mauna Loa Strip Road at 1556 m elevation, Mauna Loa flows have not been investigated.

Wentworth & MacDonald (1953) have given a description of the different types of flows and ejecta of Hawaiian volcanoes. The main building materials of the younger Hawaiian volcanoes, including Kilauea, are theolitic basalts. Basically, 2 types of basaltic lava flows with intergrades, differing only in heat and gas content, occur. Hot gaseous basalts are more fluid and flow as rivers which crust over, forming ropy or smooth wrinkled surfaces called pahoehoe. Cooler, less gaseous basalts flow as a caterpillar tractor tread, i.e., with a fluid interior and a cracking surface crust (clinker) that tumbles ahead of the flow and is continually buried under the advancing lava. This is called a'a and is characterized by a surface of very irregularly shaped large blocks of lava arranged in fantastic forms. Additionally, ejecta such as spatter, pumice, and ash can be thrown from the vent. The data in this paper only concern pahoehoe surfaces, although one flow is veneered with ash deposits.

The study areas

Kilauea: Halemaumau

The study area in Kilauea Caldera is located just south of the parking lot for Halemaumau Crater Overlook on the Crater Rim Road in the Ka'u Desert at 1110 m elevation. The substrate is composed of a partially cemented to cemented ash deposit from the phreatic explosion of 1924. This deposit overlies the 1919 pahoehoe flow from Halemaumau. The surface is dissected with numerous earth cracks of varying sizes and small lava tubes, some partially collapsed, and is strewn with small to very large boulders from the 1924 explosion.

The northeast tradewinds carry the fume cloud from Halemaumau over the area, often at ground level. This fume cloud, composed mostly of steam with small amounts of oxides of sulfur and other gases, is variable in intensity, but is often severe in its effects on the environment. There are many fumaroles and hot spots in cracks within the study area.

Because of the tradewinds, rainfall diminishes sharply as one moves from northeast to southwest over the summit area of Kilauea. Over 2500 mm of rain per year at the summit diminishes to ca 1300 mm of rain at the study site only 2 km away. The study area should be a summer drought montane forest, but is a desert because of the youth of the substrate, its poor water-holding capacity, high evaporation from the lava, and from the influence of the fume cloud from Halemaumau Crater.

The region is barren and virtually devoid of macroscopic plant life. A few stark, bleached tufts of small dead shrubs and grass dot the area. These possibly indicate very brief, more favorable conditions in the recent past, although some dead plants may have been carried to the area by wind or hikers. One very small fern, possibly

Polypodium pallucidum, 10 cm tall, was noted growing in a crack about 50 m from the pitfall trap.

Mauna Ulu: 1969 flow (Fig. 2)

Mauna Ulu is a recent shield volcano located on the east rift zone of Kilauea ca 10 km southeast of Halemaumau Crater at ca 1075 m elevation. The main vent of Mauna Ulu is at the eastern end of a long fissure which first erupted 24 May 1969 (Koyanagi et al. 1970, Swanson et al. 1971). Repeated overflows from the main vent have built a broad shield nearly 2 km long and more than 100 m tall. In 1969, 1970, and 1971, lava flows entered the ocean 12 km away (Peterson & Swanson 1974). Mauna Ulu flows have partially covered the previous historic lava flows of 1840, 1923, 1962, and 1963.

Baited pitfall trapping was carried out in February 1974. The primary study area is near the western end of the fissure which erupted on 24 May 1969, where it cut the road to Ainahou Ranch, and is at 975 m elevation and 2.4 km from Mauna Ulu. At this location the eruption lasted only 1 day, and the estimated 4.5×10^6 m^3 of lava issued as a highly fluid, thin pahoehoe flow (Koyanagi et al. 1970).

The surface is characterized by numerous collapsed bubbles, tumuli, fractures, fissures, and other irregularities (Fig. 2) and is black with a still mostly unweathered irridescent sheen. Part of the surface is lightly covered with pumice and ash, up to 2–3 cm thick in places, from both that eruption and subsequent Mauna Ulu eruptions. Many of the cracks in the lava surface are very extensive. Many partially burned trees lie fallen on the surface of the flow and are often associated with their respective tree molds.

During the period of this field work, most of the flow remained entirely unvegetated. A few ferns (unidentified) were established in cracks, most conspicuously at a hot spot, which was a large collapsed pahoehoe bubble 2 m long, 1+ m deep, and 0.5–1 m high. The ferns were growing in the shade of its overhang. When ambient air temperature was ca 13°C and the weather foggy, the air temperature inside the bubble was 22°C and higher deeper within.

A small (ca 6 m × 3 m) divided kipuka, a remnant island of older lava surrounded by the flow, is situated ca 100 m from the edge of the flow. It contains 2 large dead and 2–3 small living *Metrosideros* trees, native *Dodonaea, Scaevola,* and *Vaccinium* shrubs, the native lily, *Dianella sandwichensis,* the exotic grass, *Andropogon virginicus,* and ferns.

The vegetation cover before the lava flow was similar to the kipuka and the neighboring vegetation, which is an open *Metrosideros collina* var. *polymorpha* forest with few native shrubs and *Andropogon* ground cover. The study area has an annual rainfall of ca 2400 mm (Armstrong 1973) and is on the lower edge of the montane rain forest climatic zone (Doty & Mueller-Dombois 1966). The open character of the forest, with its grassland and fern understory, is due to the numerous volcano-originated fires and the youth of the substrate.

Mauna Ulu: 1973 flow

The small November 1973 eruption issued from a fissure just west of Mauna Ulu. The black pahoehoe lava flowed towards Mauna Ulu. This site, at 975 m, was sampled within 3–4 months of the flow (February 1974) and the lava surface was still very fresh. There were no tree molds, as this part of the flow covered a recent flow from Mauna Ulu. The environment is a little wetter than the 1969 flow, and prior to 1969, there was an open *Metrosideros* forest with mixed *Dicranopteris* ferns and *Andropogon* ground cover.

MATERIALS AND METHODS

Besides making direct observations and using bait stations on many unvegetated flows, baited pitfall traps were used to determine the presence of *Caconemobius fori.* From 11–17 February 1974, 14 pitfall traps composed of ½-gal. (1.89 liter) narrow-necked (2.8 cm diam) wine bottles, baited with rancid raw cheese, were placed in cracks and small shelter caves on the 24 May 1969 Mauna Ulu pahoehoe flow, in the small kipuka, and in the adjacent open forest. Nine traps were placed on the flow more than 150 m from the edge. One was put in the kipuka, and 4 were operated along a transect as follows: 1 on the lava within 10 m of the edge of the flow and 3 at 5–10 m intervals into the vegetation adjacent to the flow. Two of the traps on the flow were moved to new locations and 1 trap was removed after the first 2 days, making 16 locations in all. The rim of the bottle was leaned against the rock substrate under a protected overhang, and the glass was shaded completely by placing large flat lava slabs over the bottle. The traps were checked 3 times at 2-day intervals, and most specimens were collected in alcohol. All *C. fori* were retained on the 1st visit and smaller nymphs released on the latter 2 visits.

The 9 traps on the flow were set 10–50 m apart in the middle, about 200 m from either the north or south margin and about 300 m from the western end of the flow. The lobe of the flow at this point is ca 400 m wide.

Additionally, 2 similar traps were set 13 February 1974, one 100 m from the nearest vegetation on the November 1973 pahoehoe lava flow near Mauna Ulu, and 1 in the vegetation at the edge of that flow, approximately 15 m from the lava. Both traps were set inside a natural arch or shelter cave and were checked after 2 days.

On 3 March 1976, a ½-gal. (1.89-liter) wide mouth (6.5 cm diam) cheese-baited pitfall trap was set ca 50 m south of the road in the Ka'u Desert across from the visitors' parking lot at Halemaumau Overlook at 1110 m elevation on the 1919 lava flow. The trap was checked after 4 days.

RESULTS

The trapping program on the 1969 Mauna Ulu lava flow captured *C. fori* crickets only on the interior of the flow, well away from the main edge. A total of 153 crickets were captured during the 6 days (FIG. 3). Lava crickets were captured at 9 of the 10

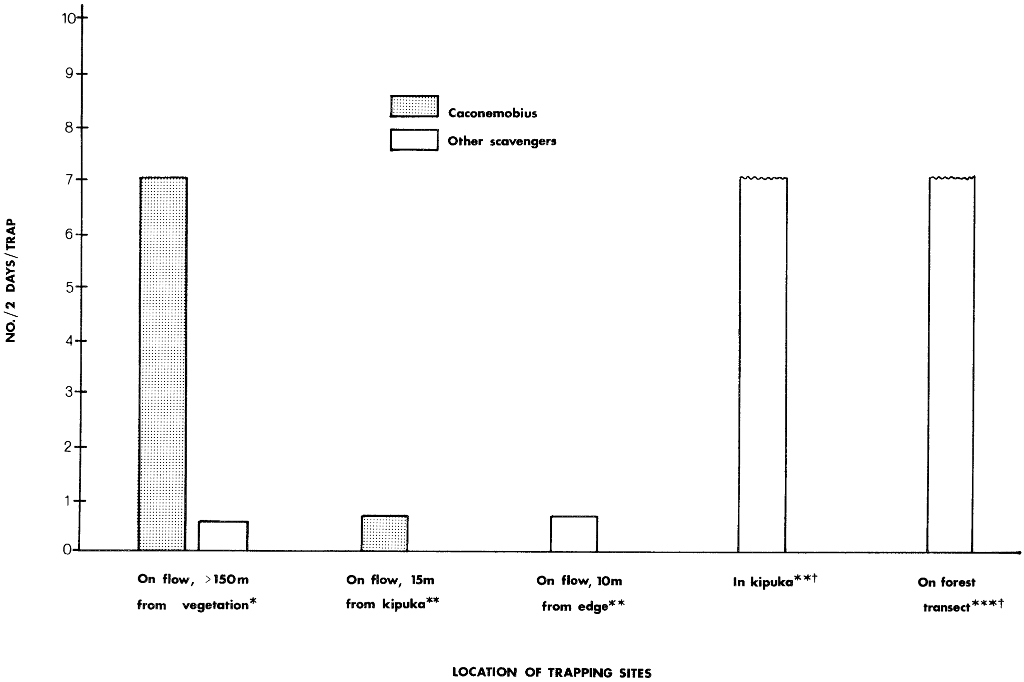

FIG. 3. Average numbers of arthropods captured at each trapping site/2-day period. *Average of 22 trapping periods at 10 locations; **average of 3 trapping periods at 1 location; ***average of 9 trapping periods at 3 locations; †small ants, Collembola, etc., estimated, not counted.

locations and in 15 of the 22 trap periods (69%), with an average of 7 specimens per trap per period. The trap at the hot spot yielded 37 *C. fori* over a 2-day trapping period. The traps had a noticeable peak in attractiveness during the second 2-day interval. Since these were live traps, the dead or previously trapped animals may have added to the attractiveness of the trap. However, some animals may have been eaten. Although each trap location on the flow was not described in detail, a positive relationship with the depth at which the trap could be set under an overhang was evident; i.e., the larger the shelter cave, the greater the catch of *C. fori.*

Besides the crickets, only 11 specimens of other arthropods of 5 species were captured in the traps on the flow. They were present at 4 of the 10 locations and in 5 of the 22 trapping periods (23%). All of these scavengers are apparently recently introduced, i.e., nonnative organisms to the Hawaiian fauna; these include 4 specimens of Isopoda (all *Porcelleo laevis*), 6 specimens of Diptera (Sphaeroceridae, Phoridae, and Muscidae) and 1 specimen of Collembola.

Of the 2 traps on the flow near vegetation, the 1 near the small kipuka yielded 2 *C. fori* and no other organisms. The other trap near the edge of the flow yielded only an exotic earwig, *Euborellia annulipes* (Lucas), and a spider web.

The trap within the vegetation of the kipuka and the 3 traps located along a transect in the vegetation captured at least 7 scavengers per trap per period, but no *C. fori.* In all 4 traps in vegetation, many of the small organisms such as ants and Collembola were not individually counted, so that these are minimum numbers. Also, some of the organisms such as the mollusca, planarians, and Collembola stuck to the sides of the jar and could not be knocked out during checking. The scavengers collected in the vegetation are all introduced, nonnative organisms and include Collembola, the isopod (*P. laevis*), the earwig (*E. annulipes*), scavenging flies of 2 families, an ant, a planarian (presumably *Geoplana septemlineata* Hyman), and a slug.

On the 3-month-old November 1973 lava flow at Mauna Ulu, the trap on the flow contained 1 immature male *C. fori* and 1 *P. laevis.* The trap in the vegetation adjacent to that flow contained a few flies and maggots. The trap set in ash at Ka'u Desert at Kilauea yielded more than 30 specimens of *C. fori.* No other animals were in that trap.

Additional animals collected or observed on the 1969 flow were 2 small argiopid spiders in orb webs, one in a crack and another in a tree mold. They were black and looked much like the lava. A large exotic mantid (*Tenodera* sp.) was seen on the flow. Exuviae of a large wolf spider (Lycosidae) were relatively abundant under the loose shelly pahoehoe crust. There were as many as 3 exuviae under some slabs, with an average of 1 exuviae for every 3 slabs.

DISCUSSION

Since concurrent baited trapping on recent lava and in adjacent forests captured lava crickets only on the flow, *C. fori* appears to be restricted to the rigorous neogeoaeolian habitat and disappears before the establishment of a complete vegetation cover. The 2 crickets captured 15 m from the kipuka in the center of the 1969 flow were the individuals found nearest to any vegetation.

Some independent negative evidence that the cricket lives only on new flows comes from the International Biological Program soil fauna studies within Hawaii Volcanoes National Park (Radovsky & Tenorio, pers. commun.). During 2 years of intensive soil fauna surveying in 1971 and 1972 by pitfall trapping and Berlese funnel sampling along a transect from ca 900 m to 2400 m above sea level, including 2 traps in vegetated areas adjacent to my study areas, not a single *Caconemobius* specimen was collected. These pitfall traps were large, with an effective (ground level) perimeter of 1 m. None of these pitfall traps were set on unvegetated flows. From its behavior, one would expect *Caconemobius* to be caught in pitfall traps if it occurred in a given habitat.

C. fori is nocturnal and was found only once on the surface during the day. No signs of it were found by turning over rocks and searching during the day. At night on 3 March 1976, during 2 man-hours of turning over rocks in the Ka'u Desert study area, 2 individuals were seen. However, on the same night the crickets readily came to cheese bait placed under rocks. Many individuals were seen and 4 were captured.

This species probably feeds and remains mainly in cracks and depressions under rocks where food is concentrated by the wind. They are shiny black animals, very close to the color of fresh lava, and in their size, shape, and color resemble the very common small beads of lava ejecta known locally as "Pele's tears." They actively jump when disturbed. The young pahoehoe substrate offers many hiding places for these animals within the numerous cracks, pahoehoe bubbles, tumuli, larger vesicles and lava slabs. It is expected that they will be found on a'a flows in similar climatic zones, but these have yet to be studied.

A large, black wolf spider, *Lycosa* sp. (unidentified), also commonly inhabits unvegetated flows, mostly as evidenced by exuviae under rocks. Occasional individuals are met with during the day on the surface of many lava flows or under lava blocks or slabs. However, judging from the large number of exuviae under such rocks, an inference to their commonness and biology can be made. The spider apparently normally hides under rocks on the surface and is ready to spring on any suitable prey which is blown to or alights in its vicinity. Since large rocks on the surface act as traps for windborne material, the spider may not have to venture out on the exposed flow often. It, or another species, was very common on a prehistoric, little vegetated a'a flow on Mauna Loa at 1556 m elevation. No sign of it, however, was seen at the Halemaumau Kilauea study area.

Of the other organisms collected on the flow, many are accidentals and would not ordinarily survive there. Some, such as the argiopid and *P. laevis,* may be able to exploit the habitat. *P. laevis* is an introduced omnivore, locally very common in the rain forests on Kilauea.

ENERGY SOURCE

The nutrient source for this biotope is primarily allochthonous windborne material originating in the adjacent forests. There are no quantitative data on the amount of such material other than casual observations, but the amount is likely to be considerable. A few obviously windborne animals have been noted on the flows. During trapping on the 1969 lava flow, numerous seeds and other organic debris were abundant in cracks.

The barren lava flows are almost constantly subject to moderate winds, due to the (1) northeast trade winds, (2) heating of the substrate by insolation, and (3) lack of windbreaks. At the Kilauea site the northeast tradewinds, which blow most of the time, carry disseminules from the adjacent tropical montane rain forest ca 2.5 km away. Some of the debris may be carried over the area, but the great surface irregularities on new lava, especially wide deep cracks, loose rocks, and overhangs, act as traps for the debris. It is expected that a'a surfaces will be at least as rich, due to their extreme irregularity and the presence of much more colonizing and hiding area on the flow, as Würmli (1974) observed on a'a flows on Mt Etna.

Swan (1963) cites studies showing that not only are macroscopic organisms and debris (spores, pollen, seeds, insects, plant fragments, and dust) which are blown in from both adjacent forests and distant sources important, but that albuminoids from windblown sea-foam may be significant. These albuminoids may be quite important in Hawaii, given the expanse of the surrounding ocean. Smathers & Mueller-Dombois (1974) found significant amounts of organic nitrogen dissolved in rainwater falling on Kilauea Iki. The source of this nitrogen may be windborne sea-foam.

The neogeoaeolian habitat shows many parallels with the cave habitat. Both the lava flow and lava tube ecosystems share a similar rock substrate with numerous cracks, and both rely on allochthonous energy. At least 2 native groups of organisms have close relatives which exploit both habitats. These are crickets (*Caconemobius*) and wolf spiders (*Lycosa*). The genus *Caconemobius* has an apparent propensity for colonizing rigorous environments as scavengers, since 2 of the other 4 species are known to be restricted to lava tubes, 1 on Maui and 1 on Hawaii (Howarth 1973).

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