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The Insect Life of Arno

by

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THE INSECT LIFE OF ARNO 1/

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R. L. Usinger and Ira La Rivers

On Arno, as elsewhere, insects are the most numerous of land animals. This well-known phenomenon is a function of their small size and their high reproductive potential. The total number of species of land anthropods on Arno is estimated at 500. This may be compared with 96 species reported from Canton Island (a somewhat drier coral atoll) and nearly 1000 recorded from Guam (a much larger, high island). The insects of Arno have to be abundant in order to maintain themselves, because most of the higher terrestrial animals live on them. Thus, insects are the first link in many of the food chains, such forms as aphids, plant bugs, caterpillars and, in fresh water, midge larvae acting as primary converters of green plants into animal food.

Of no less importance than the "grazers" are the ever-present ants and cockroaches which act as scavengers and the wood-boring beetles and termites which, with the help of bacteria and fungi, restore logs to humus. Other katabolic agents include the flies and beetles which play a dominant role in the decay of fallen fruits and others which perform a similar function in dung and carrion.

Not all insects are occupied in such vital jobs of a constructive or destructive nature. Analysis of the fauna reveals that a considerable proportion of the insects in any community are busily engaged in eating each

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1/ This report covers field work carried out in 1950 as part of the Coral Atoll Project of the National Research Council's Pacific Science Board. These studies were aided by a contract between the Office of Naval Research, Department of the Navy and the National Academy of Sciences (NR 160 175).

other. One-fourth of the insects of Arno fall directly in this category--as predators or parasites and the percentage may be even higher when careful rearing reveals the true numbers of entomophagous parasites. Then there are the small ectoparasites---the lice and mites, and one louse fly---which infest birds and rats.

Another vital though inconspicuous function of insects in most mainland areas is pollination. On Arno probably three-fifths of the higher plants are insect pollinated. Detailed studies on this are lacking but the single Arno bee, a leaf-cutting species of Megachile, collects pollen on its abdominal hairs. It nests in the dead twigs of Scaevola and visits various flowers including Triumfetta, Scaevola and Wedelia.

The above-mentioned activities are basic to any community of plants and animals and are quite independent of man. For this reason, the insects, with but few exceptions, are not much different on the uninhabited islets than in the villages. Furthermore, many of the insects undoubtedly arrived before the first natives and had achieved a state of equilibrium which may not have changed significantly with the advent of man.

There are a few important exceptions to this generalization---such as the house fly, the house mosquito, domestic cockroaches, and lice. The role of these and other insects associated with man will be discussed in detail later.

Animal Communities and Habitats

It is a well-known fact that plants and animals are discontinuously distributed over the earth's surface. Nevertheless it comes as a surprise to find that five square miles of practically level land of similar origin and relatively uniform composition should present such a variety of distinct

plant and animal associations. In spite of a superficial similarity there are at least four distinct terrestrial communities and numerous distinct but interrelated strata within each. In addition there is the marine habitat including tide pools and the open ocean which is inhabited by marine water striders.

Marine Insects. The virtual absence of the largest group of animals, the insects, from the largest habitat in the world, the ocean, has been the subject of much speculation (Buxton, 1926). It has been pointed out that insects of saline lakes can tolerate greater concentrations of salt than are found in the ocean, and insects of torrential streams and waterfalls are subjected to conditions which are comparable to wave action. What, then, are the limiting factors that prevent insects as a group from colonizing the sea? The answer is to be found in the ancestry of insects, in the fact that they evolved a special breathing mechanism (tracheae) which was admirably suited to terrestrial life and only secondarily adaptable to life in the water. But perhaps the most critical factor of all is the depth of the ocean, for deep water is uninhabitable even to fresh water forms, the profundal bottom habitat of our deepest lakes being beyond the reach of insects. Then there is the fact that the ocean is already occupied by another group of Arthropods, the Crustacea. This group, which includes the shrimps, crabs and their relatives, is so perfectly adapted to all of the available niches in the sea that would-be invaders such as insects cannot compete with them.

One group of insects has overcome the above difficulties by occupying the surface of the ocean. The marine water striders attracted the attention of early voyagers who found small, gray, long-legged creatures coursing about on the high seas. These marine forms differ from their fresh-water relatives

in that they have permanently lost their wings, there being no need to utilize this means of dispersal in the ocean which, unlike fresh-water ponds, is in no immediate danger of drying up.

Halobates micans lives in the open ocean and in the deep parts of the lagoon at Arno. Nymphs and adults are blown up on the beach by strong winds. This happened on the beach of the lagoon at Ine Village one afternoon and evening. The bugs were awkward on land and sought shelter from the wind in the smallest depressions or in footprints on the beach. Here they doubtless fell easy prey to a golden plover which patrolled that section of beach and also to the ghost crabs which glided swiftly over the sand after dark.

In protected coves such as are found on the ocean side of Tagelib and in the lagoon at the north horn of the atoll two other marine water striders are found. One of these, Halobates mariannarum, differs only slightly from its relatives in the Marianas and Carolines, but the fact that it differs at all suggests that it is endemic to the reefs of the Marshalls and has been isolated for a long time. Nymphs and adults of this local Halobates swim in groups of hundreds or thousands in shallow water. A search was made for the plankton which must serve as their food, but to no avail. Presumably, they feed on plankters which rise to the surface at night. The fact that Halobates are not eaten by fish suggests that the median metasternal scent gland repels the ever-present marine predators or, perhaps, makes the bugs distasteful to the fish.

Even more local, in small embayments, is Halovelia, a marine water strider whose body is less than one-twelfth of an inch in length. The male is even smaller and rides on the back of the female to insure that the sexes will not be separated by wind or tide.

The Strand. In the daytime the beaches of Arno are clean and support very few insects. Robber flies flash here and there, capturing mostly flies, but this is about the extent of the activity over the uninterrupted stretches of sand.

At night, Arno beaches take on a changed aspect. The Ghost crabs (Ocypode ceratophthalma), common enough during daylight hours, literally swarm over the sands after dark. They dart everywhere. At first, the insect fauna seems to be poorly represented, few species coming to lights, and then usually only one or two individuals of any given kind. As a consequence, the discovery, one night, of a small, white cricket marching about the beaches in great numbers came as somewhat of a surprise. They were particularly abundant at low tides when the greatest expanse of beach was exposed, and seemed to be coming from everywhere. They ranged in size from the quarter-inch adults down to barely visible early instar nymphs, all marching sedately by the coleman lamp on the sand. They were rather weakly positively phototropic, and after the light had been on the sand for some time, it could be noted that most of them were gradually orienting themselves toward it. They leap vigorously at the slightest motion near them. Like the storied Mormon cricket of the intermontane West (Anabrus simplex), these little beach crickets fell quickly upon an injured fellow and disposed of it with the rapidity and facility denoting the confirmed omnivore, which they were assumed to be, although no other data were obtained on their plant feeding habits, if any. Similarly, they were quite agile in catching the rather numerous small flying ants attracted to the light, and which were meandering about the sand. But, judging solely by their numbers, it is unlikely that predation was their usual way of making a living, for there didn't seem to be a large enough supply of available victims for the horde--

by contrast, the lush plant growth would seemingly have had to supply the bulk of the food such a population of crickets would require. Here, certainly, is one animal which can be reckoned an important factor in the conversion of plant materials and smaller animals into food available for other animals greater in size, and consequently occupying a more advanced spot in the food-cycle scheme. One of the larger animals patiently engaged in such conversion was the above-mentioned ghost crab; these were observed preying upon the small white cricket in large numbers. A rough count was made of the number of successful catches out of the number of attempts that any one ghost crab made, with the resulting approximation of 1 in 10.

An additional characteristic of Arno night beaches is the great number of crab spiders hunting on the rocks and vegetation bordering the sand. Directing a flashlight at eye-level usually struck up myriads of diamond-bright points of light--they could be seen flashing on all sides as the light swept along. Close inspection showed them to be the eyeshine of hunting spiders. Occasionally such a point of light turned out to be a small ground gecko, but with some experience, it soon became possible to distinguish these latter by virtue of their slightly larger size and more yellowish reflection.

Except for the beaches the shore is rocky, consisting of sharp, pitted elevated reefs. Here and in the strictly intertidal zone insects are virtually absent, contrary to the situation that exists in the Halophila tide pools of Samoa or the beaches of Hawaii. The one human element that enters into the picture in the intertidal zone is the presence of human feces--a hygienic habit involving use of the tidal waters for sewage disposal which attracts numerous flies that would otherwise be entirely absent from the

zone. Mangroves are a special association in a few places such as the lagoon at Bikariej. No insects were observed to inhabit the mangrove areas except marine water striders.

The Inner Beach is occupied by various plants such as Scaevola, which occurs singly or in pure stands and provides blossoms for the Marshallese head leis, Messerschmidia, Guettarda, Pipturus, Cordia, and, mostly on raised ledges, Pemphis. Each of these characteristic strand plants harbors a distinct fauna, a leaf mining agromyzid fly making conspicuous serpentine burrows in the thick Scaevola leaves, caterpillars of the Achaea moth on Cordia, the striking day-flying moth, Utetheisa, with red and black spots on a white background, on Messerschmidia and the beautiful blue Hypolimnas butterfly on Sida.

A particularly rich habitat in this zone is provided by the native custom of burning Scaevola and Messerschmidia thickets to provide space for coconuts. The dying or dead limbs with leaves browned but still attached, were attractive to two Scolytid beetles, one round-headed borer, and several small predaceous rove beetles. Also in the beetle galleries were two predaceous bugs of the family Anthocoridae and one curious little predator with the imposing scientific name, Ceratocombus.

The only seemingly barren tree in this association was Pemphis. Repeated search failed to reveal a single insect on this unusually hardwooded tree. Scaevola, on the other hand, supports a considerable population including a small endemic bug, Campylomma, each island group in the Pacific having a species with distinctive spots on its hind legs.

The Open Woodland. As one approaches Arno it is the erect trees that catch the eye. In profile, the tall trees give the island its place on the

horizon. Coconuts and the screw-pine (Pandanus) comprise most of the forest and are the exclusive elements that rise above the strand scrub in the narrow parts of Arno. The coconut-pandanus forest, whether seeded naturally or planted by man, is an open type with individual trees rather widely separated, allowing sunlight to reach the ground during most of the day.

Much has been written of the insect pests of the coconut in other parts of the tropics but Arno is singularly free from such troubles. The Micronesian coconut scale, an oval, reddish scale nearly one-fourth inch in diameter, is the most conspicuous pest on fronds and green husks. The boots, skirts and trunks, on the other hand, teem with insect life. Here one finds a whole community gathered largely for the protection afforded by this ubiquitous tree. Several kinds of cockroaches are found as well as small bark lice, earwigs, ants, etc. Most of these fall easy prey to the skinks which frequent the same habitat.

On Arno Pandanus is not so attractive to insects as the coconut, perhaps because it does not provide as good protection. Only at the bases of the fronds is a microhabitat found. Here rain water accumulates, sometimes in amounts sufficient to sustain dragonfly naiads and, in some parts of the tropics, mosquito larvae. On Arno during our stay moisture was sufficient only for earwigs and small beetles.

The fruit of the Pandanus is enormous and, when ripe, high in sugar content--this providing a delicacy for the natives. Decaying Pandanus fruits on the ground harbor an association of vinegar flies (Drosophila), fruit beetles (Nitidulidae) and numerous predators (Staphylinidae, Anthocoridae, Ceratocombidae). In addition there is a small but very active, white, predaceous mite.

The ground cover in the open woodland consists of various low plants such as Vigna marina, Wedelia, Fleurya and, in open areas, the sedge Fimbristylis, and associated grasses such as Lepturus. Sometimes this growth is choked by the parasitic vine, Cassytha. This ground cover is rich in insects, the undersides of Vigna leaves being heavily infested with the Micronesian red spider mite (Tetranychus), Vigna and Fleurya being spotted and withered by the hopping plant bug, Halticus, the grasses acting as hosts for the cosmopolitan green plant bug, Trigonotylus, and Fimbristylis harboring a remarkable community of true bugs including the herbivorous sedge bugs, Ninus and Orthotyllelus, and Nysius picipes, Pachybrachius nigriceps and Pachybrachius pacificus, and the predaceous Nabis capsiformis. That the lone predator is not sufficient to keep this association in check is attested by the enormous numbers of individuals present wherever the plants occur. The Nysius is of particular interest because it is found only on the islands remote from air bases in the Marshalls whereas Nysius pulchellus, from Guam, is found exclusively on Majuro and Kwajalein. Presumably Nysius picipes is an old resident in the Marshalls, yet it is indistinguishable from typical Wake Island specimens.

The Canopy Woodland. The richest zone on Arno occurs in the wider parts of the islets where humus has accumulated and breadfruit grows. Here one finds a dense growth of trees 50 and 75 feet tall with foliage so dense that the ground is shaded most of the time. Before the time of the present inhabitants, taro pits were dug in such places, thus further augmenting the accumulation of humus and the maintenance of moist conditions. Here one finds the buttressed trunks of breadfruit with epiphytic bird's-nest ferns, a moss, Calymperes tenerum, a thick, low undergrowth of Polypodium fern, and decaying logs with Polyporus and Schizophyllum fungi.

Here in decaying logs are wire worm larvae, stag beetle adults and larvae, termites, ants, Machilis and a large red Collembolan, wood roaches, earwigs, predaceous rove beetles, and other invertebrates such as scorpions, pseudoscorpions, centipedes, earthworms, isopods, and millipedes, as well as land snails of several species. On the fungi growing on the logs are fungus beetles (Ciidae and Endomychidae), fungus gnats (Mycetophilidae), and various predators that take advantage of such situations. Fallen logs are one of the most profitable foraging places for insectivorous skinks and birds.

Tree holes are frequent in this part of the forest and water stands in them for considerable periods. In this microhabitat the endemic Marshallese mosquito, Aedes marshallensis, breeds. The eggs are laid at the water's edge and the pale larvae feed on the very special type of organic matter at the bottom of such small bodies of water. That the mosquitoes thrive in spite of their rather restricted habitat is attested by the large numbers of individuals, yet these mosquitoes are of such retiring habits that they are seldom troublesome and only caused serious trouble during World War II when, on neighboring islands, dengue fever broke out. This mosquito, being an efficient vector, had to be controlled, but only in the vicinity of military installations because it has a short flight range.

Taro pits provide one of the most intriguing problems for the biologist. Surrounded by luxuriant tropical vegetation, these bodies of shallow water should, by all mainland standards, be teeming with life. Yet they are almost devoid of insects. A fresh water snail is always common but this is all that meets the eye at first glance. Mayflies, caddis flies, and all of the numerous water beetles and bugs are absent. Closer inspection reveals blood worms in the mud, from which a few midges emerge, the remainder

forming the basic, and in some instances the only, diet of the dragonfly naiades. These fierce predators with their extensible labia and powerful jet propulsion are quite the fiercest animals in the water and at least on Arno, are overadapted to their particular niche. The only other arthropod of any consequence in fresh waters is a reddish shrimp which was found occasionally.

The extremely depauperate fresh-water fauna is not surprising when one considers the nature of a coral atoll. Arno has a relatively heavy and uniform rainfall and therefore fares better than most atolls. Typically, fresh water is scant and seasonal on coral atolls and fresh-water life must be hazardous indeed. Even on Arno, the only endemic of aquatic habit is the tree-hole mosquito. The dragonflies are all strong-flying immigrants and the other forms may be accounted for by accidental transport of relatively recent date.

Adult dragonflies are swift fliers and are seen more in the open forest where they hover or dart about capturing gnats and other small insects on the wing. The slower and more fragile damselflies were seen only in the vicinity of the taro pits on the widest part of Arno Island. Damselfly naiades were not seen but dragonfly naiades were common in wells, cisterns and taro pits where they undoubtedly eke out a precarious existence in the face of occasional hurricanes and the ever-present danger of drought.

Herbivorous insects are not conspicuous in the canopy forests but nevertheless are abundant, a large red corizid bug occurring on Allophyllus and the bird's-nest fern (Asplenium nidus), a small but spry spider mite on breadfruit leaves and a host of small saprophytic and parasitic insects in fallen rotting breadfruit, as in the rotting Pandanus fruit. The productivity of one rotten breadfruit in terms of individual Drosophila flies is enormous.

Insects and Native Culture

Certain insects such as lice and bed bugs have accompanied man in all of his wanderings. The island peoples were no exception to this and it is certain that numerous species even less intimately associated with man than the above stowed away in native canoes. In this way, no doubt, the cosmopolitan house fly and its chief enemy, the predaceous Hermetia fly, came to Arno and also the Australasian and Oriental cockroaches, various ants, the rotten-fruit insects and the scale insects, mites and aphids which are attached to the coconut, breadfruit, Pandanus, banana, taro, arrowroot, papaya and lime trees. Also to be classed as a silent hitchhiker is the notorious dengue-yellow fever mosquito whose larvae have traveled over the entire tropical world in drinking water. On Arno, as elsewhere, this species is so closely associated with man that it is found only in and around houses and breeds in the cisterns and other drinking water containers, leaving the tree holes of the forest for the closely related Marshallese mosquito.

Termites attack man-made structures as well as native woods on Arno as elsewhere in the tropics. Four species, each belonging to a separate genus and each harboring distinctive Protozoa in its gut, were found on Arno. Without the Protozoa termites have been shown to be incapable of utilizing the dry cellulose of dead wood as nutritive material.

This is only a partial list of the camp followers of man in the Pacific. Nevertheless, it is a formidable array and causes one to wonder how it is that life is so pleasant on Arno. The fact is that none of these pests, except possibly the house fly, is sufficiently numerous to present a real problem in the daily life of the natives. In fact Arno is singularly free from such notorious scourges of the tropics as the coconut moth, the coconut

beetle, the Oriental fruit fly, locusts, etc. Even the ubiquitous copra beetle was not seen.

Agricultural Pests. At the time of our study there were no agricultural pests of any significance on Arno. This is a situation almost without parallel elsewhere in the world. The reasons for this happy state of affairs are complex. First, the number of crops is small and includes only those species best adapted to the conditions on a coral atoll. On Majuro, where beans and sweet potatoes are grown, hopping plant bugs (Halticus) and mealybugs are very numerous and destructive. Perhaps of greater importance, there is no intensive agriculture on Arno, the staple coconuts, Pandanus, breadfruit and taro growing with little or no cultivation and, except in the case of breadfruit, existing in amounts in excess of the actual needs of the population. The breadfruit being seasonal and especially favored as food, is more fully utilized, though no apparent attempt is made to plant new trees. Only bananas are planted in dense stands and these are protected, as young shoots, from pigs. Finally, the low level of insect pests must be attributed to the particular ecological relationship that exists on Arno between herbivores and predators. Normally, herbivores far outnumber predators in an animal community. On Arno, however, protected habitats are few and predaceous insects and vertebrates (mainly skinks) are exceedingly numerous (see Report by Marshall). Thus we have a situation in which the population level (equilibrium) of insects of agricultural crops is below the threshold of economic damage.

Ectoparasites. This subject was investigated by Dr. Marshall. A list of the parasites, both external and internal, of pigs, chickens, dogs and cats appear in his Report. Both the house rat and the Polynesian rat were

found on Arno and both were infested with lice (Hoplopleura) and two species of parasitic mites (Laelaps). Herons were infested with parasitic flies (Ornithoica) and mites, noddies with bird lice, Austromenopon, hippoboscid flies, and mites.

Insects in relation to health and sanitation. On Arno there are numerous insects and other invertebrates that affect the health of man either directly or indirectly. Scorpions and centipedes are much feared by the natives. Although we cannot say from experience, the bite of a centipede or the sting of a scorpion are usually of the same order of severity as a bad bee sting. Certainly scorpions and centipedes are sufficiently common so that their poisonous effects are experienced rather frequently. It seems safe to assume, however, that the natives' fears are exaggerated, on the basis of experiences elsewhere in the tropics.

The most serious arthropod bite in most parts of the world is that of the black widow spider. This spider has been reported from nearby islands in the Marshalls but we found none on Arno. Likewise we found no ticks, chiggers or fleas.

A rather unusual pest of man in the Marshalls is the so-called "Bao in jekaro" (BIRD IN THE JEKARO), a 3/4-inch, yellow oedomerid beetle with strong cantharitic poisoning properties. It came readily to night lights on Arno and was found on several occasions flying in cloudy weather. Everywhere we heard the same story: that it was strongly attracted to the "jekaro", the sap from the inflorescence of the coconut, while the latter was being tapped. If a "Bao" falls into the sap and is eaten or swallowed, it produces kidney disturbances, which are well-known aftermaths of cantharidin poisoning. If crushed on the skin, it would produce a blister--as we discovered from personal experience. Crushing an individual

experimentally on the forearm produced a wheal about the size of a quarter and a blister which broke after a couple of days.

The ectoparasites of man on Arno include lice and, presumably, the tropical bed bug, although bed bugs were found only on Majuro. The apparent absence of bed bugs on Arno is remarkable, since the natives say that they were found during the Japanese occupation. Whatever their true status may be they were certainly not conspicuous on Arno during the period of our study.

Lice, on the other hand, are rather common, especially head lice, and the natives engage in a louse-catching ceremony. There is no evidence of louse-borne typhus fever and this disease would not be expected in such a comparatively cleanly people in the tropics where excessively heavy, tight clothing is unknown.

Three mosquitoes are commonly encountered on oceanic islands in the Pacific, the common house or night-biting mosquito of the tropics, Culex quinquefasciatus, and the two day biters, Aedes aegypti and Aedes marshallensis. The first of these, although found on most islands of the Pacific, was not found by us on Arno, much to our surprise and pleasure, since it was not necessary to use our bed nets. However, night-biting mosquitoes have been reported by others. The pantropic dengue-yellow fever mosquito, Aedes aegypti, is common, but only in the immediate vicinity of human habitations. As is the case elsewhere in the world, this species, originally a tree-hole breeder in Africa has adapted itself to the human race even more intimately than most of our domesticated animals.

The eggs are laid at the water's edge in the concrete cisterns and other drinking water receptacles on Arno. The wary larvae are bottom feeders,

swinging with S-shaped movements from surface to bottom to provide for their constant need for air on the one hand and food on the other. Adults have silver-banded legs and lyre-shaped markings on the thorax. We found them commonly in houses, including our laboratory, where they lurked beneath tables and in dark corners biting surreptitiously around the wrists and ankles.

Dengue fever has been reported from the Marshalls, yellow fever has not. Neither disease is endemic so the only danger lies in the introduction of the virus in a human carrier, an unlikely event since the carrier would have to travel from the point where he was infected to Arno within the incubation period of the disease and be bitten by a local mosquito on or about the time of the onset of the disease. In spite of this intricate timing, dengue broke out on various islands in the Marshalls and Gilberts during World War II and the possibility of reintroduction should not be overlooked in establishing quarantine regulations.

The native Marshallese mosquito is also a day biter and a close relative of the dengue-yellow fever mosquito (they both belong to the same subgenus, Stegomyia). This is a tree-hole breeder, the larvae which look and act like aegypti larvae superficially, occurring in water-filled holes in breadfruit and other trees and in coconut half shells in the canopy forest of Arno. Adults swarm about when one stands still in the shade of a breadfruit tree but they are not vicious biters. This species belongs to the so-called "Pseudoscutellaris Group", pseudoscutellaris being a vector of non-periodic filariasis in Fiji and Samoa. We saw no evidence of filariasis on Arno (the chronic form known as elephantiasis is conspicuous in some parts of the Pacific).

Two groups of insects, the cockroaches and house flies, are of importance in general sanitation on Arno. The cockroaches, although exceedingly abundant, are less conspicuous because of their nocturnal habits. The night-feeding skinks and geckoes eat large numbers of these but the population is still sufficient so that a certain amount of contamination undoubtedly takes place.

Far more important hygienically, in fact the chief agent other than man himself in transmitting enteric disease organisms, is undoubtedly the house fly. This cosmopolitan pest occurs in enormous numbers on Arno. It is somewhat smaller and darker than mainland forms but is nonetheless abundant and bothersome. But for this pest Arno might well qualify as the "paradise" so frequently extolled in tourist posters. The combination of unscreened privies, defecation in exposed intertidal areas, unscreened houses and unprotected food, constitutes an "ideal" situation for the particular kind of contamination to which the house fly is adapted. There is little doubt that the incidence of amoebiasis as given in Marshall's Report is attributable in part, at least, to contamination of this type.

Aside from the obviously favorable breeding places, the large numbers of house flies may be attributable to the comparatively few natural enemies. Skinks cannot catch flies as readily as some other insects. There is an efficient larval predator, the larva of the large Hermetia fly. This largest fly on the island was found at all times in and about privies but unfortunately does not reduce the population of house flies effectively.

Interrelations of Insects with Plants and Animals of Arno

The "food cycle" (Elton) or "food web" (Allee, Emerson, Park, Park, Schmidt) becomes exceedingly complex, even for a small association. However,

an attempt has been made to show in the accompanying Tables (I-V) some of the food chains as they exist on Arno. Unfortunately, quantitative data on insect populations are not available so calculations of biomass are not possible. However, it may be accepted as a basic premise and this was confirmed in a general way by field observations, that the herbivores of small size were most numerous in individuals. The role of each species listed in the food chains is indicated by appropriate letters as follows: herbivores (H), predators (Pred), parasites (Par), Saprophytes (Sapr), and scavengers (Scav). In general, species are listed in order, starting with groups of herbivores, then proceeding to scavengers and then to successive groups of predators, members of each group preying on members of preceding groups. The departure from this scheme in Table V (The Human Community) is self-explanatory.

It is noteworthy that most of the food chains end with lizards. This is a partial explanation for Marshall's statement that lizards (the blue-tailed skink in particular) are the the most numerous land vertebrates on the atoll. This does not mean that the skinks have no enemies for they were eaten on occasion by cuckoos, herons, chickens and even by a land crab, Geograpsus. However, none of these predators is generally distributed and none depends primarily on lizards for food. Therefore the lizards are relatively free from predators. They do have numerous endoparasites, including stomach nematodes and rectal flagellates.

The significance of these data from the viewpoint of atoll ecology is that the majority of the food chains are independent of man. Only in the immediate vicinity of villages is the picture significantly altered and in such places man enters the basic atoll food chains mainly via chickens and pigs. Aside from this, man has moved into the atoll biota and made his own niche.

Origin, Dispersal, and Speciation

The origin of the fauna and flora of Arno is lost in antiquity but it is possible to piece together in a general way the probable history on the basis of present day observations and certain logical inferences.

First, if one of the presently accepted theories of formation of coral atolls is true (see Wells' Report), then the insects and all other animals and plants must have reached Arno fortuitously, that is, by accidental transport. Various types of overseas' dispersal are known to occur (see Zimmerman, Ins. of Hawaii), among which are wind and convection currents of the air, birds, rafts of debris carried by ocean currents, native canoes and, more recently, trading boats and airplanes. Probably all but the last of these have contributed to the present biota of Arno. While it is difficult definitely to attribute the presence of a particular species to a certain type of dispersal, here again we have certain facts and certain logical inferences to go on.

Certainly the insects associated with man, such as lice, cockroaches, and the house fly, came with man and probably with early man in native canoes. The dengue-yellow fever mosquito was probably a more recent immigrant, since its dispersal elsewhere in the Pacific (Hawaii, Usinger) is known to be associated with the voyages of exploration and profiteering during the 19th century.

Insects which are attached to breadfruit, coconut, Pandanus, arrowroot, banana, and lime (e.g., scale insects, aphids, etc.) surely came with these crops when they were introduced by the natives.

Many insects of small size have been collected at high elevations (a mite at 30,000 feet, for example) in a study of several years' duration

(Glick). Especially during the infrequent but violent hurricanes, small forms, whether winged or not, must have been blown to Arno. Stronger flying insects such as the dragonflies and the monarch butterfly, we know are capable of long distance flights, aided no doubt by the wind. Thus Anax has flown to ships at sea and readily establishes itself on remote islands, wherever fresh water is to be found. Similarly, the monarch butterfly, though absent when its milkweed host is wanting, arrives soon after the accidental or deliberate establishment of Asclepias curassavica.

Though rafts may be necessary to account for endemic skinks, many of the animals which present apparently insuperable problems of dispersal (e.g., land snails, wingless weevils, etc.) could have been transported on the feet of migratory birds (Zimmerman).

Beyond a certain point this type of reasoning degenerates into idle speculation amd is of little or no use to anyone. However, it is instructive to carry the analysis as far as possible in order to piece together the separate parts that contributed to the present biota of Arno. To a certain extent the same sequence of events can be traced when a new islet is built up from reef to sand bar and thence, through accumulation of vegetation, to a cemented and subsequently decomposed substrate capable of supporting life as we find it on the densely covered islets. Literally all stages in this succession can be seen today. But this is not the end. Acultural processes are proceeding at an accelerated rate on Arno as elsewhere in the world (see Mason's Report) and the biota is bound to change too. In the long run this may be regarded as inevitable and therefore of no particular concern. However, the depauperate nature of the biota (e.g., the small number of different kinds of plants and animals as compared with an equivalent mainland area) and of even greater importance, the disharmonic

nature of the biota (e.g., the complete absence of certain types with consequent gaps or ecologic vacua) makes Arno peculiarly susceptible to disruptive influences. Furthermore, the limited economy of the people, based as it is on so few crops, could be brought to a standstill by failure of one of the staples. Hence, it is important to look to the future and try to foresee immediate and long-term dangers which might ensue from the dispersal and establishment of noxious plants and animals from nearby or farther distant islands and mainland areas.

The most imminent cases of this kind are on the neighboring atoll of Majuro. Due to wartime activity and air transport, Majuro, and to an even greater extent, Kwajalein and Eniwetok, now support several immigrant insects which, if introduced to Arno via the native canoes or the copra boat, would prove to be detrimental to the natives. Foremost among these potential immigrants are the infamous migratory locust and a second, slightly smaller grasshopper, the black widow spider, the night mosquito, an Odynerus wasp and a tick. In addition, bed bugs, fleas, the coconut Brontispa beetle and the copra beetle are either absent from Arno or are so scarce that we did not find them. Obviously an effort should be made to prevent or delay their establishment or increase on Arno.

Serious pests from more distant islands of Micronesia include the giant African snail, the Rhinoceros beetle (Oryctes), and a malaria mosquito, any of which could reach the Marshalls from Guam or Saipan unless quarantine regulations are strictly enforced.

Table I

Strand Community

A. Open Beach Stratum - Mostly Nocturnal

Sand crickets - H.
Sand fleas - S.
House flies - (human feces). Sapr. (daylight).
Robber flies - Pred. (Daylight).
Marine water striders (blown onto beach) - Pred.
Crab spiders - Pred.
Ghost crabs - Pred.

Rock geckoes - Pred.

Plover - Pred.
Curlew - Pred.
Tattler - Pred.

Marine Insect "Community"

A. Surface Stratum

Pelagic plankters - Pred. H.
Marine water striders (Large - Open ocean / Large - Tidepool species / Small - Protected coves) Pred.

Table II

Inner Beach Community

A. Foliage Stratum

Leaf-mining fly - H. Scaevola
Plant bugs - H. Scaevola
Caterpillars - H. Cordia, Messerschmidia, Sida
Leaf-cutting bee - H.
Aphis - H.

Ants - Scav.

Ladybird beetles - Pred.
Green lacewings - Pred.
Syrphid flies - Pred.
Spiders - Pred.

Geckoes - Pred.
Skinks - Pred.

B. Bark and Dead Wood Stratum

Bark beetles - Wood borers
Round-headed borers - Wood borers

Rove beetles - Pred.
Predaceous bugs - Pred.
Spiders - Pred.

Geckoes - Pred.
Skinks - Pred.

C. Ground Stratum

Sand crickets - H.

Crab spiders - Pred.
Ghost crabs - Pred.

Rock geckoes - Pred.

Golden plover - Pred.
Heron - Pred.

Table III

Open Woodland Community

A. Coconut - Pandanus Stratum

Coconut scale - H.
Sugar-cane weevil - H.
Bark lice - Scav.
Ants - Scav.
Cockroaches - Scav.

Earwigs - Pred.
Luteva - Pred.
Spiders - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

B. Ground Cover - Vigna, Wedelia, Fleurya, Fimbristylis, Lepturus, Cassytha

Red spider mite - H. Vigna leaves
Hopping plant bug - H. Vigna and Fleurya
Green grass bug - H. Grasses
Leafhoppers - H.
Sedge bugs - H. Fimbristylis
False chinch bugs - H. Fimbristylis
Thrips - H.

Bees - H.
Caterpillars - H.
Mealybugs - H.
Aphids - H.
Ants - Scav.

Damsel bugs, Nabis - Pred.
Spiders - Pred.
Thrips - Pred.
Stink bugs - Pred.
Ladybird beetles - Pred.
Green katydids - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

Table III (continued)

C. Fallen Green Coconuts

Rats - H.
Coconut crabs - H.
Mosquitoes - Larvae-detritus.

D. Rotten Pandanus Fruit Stratum

Vinegar flies - Sapr.
Fruit beetles - Sapr.

Rove beetles - Pred.
Spiders - Pred.
Predaceous bugs - Pred.
Predaceous mites - Pred.

Geckoes - Pred.
Skinks - Pred.

E. Soil Stratum

Earthworms - Sapr.
Millipedes - Sapr.
Sowbugs - Sapr.
Garden centipedes - Sapr. H.
Silverfish - Scav.
Ants - Scav.

Hermit crabs - Pred. Scav.

Rock Geckoes - Pred. Night
Ground skinks - Pred.

Table IV

Canopy Woodland Community

A. Breadfruit Stratum

Corizid bug - H. Bird's nest fern
Leafhoppers - H.
Spider mite - H. Breadfruit leaves

Mosquito larvae - Detritus. Tree holes

Ants - Scav.

Spiders - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

B. Underbrush Stratum - Alophyllus, Pipturus, Terminalia, Pisonia, Cordia

Aphids - H.
Mealybugs - H.
Leafhoppers - H.
Corizid bugs - H.
Fruit flies - H.

Ants - Scav.

Spiders - Pred.
Ladybird beetles - Pred.
Syrphid flies - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

C. Fallen Log Stratum

Fungous flies - Sapr.
Fungous beetles - Sapr.

Weevils - Woodborers
Termites - Wood feeders

Wireworms - Sapr.
False wireworms - Sapr.
Stag beetles - Sapr.

Ants - Scav.

Table IV (continued)

C. (cont.)

Earwigs - Pred.
Spiders - Pred.
Pseudoscorpions - Pred.
Scorpions - Pred.

D. Rotten Breadfruit Stratum

Vinegar flies - Sapr.
Fruit beetles - Sapr.

Rove beetles - Pred.
Spiders - Pred.
Predaceous bugs - Pred.
Predaceous mites - Pred.

Geckoes - Pred.
Skinks - Pred.

E. Soil Stratum

Earthworms - Sapr.
Millipedes - Sapr.
Sowbugs - Sapr.
Garden centipedes - Sapr. H.
Silverfish - Scav.
Springtails - Sapr.
Ants - Scav.

Rock geckoes - Pred.
Ground skinks - Pred.

F. Taro Pit Aquatic Stratum

Midge larvae - Detritus
Shrimp - Pred.
Snails - H.
Dragonfly naiades - Pred.

Table V

Human Community

Man - Omnivorous. Eats fish, coconut, breadfruit, taro, pandanus, bananas, papaya, and various imported foods.

Ectoparasites - Lice, bedbugs
Endoparasites - Amoebae, hookworms, etc.

Domesticated Animals

Dogs - scavenger - copra - garbage
Pigs - scavenger - soil insects, roots
Chickens - Omnivorous. Copra, ground insects, skinks
Cats - Omnivorous. rats

Household Vermin

Rats - Eaten by cats

Ectoparasites - mites and lice

Cockroaches - Evania parasites
Termites
Mosquitoes - cisterns - Dragonfly naiad predators
Houseflies - Hermetia parasites - Privies
House gecko eats all household insects