

Island Biology: We've Only Just Begun

Sherwin Carlquist

At the time I write this article, I have just completed a scientific-style book on island biology. Especially because this will be my third book-length essay on insular plants and animals, and since it overlaps very little with the previous two, one might expect that I would sense the massiveness of what biologists have to tell us about life on islands and would be overwhelmed by the enormity of our knowledge.

Quite the contrary. I have been impressed, instead, with the number of topics on which I could report nothing meaningful, or offer only speculation, because we lack information. I have repeatedly noticed numerous problems on islands, problems that appeal to me as basic and exciting. I have simultaneously wondered why so few biologists seem to want to work on them. We are, today, in an era when "ecology" and "natural history" are favored words. Access to islands is far easier than it has ever been, and island biotas, many relatively intact now, are going to be devastated soon to the point where all we will have to study are shreds of the marvellous fabrics of evolution that inspired Darwin and Wallace, yes, and so many other biologists as well. Even forgetting this urgency, I am tempted to editorialize — and will. There are, of course, some biologists doing excellent work on islands — more about them later. Others might welcome the opportunity to work on island areas. I would ask those others, "Are you going to inflict the narrowness of your declared area of specialization on insular biotas, or are you willing to let islands open your insights so that you can ask new questions, solve new problems, and indulge in personal growth as well?" I don't mean to sound sarcastic; I only mean that many discoveries yet to be made on islands cannot be predicted, and are made by the open-minded biologist.

One example that comes to mind is the Darwin's Finches and the history of their study. We know that Darwin reported on them in the *Journal of Researches* of the Beagle voyage. About

80 years and several major expeditions elapsed between Darwin's visit and that of David Lack. One might wonder why so much time had to elapse before David Lack's (1947) classic book, which adds so much to our knowledge of these birds. I would guess that Lack on the Galápagos was a keen and imaginative observer, who did not have preoccupations about what he ought to find or what methods he should use. Rather, he merely tried to find out all he could about the Darwin's Finches. Even so, more remained for workers such as Robert I. Bowman to uncover and describe. So I am simply asking, "How many truly outstanding problems, like the Darwin's Finches prior to David Lack's studies, are still waiting to be studied?" The answer I am obviously going to give is that there are far too many problems which have been studied only in a preliminary way, and many more studied not at all. The fact that MacArthur and Wilson (1967) can construct intricate mathematical models of island situations involving integral calculus does not mean that work on islands is in a concluding phase — or that we must all use mathematical models now. It only means that those two workers have explored one particular way of looking at island problems, and done well.

Evolution of Insular Plants and Animals

First, I want to cite some examples from the field of dispersal. This is a basic problem, for if we don't understand how oceanic islands have become populated, we really can't speak meaningfully about the subsequent evolution of plants and animals on islands. A few years ago, I met a graduate student at the University of Hawaii, Carolyn Corn. She asked me about potential research problems in the Hawaiian Islands. I suggested she might do some work on the chief forest tree of the Hawaiian Islands, *Metrosideros polymorpha* (Myrtaceae). This genus occurs on many high Pacific islands, although we don't know how it got there. However, botanists avoid the Hawaiian *Metrosideros* populations (they seem to hybridize a lot and

specimens are difficult to name). Merely mentioning *Metrosideros polymorpha* in some quarters evokes despair or annoyance. However, as a footnote, I would like to say that a taxonomic morass can be a great opportunity for evolutionary study.

Metrosideros has small seeds, a fact that suggests it can disperse easily — it colonizes new lava flows in the Hawaiian Islands, in fact. Studying dispersal of this tree may not seem as glamorous as studying problems that involve spectrophotometers and electron microscopes and computers. However, Corn was apparently not intimidated by the tendency to consider studies in dispersal as old-fashioned and out-moded, nor by the tendency to avoid *Metrosideros polymorpha* as a research subject because it is complicated. To fulfill requirements for a term paper in an undergraduate course at the University of Hawaii, she undertook experimental studies on *Metrosideros polymorpha* seeds. She discovered, by using homemade equipment or readily available items (freezer, refrigerator), that *Metrosideros* seeds can become airborne in air currents of 5-19 k.p.h. Seeds can survive temperatures of -30°C for at least 6 hours. After soaking in seawater for 39 days, then drying for an additional 7 days, seeds can still be germinated:

Corn has virtually explained how this important tree spread throughout the Pacific Basin. If seeds can become airborne so easily, they can be carried aloft into the high-speed air currents (up to 206.5 k.p.h.), known as jet streams, which travel from Indo-Malaysia to the area of the Pacific in which the Hawaiian Islands are located. The seeds can withstand the cold of these air currents, which occur at 9144-12,294 m. Seeds could then drop as these currents decelerate over the Hawaiian Islands. Seeds could even drop into the surf, be washed ashore, dry out, be blown upwards to suitable sites, and still germinate successfully. Corn, without grant funds or special equipment, has made a very important contribution to Pacific biogeography. Even though it's "just a term paper," I hope she publishes this work — I feel it is much more significant than many

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papers I have read in the field of Pacific biogeography.

Of course, I would like to congratulate J. L. Gressitt, C. M. Yoshimoto and their co-workers, whose studies on aerial dispersal of insects (by trapping in nets on ships at sea, in traps on airplanes, or nets on land areas), published mostly in the journal *Pacific Insects*, have virtually proved how insects reached the Hawaiian Islands and various other Pacific islands.

I would also like to mention some very significant studies (Proctor, 1968; Vlaming and Proctor, 1968) that show how shore birds and waterfowl can, in fact, eat and retain seeds (especially moderately large seeds) for long periods of time (hundreds of hours) under experimental conditions, excrete them in viable condition, and thus serve as potential vectors for such seeds. I had hypothesized (1967) that internal transport of seeds in shore birds and, to a lesser extent, in waterfowl, must have been responsible for introduction to the native Hawaiian flora, because these birds are both migratory and eat seeds and other plant materials. The results of Proctor and Vlaming come close to confirming this. Now, it would be valuable to perform similar experiments with the migratory shore birds that actually visit the Hawaiian Islands (bristle-thighed curlew, Pacific golden plover, ruddy turnstone, sanderling, wandering tattler), using fruits and seeds of plants actually native to the Hawaiian Islands (such as those of *Dianella*, *Coprosma*, *Santalum*, etc.). With such results, we should be able to prove just about definitely that land-bridges to the Hawaiian Islands are egregious fictions, and that continental drift is completely irrelevant where oceanic islands (and perhaps many other situations) are concerned. This seems extremely important to me, despite the fact that expensive equipment is not needed.

I recently supervised a seminar on adaptive radiation. I was faced with the ugly task of having to say to student speakers that despite the wide and intriguing ranges in morphology seen in insular genera, we don't have any ecological observations on most of these to show how these cases of adaptive radiation "work," or have evolved, and so I couldn't allow them to be presented as examples of adaptive radiation (they are examples that could be studied, of course). We don't know why there are so many different sizes and shapes in the Hawaiian amastriid snails. We don't

know the ecological requirements and habits of many insular insect groups that appear to have undergone adaptive radiation. We don't know the climatic, elevational, and edaphic requirements of plant species that are obviously products of adaptive radiation (we find only a few hints in good floras, none at all in less complete floras).

Herre (1933) issued a plea for study of the fantastic assemblage of endemic genera and species in Lake Lanao, Philippines, an assemblage that has evolved in about 10,000 years. Apparently this call has not yet been answered (Lowe-McConnell, 1969). We know as much or less about this remarkable example of adaptive radiation than Darwin knew about the geospizid finches of the Galápagos. Will we ever learn about their differing ecological requirements, anatomical modifications, etc.? And this is just one of many examples I could cite.

Speaking of adaptive radiation, I could mention several plant groups that show exceptional adaptive radiation on islands. Among these are *Echium* (Boraginaceae) and *Sonchus* (Asteraceae) on the Canary Islands and Madeira; the *Dubautia-Argyroxiphium-Wilkesia* complex (Asteraceae) and many other genera in the Hawaiian Islands. I have seen some of these in cultivation in California; some appear to grow successfully only along the coast, some appear just as healthy, if not healthier, at inland locations. One could study the tolerances of species in these groups to various conditions, from coastal to inland, in a locality like California or in one of the archipelagos themselves. One could employ a series of transplant stations like those used by Clausen, Keck, and Hiesey (to my knowledge, no insular plants have ever been studied in this way). One could, of course, use the more precise and elaborate conditions that controlled growth chambers or "phytotrons" offer. For the first time, we might be able to *measure* adaptive radiation. We really do not know whether some of these plants have very broad or narrow tolerances, or what extremes they can withstand, or what adaptation to various island climates, supposedly distinct in their "moderation," constitutes. A planting of various *Echium* species at the Rancho Santa Ana Botanic Garden by Cornelius Lems proved how interesting these studies could be, although the untimely death of Lems prevented full utilization of these plantings. During one

winter while the *Echiums* were in cultivation, a sharp freeze occurred, and showed dramatically that the species of *Echium* differ markedly, corresponding to their coastal versus upland native habitats, in resistance to frost.

An interesting by-product of experimental physiological work with insular plants might be the demonstration of how arborescence takes place during the evolution of herbaceous or non-arboreal plants under the relatively uniform conditions of oceanic islands. When one sees the ordinary cultivated cabbage form rosette trees in islands such as the Canary Islands or some of the West Indies, one can imagine how we might determine whether and to what extent moderated temperature throughout a year, lessened seasonal differences in day length, or other factors could induce increased woodiness.

Another series of insular problems amenable to experimental approaches include those of flightlessness of insects on islands. Although a few experiments have been done, they are inconclusive in nature and other conflicting conclusions. We need to know whether flightlessness on tropical islands derives from such factors as restricted stable habitat and geophily, such as Darlington (1943) cited, or whether Darwin's idea that wind pressure plays a part is at all operative. Does flightlessness of insects on subantarctic islands involve factors different from those invoked by Darlington, as Gressitt (1970) claims? Also, the high proportion of flightless insects on high equatorial peaks may have explanations other than those that apply on tropical islands. Cold temperature might be a factor, for nightly temperatures drop sharply on equatorial peaks. Inability of insects to fly when temperatures are lowered, once investigated with cockroaches, could be tested. Are flightless insects hardier, do they have "greater vitality," as Darlington claimed? This could be studied easily enough, as could the supposed effect of wind pressure. Why is there sexual dimorphism in the subantarctic moths in degree of wing presence — nearly fully winged in males, vestigial-winged in females?

Nature of Speciation

Experimental work of another sort awaits enterprising botanists who might be interested in the nature of speciation on islands and whether its genetic modes are different from those on continental areas. For example, Gillett

and Lim (1970) found that the numerous Hawaiian species of *Bidens*, when cultured and artificially crossed, show virtually no sterility barriers. Apparently geographic isolation is basic to speciation in this group. Is this true in all insular groups that have speciated on islands? One study is hardly a fair sample. Recently, S. H. Sohmer (unpublished manuscript) has suggested on the basis of his experimental work that *Charpentiera* (Amaranthaceae) species on the Hawaiian Islands are interfertile, but evidently are maintained as entities by distinctive ecological preferences. Are insular "species" different from mainland "species?"

Likewise, although hybridization is abundant in such insular floras as the Canary Islands, the Hawaiian Islands, and New Zealand, some of these hybridization events are recent, some perhaps so old that they no longer appear to be hybrids. One careful analysis of stable hybrids, resembling "species," is that of Gillett (1966). We obviously need many more such studies. I do not know of any "progeny test" work on natural hybrids on insular areas; the degree of variability, segregation to parental types, and fertility would be interesting to know. The modalities of reproductive biology may be quite different on islands, but we should have more than circumstantial evidence.

Some plant species have clearly diminished dispersibility on some islands (especially Juan Fernandez, Hawaii, Samoa), often in relation to ecological shift into wet forest. Although this is morphologically visible in increased seed size or loss of a mechanism like gelatinous coating on seeds, is there also a concomitant shortening of seed viability? Is fertility of insular plants lower than that of comparable mainland species, as appears to be the case in some? If so, in which and why?

One phenomenon long ago noted by botanists such as Joseph Hooker is the tendency for flowers in insular floras to be relatively colorless — chiefly white, green, and yellow. This must be related to the fact that different pollinators are available on oceanic islands as compared to mainland areas, but we really do not know any details of this story. The same appears to apply to equatorial alpine areas, but no one has compiled percentages of flower colors in such an area, to my knowledge (one would expect special pollination difficulties in the equatorial alpine floras). Likewise,

flowers on certain islands, such as the Hawaiian islands, New Zealand, and the Juan Fernandez Islands are (with the exception of bird-pollinated flowers) relatively small and lacking in fragrance. Is this related to absence of long-tongued bees? We simply do not know how most insular flowering plants are pollinated — there are so few observations. There have been a few on the Galápagos Islands recently — those of Linsey (1966), Linsey, Rick and Stephens (1966), and Rick (1966). Comparable work in the Hawaiian Islands is very much needed, and would yield much more interesting results. Studies on pollination biology can be time-consuming, but the information to be derived on islands and on equatorial alpine areas is potentially of great importance in understanding the total picture of evolution in these areas.

The reason for some notable gaps in our knowledge of evolutionary nature of island floras and faunas is probably that most forays take the form of collecting trips, rather than observation sessions. While I could protest the making of additional collections from those areas already well-collected, the lack of ecological information about species is really a more important cause for alarm. Labels on most specimens of island plants and animals are, to be kindly euphemistic, models of brevity. One notes that, for example, the careful observations on behavior of birds, landshells, and insects made by Perkins (1913) during extended stays in localities in Hawaiian forests have few sequels or equals. If we are to understand the adaptive radiation in a group, we must understand its ecological requirements and habits rather thoroughly.

In this regard, I would like to mention the achievements of those who have studied the Hawaiian drosophilids (e.g., Spieth, 1968; Carson et al., 1970). Here, there has been an admirable combination of taxonomic work, field studies, and laboratory work. This synthesis promises to provide us with some of the richest and clearest stories of speciation in insular biotas. For example, we now know on which islands of the Hawaiian chain origins of species groups in *Drosophila* took place, and which islands were subsequently invaded and in which order (Carson et al., 1970). The very curious "lek" behavior of Hawaiian drosophilids during mating could only have been discovered during field studies (Spieth, 1968).

Likewise, Zimmerman (1948) has reported some very drastic shifts in habits and habitats for Hawaiian insects. For example, bugs of the genus *Saldula*, typically aquatic elsewhere in the world, are arboreal in the Hawaiian Islands. The damselfly *Megalagrion oahuense*, unique among the Odonata, has nymphs not aquatic but terrestrial. I have hypothesized in my current book that perhaps these transgressions into new habitats may relate to the nature of the Hawaiian environment. Lakes and permanent streams are limited in extent because of the porosity of Hawaiian soils and rocks. There is sufficient area for establishment of aquatic organisms, but I would guess that further evolution must perforce feature crossing of ecotones. This may be possible because the Hawaiian wet forest is not really "dry land," but a series of quite wet microhabitats. Forest litter may be water-rich, and the bark of trees, often dripping, may in many cases be covered thickly by mosses, liverworts, ferns, and lichens which form wet pockets. In an analogous way, three species of the weevil genus *Proterhinus* have shifted in the Hawaiian Islands from mining of decayed wood to boring in living tissues. One species has entered leaves of *Astelia*, an often-epiphytic liliaceous plant; two others have entered leaves and living stems, respectively, of the saxifragaceous shrub *Broussaisia*. I am guessing that transition to *Astelia* leaves has occurred because of the contact between *Astelia* plants and rotting bark and wood. Likewise, in the case of the *Broussaisia* weevils, perhaps they have shifted because old *Broussaisia* shrubs, common components of wet forest, contain both rotting and living portions, so proximity once again may have provided the opportunity for "character release." Likewise, the tipulid crane-fly *Limonia foliocuniculator* has abandoned the soil, rotting vegetation, or water typical of tipulids in favor of mining leaves of *Cyrtandra* (Gesneriaceae). *Cyrtandra* does grow in exceptionally wet, shady gulches of the Hawaiian Islands. Are the above hypotheses correct for these interesting shifts in habits? Field studies might show.

Likewise, we have other interesting examples of changes in habits by animals. The Philippine genus of skink lizards *Brachymeles* shows an interesting series in reduction of legs, from normal to legless. We do not know what the ecological requirements of the various species are, and how different habits

might be related to degrees of leglessness. I would guess that there must be a relationship.

Gigantism has apparently occurred in groups of land shells on New Caledonia, Hawaii, and other island groups. Why? Do gastropods with small shell sizes migrate to islands more easily, and once there, do they undergo increase in size during evolution into new habitats, where nature of food supply is commensurate with a larger body size? Do gastropods with smaller shell sizes form the immigrants to islands? One could calculate this, or find other factors which favor long distance by land snails (we know very little about how land snails migrate, but we know from distribution of families such as Tornatellinidae that they are very adept at long-distance dispersal). Gigantism in island lizards has been noticed on a number of occasions, but studied in detail only in a very few cases. The results of Soulé (1966) are promising in this regard, but many questions remain unanswered. For example, Soulé suggests that absence of predation may be related to larger sizes of lizards on the Gulf of California Islands, but he readily concedes we have no data on predation there. Changes in bill, wing and tarsus length in insular birds (such as in the work of P.R. Grant on the Tres Marias Islands) show us subtle facets of how congeneric species on islands occupy non-overlapping ecological niches.

I like to consider southwestern Australia as an island – it has many aspects of one. This climatically and geographically isolated province is like an “island within an island.” As such, it presents many rather amazing phenomena. One I always enjoy mentioning is the tree mistletoe, *Nuytsia floribunda* (Loranthaceae), which parasitizes grasses and other ephemeral vegetation in its vicinity. Biological problems remaining to be solved in southwestern Australia are legion. We know little about pollination in this amazingly colorful flora. Half of the family Droseraceae as a whole is endemic to the southwestern corner of Australia, and there the genus *Drosera* has radiated into habitats unlike those of *Droseras* anywhere else in the world. Southwestern Australian species of *Drosera* include broad-leaved rosette perennials, minute ephemeral annuals, “bulb”-forming perennials, vines, “miniature trees,” and stoloniferous plants. This genus is only one example – there are very many genera in this flora with unusual habits and adaptive

radiation. Why are there so many cladodial-shrubs in southwestern Australia? Why do *Banksia* and *Hakea* (Proteaceae) show such an incredible diversity of leaf types? Is there reversibility among these? Why does southwestern Australia have the highest rate of speciation (as figured by species per family, for example) of any region in the world, despite the fact that this area is rather flat topographically and has a relatively even gradient of rainfall from interior desert areas to the southwesternmost corner? What is the adaptive significance of curious plant and leaf forms (such as the perfectly dichotomous leaves of *Stirlingia* and *Franklandia* of the Proteaceae, for example)?

As the above indicates, we lack knowledge of ecology, and therefore of factors influencing evolution on many islands. In many instances, we do not even have the benefit of “alpha taxonomy” in these areas in the form of monographs or floras or faunas. Ironically, this rudimentary state of knowledge based on field experience coexists with a high degree of instrumentation in American science, so that highly sophisticated studies are possible yet we have only limited basic knowledge of many islands. New species continue to be discovered rapidly in Western Australia (as many as 15% of that flora's species may currently be undescribed). As for the floristic works, we do now have good floras of New Zealand and of the Galápagos Islands, but we have no complete and current floras of such important areas as the Hawaiian Islands, the Canary Islands, Madagascar, New Guinea, and most portions of Australia and the Malaysian islands. While I am not as familiar with the faunistic coverage, I suspect our knowledge is equally poor, especially in insect groups. Without this foundation, building ecological and evolutionary knowledge is hampered. I note that MacArthur and Wilson (1967) have drawn heavily for their computations on island avifaunas. Birds of islands are relatively well known, but few other groups of insular organisms are known with any degree of completeness.

Future of Island Biology

We know that many species of animals and plants are going to become extinct over the next few decades. Perhaps the majority of these extinctions will be on insular areas. If we

consult, for example, the I.U.C.N. Red Data Books, we see that extinction or endangerment on insular areas is well out of proportion to a random condition. That insular organisms should be vulnerable on account of limited land area and several other reasons is quite understandable. In many instances, we will be able to do little more than slow this extinction. This places a great responsibility on biologists. It may shock some conservation-oriented biologists when I say that, in all candor, I cannot see a realistic possibility for saving most of these areas or organisms. The future may well scorn today's biologists not for failing to be activists in the cause of conservation, but for *failing to study endangered organisms while they are still extant*. I can visualize future generations wondering in just what kind of locality a plant alive as of 1972 grew, or what the habits and diet of a particular bird or lizard or insect on an island were.

Islands are great museums for the biologist, and many mainland biologists will and should want to visit them. If they do, they can make contributions, however small they may seem. Just good photographic records of rare species would be very helpful (and I would hope for photographs of good resolution and depth, not just color snapshots). Many species, now extinct, have never been photographed, or photographed adequately. Few extinct or endangered species have specimens on which location and ecology are described accurately. Very few extinct or endangered species have been collected in the form of liquid-preserved specimens suitable for anatomical studies. We cannot predict what extinctions will take place; even species relatively common now may be completely extinguished by agriculture or mining (this is currently occurring rapidly in southwestern Australia). Faced with this, the biologist may wish to take part in efforts toward conservation. However, realizing that many such efforts will inevitably fail, he would, I hope, undertake studies possible only on the living organism, and would collect full data, specimens, and photographs. If you had to choose between letting an organism become extinct without gathering any additional information, or collecting as much information possible about it, which would you choose? The answer is obvious, but in fact, we are by default choosing the former alternative all too often.

At any rate, islands remain the marvelous laboratories of evolution that Darwin and Wallace found them to be more than a century ago. These laboratories, however, have hardly been used, in comparison to what they offer. I could have expanded my listing of important problems and questions above by several times easily. While some areas may appeal as very glamorous (the Galápagos Islands have recently been enjoying a tremendous vogue, for reasons not entirely comprehensible to me), a wide variety of islands deserve attention and offer enormous opportunity. I could also add that islands are often truly delightful sites for research.

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Errata

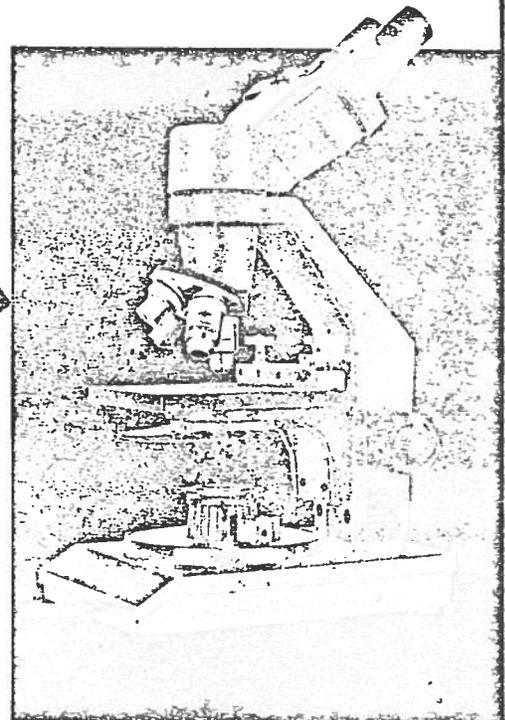
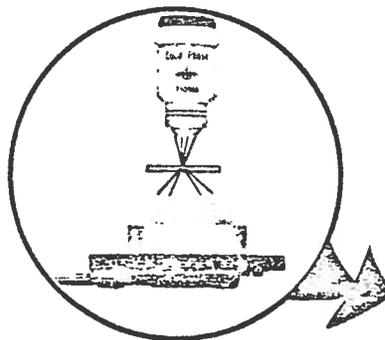
On page 47 of the January 1972 issue, the affiliation for Martin D. Brown should be: Fullerton College, Orange County, California, not California State College.

In the section on New Titles (*Bio-Science*, 22(1): 60, 1972), the title of the book by Seymour S. Cohen should have read: *Introduction to the Polymers*, not *Introduction to the Polymers*.

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