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THE BIOTA OF LONG-DISTANCE DISPERSAL. I. PRINCIPLES OF DISPERSAL AND EVOLUTION

By SHERWIN CARLQUIST

Claremont Graduate School and Rancho Santa Ana Botanic Garden, Claremont, California

ABSTRACT

A growing consensus of biologists now favors the effectiveness of long-distance dispersal as a means of populating islands. The observational and experimental bases on which this opinion rests are strong, but additional work is needed. A clear understanding of long-distance dispersal is essential to an understanding of evolutionary trends on oceanic islands, because immigrant patterns are different from relict patterns. Since oceanic islands are short-lived, the evolutionary history of waif immigrants is also short. If a continental island maintains long isolation, arrivals by long-distance dispersal may show evolutionary patterns more completely, as is true on New Zealand, for example. The evolutionary patterns of waif biotas are influenced by isolation, by the broad range of available ecological opportunities, and, to a lesser extent, by the moderation characteristic of maritime climates. In addition to problems involved in becoming established, immigrants must overcome genetic disadvantages inherent in the fact that the number of original colonists is small. Increase of genetic variability may be governed by ecological diversity, and persistence of a phylad may be increased by maximizing outcrossing and hybridization. Among features which are exhibited by waif biotas are adaptive radiation, flightlessness in animals, loss of dispersal mechanism in plants, and development of new ecological habits and growth forms. Each of these adaptations is evidently governed by a wide variety of factors. "Weedy" groups seem to possess the greatest ability to disperse and become established; they also excel at sensitive adaptation to island conditions. The waif biota contains few relicts except for "recent relicts."

INTRODUCTION

THE faunas and floras of oceanic islands possess many distinctive characteristics which have long attracted attention. Interest in these lands as "evolutionary laboratories" was crystallized during the Darwin-Wallace era and has not diminished since. Floristic and faunistic studies of islands have been frequent (cf. Blake and Atwood, 1942; Darlington, 1957; Thorne, 1963), although more are needed and will undoubtedly be produced. Discussions of the possibility of dispersal to oceanic islands, and of whether particular islands are oceanic or continental, have occupied an inordinate number of pages and created considerable controversy. Among the many discussions there have been a few outstanding contributions dealing with the problems of dispersal and patterns of insular evolution. Among those commendable for their comprehensiveness and rational outlook may be cited those of Gulick (1932), Zimmerman (1948), Darlington (1957), and Thorne (1963). To a surprising degree, the assessments which most appeal to the writer are those which confirm and extend the concepts of Darwin (1859) and Wallace (1880). Although adherents of alternative proposals may still be found, there seems to be a growing consensus among biologists regarding many of the ideas discussed below.

The reasons for presenting an additional essay at this time are several. Interest has shifted recently from a primarily floristic-faunistic outlook to a concern for evolutionary processes on islands. Principles which have emerged clearly, as well as those which can only be tentatively enunciated, are reviewed here because a foundation for further research seems needed and because a critical sifting of past hypotheses may prove helpful. An earlier generation of biologists stressed the amazing speciation which has occurred on oceanic islands. Today's biologists are inquiring into the background of this speciation: its origin and direction and its underlying mechanisms. The basic mechanisms of evolution on oceanic islands are the same as those on continental areas and no new "laws" are needed, yet the direction evolution takes and the products which result on islands are often quite distinctive, at least modally. Understanding of these evolutionary concepts must be based on sound principles of dispersal and biogeography. Therefore, these topics as they apply to the waif biota must be reviewed, however briefly. For example, the peculiar rosette trees of the Juan Fernandez Islands must be interpreted as relicts by those who see long-distance dispersal as an inadequate explanation for the Juan Fernandez flora. Those who can envisage these islands as recent and populated by means of long-distance dispersal can, on the contrary, regard the rosette trees as innovations —the products of recent evolution.

Literature on the evolution of island biotas is widely scattered among zoological, botanical, evolutionary, and other journals and books, and needs to be synthesized. Too often, patterns of one group only, of animals only, or of plants only, are considered. There is a definite need for integrating the data from various disciplines. Information from one field not only often proves valuable to studies in other fields, but must eventually be coordinated into larger patterns.

The biota characteristic of oceanic islands is, ironically, not always found on such islands and may occur in other situations as well— hence the title of this paper. Oceanic islands near continents may show an essentially continental pattern. A completely glaciated continental island will bear a biota entirely oceanic in character (Fleming, 1963). A remote oceanic island may be too new or ecologically too poor to have shown the evolutionary patterns described below. Despite incongruities such as these, the concept that there are oceanic and continental islands, the differences between which reflect their geological history, still seems useful and is generally accepted (Fosberg, 1963). No scheme for classification of islands, however, can hope to reflect unexceptionably both geological history and the nature of the biota.

Most oceanic islands are volcanic, and volcanic islands are, on a geological scale shortlived. Therefore, true oceanic islands clearly display the early and middle stages in the phylesis of a waif biota; but such islands may vanish before evolutionary products are well advanced (for example, before they are differentiated to the level of distinct families). Ironically, later stages in the evolution of the long-distance-dispersed biota are often shown on old continental islands. For example, New Caledonia and New Zealand have been isolated for a very long time — since the Createaceous, if not much longer. Waif arrivals to these islands have had a much longer time in which to evolve than have arrivals to the Hawaiian Islands, which are probably no older than Miocene. The discerning biologist can, in most instances, detect which elements in the New Zealand biota are waif immigrants, and can follow their evolutionary patterns separately from those which probably are relicts from an era of continental interconnection or near-interconnection (such as conifers, primitive flowering plants, *Sphenodon* and *Leiopelma*). With an extended period of isolation and with a sizable land mass available for occupancy, the waif biota of New Zealand has been able to evolve extensively, to show waif evolutionary patterns better than such biotas on most oceanic islands. It is ironical to say that the evolutionary products of waif biotas are perhaps best studied on old continental or continental-like islands; nevertheless, it is possible to cite oceanic islands on which insular patterns are well fulfilled. Among these, the Hawaiian Islands surely deserve first place, although part of the evolutionary history of Hawaiian organisms may have taken place upon now-vanished island chains adjacent to the present Hawaiian Islands. The Hawaiian Islands are favored by ecological richness, extreme remoteness, and (for oceanic islands) relative oldness. The Galápagos Islands, although famed for their insular biota, are relatively young, relatively poor ecologically, and relatively close to continental areas. With the possible exception of Darwin's finches, the Galápagos biota best serves to show earlier stages in the evolution of insular groups. Completing this spectrum from old to young waif biotas, the earliest stages in evolution are perhaps best studied in animals and plants which have been introduced to islands by man. Mice have proved good examples (Berry, 1964).

Some persons will note that waif biotas are represented in non-insular but isolated situations as well: mountain-tops, caves, lakes, and the like. This is true. Islands differ from such situations, however, by offering a broad gamut of ecological opportunities (shore to alpine, aquatic to xeric) instead of a single extreme habitat (such as alpine). Some non-insular waif biotas can be informative, however, and are used among the examples to follow. Thus, a waif biota can occur wherever arrival is by means of long-distance dispersal and where isolation is high for a prolonged period of time. The assumption made here that waif arrivals on continental islands can be distinguished from preinsular arrivals will no doubt be challenged. Our methods of separating the two groups are inferential, but should improve as our knowledge of waif-biota characteristics become surer. I believe that most groups on an old continental island, and especially on a remote one, can be discriminated, and that we should aim for such discrimination. The basis for this distinction is now, and will continue to be, largely a comparison with oceanic islands. For example, if conifers and primitive flowering plants are subtracted from the New Zealand flora, and if differences in climate are taken into account, the composition of that flora is remarkably similar to the Hawaiian flora with respect to families and even genera.

Hypotheses respecting the dispersal and evolution of waif biota are presented here as a series of principles, or if one prefers, topic sentences. The number of such principles could be enlarged or reduced, and ideas placed under some headings could just as well have been entered under others. Many of the ideas are closely interrelated, and lead me to conclude that there is an "insular syndrome" which derives (1) from difficulties of long-distance dispersal; (2) from isolation; (3) from ecological opportunity; and (4) to a much lesser extent, from climatic moderation of a maritime climate. The consequences of these factors are, however, quite manifold. Some of the principles stated below will appear restatements of the obvious, but others will represent views which have not hitherto been discussed to any appreciable extent in the literature on waif biotas. For definitions of which islands are continental and which ones are oceanic, the reader can consult Darlington (1957) or Carlquist (1965).

PRINCIPLES

1. *Disharmony in composition of an insular biota is considered a prime source of evidence for the occurrence of long-distance dispersal.*

The distinction between the concepts of harmonic and disharmonic biotas is a simple one, namely, that a harmonic flora or fauna contains a spread of forms with poor to excellent dispersal ability, whereas waif biotas will contain only the more easily dispersed end of the dispersibility spectrum. An excellent criterion for dispersibility is the maximum gap of salt water which may have been crossed by natural means by particular groups of plants or animals. A distance measured from a continental area to an oceanic island is the most reliable. Admittedly, the gap crossed may have been greater because the continental source population may have been inland, or narrower if a strait has widened since dispersal occurred. A rating of dispersibility was developed by Darlington (1957) for animals, and has been extended to plants by Carlquist (1965). Within taxonomic groups, dispersibility is related to size of the disseminule and to specific mechanisms which can vary widely even within a genus. The idea that particular groups have differential thresholds, or hurdle-values, roughly calculable in miles, is basic to the concept of disharmony, however.

A demonstration of disharmony is rendered more difficult by the fact that some regions, insular and otherwise, have biotic depauperation for ecological reasons. Poorer faunas or floras, however, are usually deprived of species with good dispersibility as well as those with poor dispersibility. Some poorly dispersing groups, by coincidence, also happen to be restricted to ecologically "good" situations (e.g., conifers). Also, good dispersal is often correlated with ability to occupy pioneer habitats — a wholly reasonable correlation because pioneer habitats are widely scattered (e.g., beaches) and often open up for occupancy suddenly, whereas stable habitats, such as rain forests, are limited in extent and do not change rapidly. The possibility of confusion between biotic depauperization owing to distance and that due to ecological factors is great, and has caused some workers, who are unwilling to make a distinction, to reject the concept of disharmony — usually in favor of the existence of hypothetical land-bridges or continental drift.

Strong support for the concept of disharmony comes from the fact that it occurs not once, but in as many replications as there are oceanic islands. The limit of dispersal ability of lizards is shown not only by their absence from the Society Islands, but from their absence on Easter Island, the Austral Islands, Samoa, etc. *Metrosideros* (Myrtaceae) is a tree which has reached not just Samoa, but all of the major groups of high islands of the Pacific, starting from an Indo-Malaysian source or sources.

An island can harbor both harmonic and disharmonic biotas if it is a continental island. New Zealand, Fiji, and New Caledonia are floristically notable for old harmonic elements (e.g., Araucariaceae) presumably derived from times when this arc was connected, or nearly connected, with an Antarctic route, perhaps in Cretaceous times (Thorne, 1963). Since that time, waif elements have also populated these islands; they bulk larger presumably both by virtue of continual immigration and the diversification of arrivals.

An oceanic island, by definition, will have only a disharmonic biota. Some biologists tend to overemphasize the difficulties of dispersal for groups with which they are most familiar. For oceanic islands, however, there can be no exceptions to over-water dispersal. Not generally appreciated is the tendency for loss of dispersal ability following arrival (see principles 16 and 17). Consequently, current dispersibility of island species cannot be used invariably as a basis for estimates of dispersibility. The pivotal controversy, as to which islands are continental and which are oceanic, seems to be dwindling. Only a few islands remain difficult to interpret, and the growing consensus regarding the interpretation of islands suggests that there is likewise increasing agreement on some of the principles discussed in this paper.

2. *Positive adaptations for long-distance dispersal and establishment are the key to disharmony, and disharmony is thus not a negative concept. All elements in a disharmonic biota are capable of long-distance dispersal or are derived from ancestors which were capable of it.*

Organisms which are clearly adapted to dispersal across very long or unlimited distances include spore-bearing plants, strand plants, and some birds and insects. Species with virtually unlimited dispersal (e.g., strand plants) are a virtually constant element on islands, and provide no problems in interpretation, nor do they develop patterns of evolutionary interest on islands. The strand flora usually remains a strand flora, and rarely evolves into montane species. Exceptions include *Erythrina* and *Acacia* (Rock, 1919b) on the Hawaiian Islands. Although dispersal by sea-water flotation has contributed little to montane floras of islands, one must remember that some plants for which sea-water dispersal may seem unlikely are, in fact, capable of it (e.g., *Gossypium:* Stephens, 1958a,b, 1963, 1964; *Lagenaria:* Whitaker and Carter, 1954, 1961).

Rafting is probably most effective over relatively short distances, but is doubtless responsible for cases of land-animal transport (for reviews and observed examples, see Wheeler, 1916; Darlington, 1938; Zimmerman, 1948; McCann, 1953).

For the remainder, birds or winds must be the vector. Gressitt and coworkers are to be congratulated for extensive aerial trapping experiments which demonstrate clearly not only that aerial transport of insects and spiders is likely, but that the species caught represent groups in the same proportions as they occur in insect faunas of oceanic islands (Gressitt, 1956, 1961a; Gressitt and Nakata, 1958; Gressitt, Sedlacek, Wise, and Yoshimoto, 1961; Gressitt and Yoshimoto, 1963; Yoshimoto and Gressitt, 1959, 1960, 1961, 1963, 1964; Yoshimoto, Gressitt, and Mitchell, 1962). Actual dispersal events can be witnessed with such rarity that Gressitt's experiments are as close to definitive proof as can be expected. Thus the contentions of such workers as Visher (1925), Ridley (1930), Setchell (1926, 1928, 1935), Andrews (1940), Zimmerman (1948), Myers (1953), and Fosberg (1963) that aerial dispersal is a reality wherever small or air-floated disseminules are formed seem justified.

Transport of fruits, seeds, and eggs externally, or of fruits and seeds internally by birds must be regarded as the dispersal mechanism of many species (Ridley, 1930; Gulick, 1932; Zimmerman, 1948; Falla, 1960; Holdgate, 1960; Wace, 1960). Observational and experimental evidence for these modes of transport is not as sufficient as one could wish, although morphology and texture (barbed fruit appendages or viscid surfaces of fruits or seeds, etc.) are highly suggestive. More experimental work needs to be done, because the striking array of species transported on intercepted birds demonstrates that birds definitely can function as vectors. Analysis of the montane flora and fauna of islands shows that the majority of species are adapted for transport externally or internally by birds. Detailed analyses of floras and faunas with respect to these mechanisms would be valuable; it has been done in only a few cases (Skottsberg, 1928; Lems, 1960b). Such analyses must be tempered by understanding that dispersal mechanisms change on islands, and may not be as good now as they once were (see principles 16 and 17). Continental disjunctions, such as the famed Chile–western North American pattern (Constance, Heckard, Chambers, Ornduff, and Raven, 1963) can be as helpful in discovering means of long-distance transport by birds as can insular patterns.

High ability for long-distance dispersal is shown in the Pacific by the points at which genera terminate with reference to source areas. Smith (1955) has shown that 101 genera of flowering plants have their eastern terminus on Fiji, the most easterly major island within the line delimiting andesite rocks (which suggest the former presence of a larger land mass). Of the genera which do continue beyond Fiji – to Samoa, for example – many (or endemic genera derived from them) go all the way to Hawaii or the Society Islands, a fact which suggests that the flora of Polynesia is, in fact, the flora of long-distance dispersal. Careful analyses of distributions in Polynesia are needed, however.

3. *Long-distance dispersal is probably not achieved primarily by single introductions but by repeated or simultaneous introductions.*

There is a tendency to believe that introduction of a single seed can and will suffice to establish a new plant species. This possibility certainly cannot be denied, but several circumstances point to a different conclusion. First, animals require at least a breeding pair or a gravid female. A single gravid female would introduce less genetic material than a flock of adults and would be expected to be a poorer mode of introduction of an animal species. Second, this requirement holds true for dioecious or other obligately outcrossed plants (see principle 20). Third, a single individual seems less likely to yield progeny destined for long-term success because of its limited content of genetic variability (see principle 10).

In addition to these relatively demonstrable reasons one can suggest other cogent ones. The very frequent observation of stragglers among migratory birds (e.g., Munro, 1960) suggests repeated introduction. Repetitive stragglers succeeded in establishing a breeding colony of purple gallinules on Tristan da Cunha recently (Rand, 1955). Repeated arrival of straggling monarch butterflies on Canton Island was observed by Van Zwaluwenburg (1942). Shifts in ocean currents may result in unprecedented deposits on beaches of seeds of a previously absent species. Such populations of *Mucuna* seeds were observed on New Zealand beaches in 1956 (Mason, 1961). *Mucuna* seedlings were observed for the first time on not one but several of the Leeward Islands of the Hawaiian chain in 1964 by Charles Lamoureux (pers. commun.). Rafting would tend to bring not one individual, but a small population, as with the ants observed by Wheeler (1916). The pattern of distribution of some genera which occur on virtually all of the high islands of the Pacific, such as *Metrosideros,* suggests not introductions of single seeds but repeated dissemination of large quantities of seeds. Logic dictates that for every successful establishment, there are many unsuccessful arrivals.

Rapidity of colonization of the Krakatau islets by animals (Dammermann, 1948) and plants (Docters van Leeuwen, 1936) following the devastation of Krakatau, suggests introduction of many disseminules of a species. The equilibrium theory of MacArthur and Wilson (1963), a theory which seems well justified, depends on a continuous rate of immigration, rather than a few random accidents.

The majority of seed plants are cross-pollinated. This characteristic, together with a tendency to evolve toward self-pollination from cross-pollination but not the reverse, suggests that whenever there is a requirement for two or more individuals, they must not only grow and flower simultaneously, they must also grow within a short enough distance of each other for pollination to be possible. These requirements clearly favor simultaneous introductions for successful establishments. Such introductions may not be on a yearly or continual basis, of course, but rather the result of a violent occurrence such as an unusual storm that may deposit large quantities of alien trash on an island.

4. *Among organisms for which long-distance dispersal is possible, in the long run introduction is more probable than non-introduction to an island.*

This principle, together with appropriate calculations, has been clearly enunciated by Simpson (1952). Calculations demonstrating probabilities of this sort were offered by Matthew (1915) and Darlington (1938). The calculations of Fosberg (1948) on the origins of the Hawaiian flora suggest the inevitability of the outcome. Attention is called to Fosberg's estimate that the Hawaiian species of no fewer than 23 genera of flowering plants have resulted from two independent introductions, whereas three or more than three introductions are hypothesized for Hawaiian species of 11 other genera. Similar calculations probably could be made of hypothetical immigrants in other groups of organisms and in various waif biotas.

Odd chance distributions do, of course, occur. *Lepinia* (Apocynaceae), which occurs on Tahiti and Ponape, is probably such an example (Fosberg, 1963). Peculiar distributions of this sort are discussed by Falla (1960), who suggests that habits of those birds which are possible vectors may be responsible. The distribution of *Bidens* in the Pacific suggests the operation of chance (Carlquist, 1965). Drastic disjunctions sometimes prove to be the result of incorrect taxonomic interpretation. The supposed occurrence of *Lipochaeta* (Compositae) on the Hawaiian Islands, Galápagos Islands, and New Caledonia now proves to be a case of three different genera which had not been distinguished because of insufficient study (Harling, 1962).

5. *Elements are present not only in proportion to dissemination ability, but also establishment ability.*

Difficulties of establishment seem much greater than those of transport. One can safely say that among successful introductions of disseminules in good condition, only a fraction manage to survive, reproduce, and establish a continuing colony. Animals with wide food preferences and plants of pioneer habitats and easily satisfied pollination requirements seem especially favored. Carnivores are less favored than herbivores, an example of the fact that primary elements in a food chain must become established on an island before later ones can be. This fact is shown on Tristan de Cunha, where the insect fauna contains an exceptionally high proportion of phytophagous species (Brinck, 1948). According to Gressitt (1961b), insects which inhabit plant debris or are leaf-miners or wood-borers are especially successful on oceanic islands.

Most forest trees or forest plants can become established only when soils suitable for them are present. An exception is the chief forest tree of the Hawaiian Islands, *Metrosideros*, which can grow and eventually form a forest on new lava flows (Robyns and Lamb, 1939; Skottsberg, 1941). Lava pioneers are especially likely to succeed on oceanic islands, and by no coincidence, many plants of oceanic islands fall into this category. Rangitoto, a recent volcanic island in Auckland harbor, New Zealand, is vegetated by plants of the New Zealand flora which are capable of growth on bare lava. The floristic composition of Rangitoto contains few genera which are not also found on Hawaii and Tahiti (Carlquist, 1965).

Climatic requirements for establishment are numerous, and inadequate ecological conditions must screen out numerous potentially successful colonists. Examples on Canton Island described by Van Zwaluwenburg (1942) show this phenomenon clearly. Wilson (1959) has shown that in the Pacific, ants of open and marginal habitats have been the migrants to new island areas. Following arrival on islands they evolve into more specialized interior situations. More observations and experimental work on ecological requirements on island animals and plants need to be done.

Animals have the advantage of being able to seek suitable environments upon arrival, whereas plants, to survive, must be deposited upon locations suitable for their growth and maturation. Moreover, suitable pollination agents must be present. The claim that hermaphroditism or self-pollination is advantageous at the time of establishment (Baker, 1955) must be weighed against the undeniable value of outcrossing (see principle 19).

Perennial plants have been alleged to enjoy an advantage over annuals because longevity increases the likelihood for securing sufficient pollination to produce seeds to establish and maintain a species (Wallace, 1895), but alternative explanations for the lack of annuals on islands may take precedence (see principle 14).

6. *Migration to islands is governed by chance and probability, and ordinary concepts of migratory routes and biological provinces do not apply well to many islands.*

This statement is designed as a critique of the division of islands (chiefly those of the Pacific Ocean) into provinces, subprovinces, and the like. The concepts of biological provinces and migratory routes are primarily derived from, and therefore best applied to, continental situations. The best systems of biological provinces, such as those of Thorne (1963) and the workers he has cited, still remain unsatisfying to me for the following reasons:

(1) Groups of plants and animals on a particular island are present roughly in proportion to the distance from source areas. Many islands have acquired their biota from several source areas. Can the Hawaiian Islands logically be put into an Oriental province when an appreciable portion of their flora and fauna is American in origin (Fosberg, 1948)? The diverse sources of the New Zealand flora and fauna defy categorization into anything but multiple provinces and multiple routes (Dawson, 1958, 1963; McDowall, 1964). Darlington (1957) has shown that animals have entered the West Indies from many sources, and have used many ports of entry. These and other examples provide difficulties which in my opinion override whatever merits the province and route devices may have.

(2) Although there is merit in emphasizing major faunal regions, such as those delimited by Wallace's Line and Weber's Lines, these concepts apply to large land areas, not to oceanic islands. For example, the marsupials, which are a chief criterion of the Australo-Papuan region, do not reach oceanic islands or New Zealand.

(3) Criteria for one province differ from those for another. Placental mammals characterize the Malayan area, whereas biotic depauperation is the best criterion for Micronesia. In this connection, the Tuamotus must fall floristically into Micronesia, although geographically they are Polynesian.

(4) Each biologist will erect provinces and routes differently from others because, inevitably, each one will stress some groups not stressed by others, or will regard as of different importance historical, climatic, ecological, or geographical factors. No two biologists appear to be in agreement about the designation of provinces or routes, nor would agreement necessarily be desirable.

(5) The concepts of provinces and migration

routes result from an analysis of data but in their final expression do not of themselves yield information. They are a shorthand which cannot be translated. Because there is no substitute for knowledge of original data, the hypothetical construction of routes and provinces serves only their authors' ideas. Other persons would be well-advised to acquire the original data, if they would comprehend distribution patterns on islands.

7. *Guyots and other now-vanished high islands or lands more extensive formerly than now may have aided dispersal to oceanic islands as subsidiary source areas or "steppingstones," but not as dry land bridges.*

One can suppose, with Zimmerman (1948), that disseminules are abundant close to a source, and become progressively fewer with distance. In this case, presence of an island chain would attenuate the dispersal possibilities of a species. That this arrangement is indeed effective is shown by the Hawaiian Islands. Although the nearest area with any appreciable land surface is the North American continent, the Hawaiian biota is predominantly Indo-Malaysian. Moreover, the prevailing winds do not seem to favor immigration from Indo-Malaysia. However, the many small islands and atolls which lie west and south of Hawaii very likely aided, when they were larger high islands, in transmitting plants and animals to the Hawaiian Islands. Realizing the potential importance of these now-vanished lands, Zimmerman (1948) called for the development of paleontological information about the Pacific basin. Such data are now rapidly accumulating (Hamilton, 1953, 1956; Ladd, Ingerson, Townsend, Russell, and Stephenson, 1953; Ladd, 1958; Cloud, 1956; Cloud, Schmidt, and Burke, 1956; Menard, 1956; Menard and Hamilton, 1963; Stark and Schlanger, 1956; Durham, 1963). These authors have contributed to a picture of large former archipelagos, some as early as the Eocene, lying in the mid-Pacific. The maps by Menard and Hamilton (1963) strongly suggest a dispersal potential for now-vanished islands and should serve greatly to reduce skepticism concerning long-distance dispersal as a means for populating the Hawaiian Islands.

"Steppingstone" islands are potentially less effective as a source for dispersal than large land masses, because dispersal may be expected to be in proportion to the number of individuals in a source area (Johnson, 1960a, b). Moreover, autochthonous loss of dispersal mechanisms may lower the dispersal function of "steppingstone" islands. That such islands may function as staging areas in dispersal cannot be denied, however.

Within archipelagos redispersal occurs, often with interesting consequences as a result of successive events of isolation and reinvasion (Hamilton and Rubinoff, 1963). Many theoretical possibilities of how archipelagos may affect dispersal have been summarized by Carlquist (1965). One can say that any species with dispersal ability sufficient to bring it to an archipelago can be expected to succeed in dispersing (but not, perhaps, in establishing) itself throughout the archipelago. A species may lose pioneering ecological characteristics or dispersal mechanisms, however (Wilson, 1959).

8. *The size and systematic composition of particular insular biotas are determined by many factors which differ in relative importance from island to island.*

To attempt to say which factor is of prime importance is difficult. Even for particular islands factors are not easily ranked, although attempts have been made (Hamilton and Rubinoff, 1963; for a critique, see Carlquist, 1965). Among factors which have been claimed to be of importance are island area and altitude (Darlington, 1957); size, nearness, and richness of source (Zimmerman, 1948); latitude, climate, age, and geological events. Archipelago effects (size of island; size of neighbor island, nearness to neighbor island, altitude, altitude of neighbor island) are manifold (Hamilton and Rubinoff, 1963).

Factors which are influential in an island's biotic richness are measures of (1) ecological opportunity, (2) the degree to which barriers to dispersal to an island can be overcome, (3) the number of barriers within an island which can serve for isolation during speciation, and (4) the requirement for a certain minimal area for maintenance and evolution of a population (see principle 10).

9. *Relicts in the strictest sense are few or absent on oceanic islands, although every immigrant group has a history, and one can designate more primitive island autochthones as "recent relicts."*

Good dispersal ability is not entirely restricted to phylogenetically advanced groups. If primitive forms migrated to oceanic islands while the mainland remnants have become extinguished recently, they appear as relicts. This is probably the case with the primitive flowering plant *Lactoris* (Carlquist, 1964) and the fern *Thyrsopteris* on the Juan Fernandez Islands. These islands do not appear to be ancient, and the remainder of their flora and fauna contains no relicts. In the West Indies, the cycad *Microcycas* and the insectivore *Solenodon* (together with its fossil relative *Nesophontes*) may be considered relicts (McDowell, 1958; Darlington, 1957). Other than the above, no spectacular phylogenetic relicts can be found on oceanic islands.

Insular groups may tend to have a rapid cycle of speciation and extinction, and the latter stages may be said to contain, in a sense, "relict" species (see principle 18).

Why are there so few real relicts among the waif biota, whereas continental islands, such as Tasmania, are notable for relictism? One answer may lie in the fact that the most successful groups in the waif biota appear to be those which are evolutionarily "upgrade" or "weedy" and which have a greater degree of genetic "momentum." Most antique groups make relatively poor immigrants, both because of their generally poorer adaptability, and also because they often have poorer dispersal mechanisms.

10. *Immigrant species must overcome the restriction of genetic material related to the very small size of the initial population.*

The small size of populations with which waif groups begin is one of the unique features of insular existence. With few exceptions (such as the strand flora), an immigrant population will receive no new genetic material from the parent population. Indeed, if such infusions occurred with frequency, endemism on islands would be much lower than it is. Such infusions do occur with relatively great frequency among the strand flora, so endemism among those species is, in fact, relatively low (Fosberg, 1963).

Genetic variability must be manufactured following migration. The degree to which mutations are retained depends not only upon the mutability of a species but upon the ecological opportunity. Chromosomal polymorphism in West Indian populations of *Drosophila willistoni* is greater on islands which are ecologically diverse (Dobzhansky, 1957). *Metrosideros polymorpha,* the chief forest tree of the Hawaiian Islands, is extraordinarily diverse and has proved difficult for taxonomists. This multiform tree ranges from bare lowland lava to high bogs, where it is a shrub (Rock, 1917). Polymorphism in morphology characterizes many island species. Notable examples of variable island species in stages of expansion were demonstrated in the land shell *Partula* by Crampton (1916, 1925, 1932). There is every reason to believe that physiological and ecological opportunities play a controlling role. Small area and ecological poverty are cited by MacArthur and Wilson (1963) as reasons why extinction is high on some oceanic islands. The requirements of populations of a species for a land area large enough for maintenance of genetic variability, and thus, for the maintenance of the species itself are cited by various authors. Darlington (1957) believes that this explains the extinction of large mammals on Ceylon.

"Weedy" immigrants would be expected to have the advantage of high mutability, in my opinion. Moreover, the broader ecological tolerances of "weedy" plants and animals would permit occupancy by more numerous individuals, thus increasing potential genetic variability. Smaller body size would also favor development of larger populations, which similarly could be genetically more viable.

A species which immigrates as a flock of individuals rather than as one or two would seem to enjoy a great genetic advantage. The genetic disadvantage of self-pollination in an immigrant population of plants seems considerable.

The colonizing individuals represent only a portion of the genetic content of a species, and this portion will influence the characteristics of the eventual island population and its distinctions from the remnant mainland populations (Berry, 1964).

11. *Rapid evolution of island immigrants is not only possible, it is frequent. Change following arrival is inevitable.*

"Explosive" evolution is demonstrated by various groups which have been afforded good ecological opportunities. Among outstanding examples may be cited the Hawaiian Drosophilidae (perhaps 400 species according to Elmo Hardy, pers. commun.) or the Hawaiian species of *Cyrtandra* (Gesneriaceae): about 130 species of *Cyrtandra* on Oahu alone are claimed by Harold St. John (1966).

Actual times have been estimated for some cases of rapid insular evolution. Five species of endemic Hawaiian banana-constant moths have evolved in the approximately 1,000 years since human introduction of the banana there (Zimmerman, 1960). Freshwater lakes can be considered insular situations. In Lake Lanao in the Philippines, four endemic genera of fish with 18 species have evolved from a probable single species in 10,000 years or less (Myers, 1960). In Lake Baikal, endemism has reached the familial level in the case of the fish family Comephoridae (Kozhov, 1963).

Biologists are increasingly aware that geological time is short on volcanic islands. Evolution must proceed within this time span, although to this length of time can be added that available on an archipelago as a whole, as well as that on "steppingstone" islands, if any.

Factors favoring rapid evolution on oceanic islands include the lack of competitors and predators, presence of a wide spectrum of ecological opportunities, and numerous potential barriers. Geographical isolation is abundantly provided by the sharp relief of deep valleys and narrow ridges formed as volcanic islands erode. This may, in part, have been responsible for the remarkable speciation of *Partula* (Crampton, 1916, 1925, 1932). Lava flows may subdivide populations and provide isolation (Zimmerman, 1948), and catastrophic episodes of volcanism may well spur evolution. The barriers among islands of an archipelago seem important in the speciation of insular groups (Darlington, 1957). Other forms of reproductive isolation among insular species are possible, however, and should not be overlooked (Bailey, 1956).

Where distinct endemic species and genera evolve, one may expect changes in any part of a plant or animal. For example, it is illogical to expect that the dispersal mechanism in the Hawaiian silversword, *Argyroxiphium*, is the same as that of the ancestors of this endemic genus. Possibilities that genes may have pleiotropic effects should not be overlooked.

12. *Situations on islands new to immigrants will dictate their courses of evolution. Adaptive radiation is the inevitable result on an island or archipelago where a small number of immigrant groups is faced with a broad spread of ecological opportunities.*

The "genus-and-family-poor but species-rich" condition of oceanic islands is one reflection of adaptive radiation. What is not reflected in taxonomic terms is the tendency for island species to evolve into ecological niches that would be occupied by a member of an entirely different group on a comparable mainland area. The consequence of the absence of mammals on most oceanic islands is the assumption of mammalian roles by birds and reptiles. For example, the dodo of Mauritius, a large terrestrial herbivore, represented a sort of avian rabbit. Phases of adaptive radiation are related to topics discussed under principles 14, 15, 16, and 17 below, in which diversification of habits within groups is cited.

Well-known examples of adaptive radiation such as Darwin's finches (Lack, 1945, 1947; Bowman, 1961, 1963) or the Hawaiian honeycreepers (Amadon, 1950) are only a few of the excellent ones which could be named. Other instances, particularly among plants, deserve greater currency. Among these are the Hawaiian tarweeds (Carlquist, 1959) and the Canary Island Aeoniums (Lems, 1960a). Descriptions of these and others and a catalogue of instances of adaptive radiation are offered elsewhere (Carlquist, 1965).

Time is a requisite for completion of a cycle of adaptive radiation. On some islands, time (as well as other conditions) has been insufficient for achievement of spectacular radiation. In some cases, secondary cycles of radiation can begin. For example, the genus *Psittacirostra* (Drepanididae) not only represents one product of adaptive radiation, it contains species which differ in bill size and shape and in food sources (Amadon, 1950).

13. *An immigrant group which is not confronted with, or cannot take advantage of, a broad spectrum of ecological opportunities on an island may evolve into one or a few niches.*

This statement is a way of saying that in addition to "definitive" adaptive radiation, islands may bear portions of a gamut of adaptive radiation. Examples of "incomplete" or "lopsided" adaptive radiation are abundant on islands. These examples usually demonstrate entry into a few new habits or mechanisms. The Hawaiian species of *Viola* and *Bidens* range from herbs to small shrubs, but not large shrubs or trees.

Islands may play a role in fostering peculiar adaptations, such as unusual diets (seaweed is eaten by the Galápagos iguanid *Amblyrhynchus*), specialized pollination mechanisms (ornithophily has been developed by Hawaiian lobeliads), peculiar dispersal mechanisms (the Hawaiian lobeliad *Trematolobelia*), new food-getting mechanisms (the tool-using Galápagos finch *Cactospiza*), etc. Unique developments in these general categories do occur, of course, on mainland areas as well as on islands. One can speculate that the specific examples cited in parentheses not only represent responses to opportunities on islands, they also may be preserved in the less competitive island situation (Carlquist, 1965).

14. *New growth forms evolve among plants on oceanic islands. Most conspicuously, there is a tendency toward increased stature.*

The chief changes which seem to occur are from herb to rosette-tree or rosette-shrub, herb to shrub, shrub to rosette-tree, shrub to "true" tree. Examples of these tendencies are described elsewhere (Carlquist, 1965). The reasons for these alterations in growth form are several, and one or more of these may serve to explain the habits of particular species:

(1) A high volcanic island potentially could support the same growth forms in the same taxonomic groups as a continental area with similar climate. Dispersal to such an island tends to favor not the entire spectrum of plants, but mostly herbaceous and shrubby plants, chiefly those of pioneer or "open" habitats. Plants of stable forest areas, many of which are often large-seeded, are disadvantaged as waif immigrants not only because of poor dispersal but because of specialized ecological requirements. From the limited spectrum of growth forms which dispersal brings, the entire gamut tends to be evolved on islands.

(2) Herbs which follow a strongly seasonal regime on continents are "released" on tropical, subtropical, and even temperate islands where latitude and the tempering effect of maritime surroundings moderate climate. Under these conditions, the growing season lasts throughout the year and a rosette-plant which would ordinarily die down to the ground each winter forms elongate stems. Moreover, this is a more efficient growth form where climate permits, for vegetative growth and flowering stems can be produced continuously, by-passing seedling stages required by annuals each year. These seem to be major factors in the development of rosette shrubs such as the large *Plantago* species which have evolved independently on St. Helena, the Juan Fernandez, Hawaiian, and Canary Islands. Similar considerations apply to the Hawaiian lobeliads. Climatic factors have been cited as responsible for development of rosette-shrubs in the Canary Islands (Schenck, 1907; Rikli, 1912; Johnston, 1953). Climatic considerations also seem basic to evolution of rosette trees in equatorial-alpine regions on continents (*Espeletia* and *Puya* in the Andes; *Senecio* and *Lobelia* in the African Alps).

(3) A relative lack of herbivores may permit survival of succulent and large-leaved shrubs and trees, once they have evolved on islands, although this circumstance may not be basic to their evolution.

(4) Competition among individuals of an herbaceous species was claimed by Darwin (1859) to be a selective force. Larger individuals which overtopped their neighbors were interpreted by him as leading to shrubby habits. This seems rather unlikely in the example selected by Darwin, *Scalesia*, shrubby species of which grow mostly not in dense stands, but in a scattered fashion on rather bare lava areas of the Galápagos Islands (Harling, 1962).

Reasons (1) and (2) above are considered most significant in alteration of growth forms. The tendency for typically herbaceous groups — such as the Compositae — to develop into rosette-trees, rosette-shrubs, or true trees is represented by the abundance of such Compositae on the Hawaiian Islands (Rock, 1913), the Juan Fernandez Islands (Skottsberg, 1953), St. Helena (Melliss, 1875), the Canary Islands (Schenck, 1907; Børgesen, 1924), and other islands (Hemsley, 1885; Carlquist, 1965). Compositae have been successful at these innovations both because they are, as a group, rapid-evolving, adaptable, well-represented on islands because of good dispersibility, and because, although many are herbs, most are at least somewhat woody and can presumably evolve increased woodiness easily.

The alternative proposition — that strange growth forms such as those cited above are relicts (Skottsberg, 1956; Lems, 1960a, 1961) — seems clearly contradicted by data referable to the above concepts. Where comparative studies of the island forms and their mainland relatives are undertaken, the interpretation of insular rosette-trees and the like as innovations, rather than relicts, becomes inescapable. Anatomical evidence on the nature of insular rosette trees shows that they are juvenilistic; the stem and wood structure suggests an herb pattern the ontogeny of which never, or only slowly, reaches adult characteristics (Carlquist, 1962).

Particular ecological conditions undoubtedly play a role in determining the nature of the growth form evolved — e.g., whether a large-leaved rosette-tree or a rosette-shrub, whether a stem-succulent or a wiry fountain-shaped shrub (Carlquist, 1965). Further anatomical studies are in progress in an effort to elucidate the nature of changes in growth forms on oceanic islands.

A corollary to insular change in growth form is that mainland relatives will have different growth forms. This truism must be remembered when attempts are made to establish the relationships of "anomalous" insular endemics. One must often investigate groups with rather different growth forms. For example, Keck (1936) thought that the Hawaiian silversword *Argyroxiphium* might be related to a Juan Fernandez rosette-tree with similar habits, *Robinsonia,* but the closest affinities actually seem to be with the California tarweeds (Carlquist, 1959), which are relatively non-woody annuals and perennials.

15. *Changes in form, size, and color of animals often occur on islands: gigantism, dwarfism, changes in body proportions, and melanism are among the changes represented.*

The animals which show these trends well are those which are best represented on islands and which are evolutionarily plastic. Insects, birds, reptiles, and land molluscs are chief among these. The former two groups, being mostly volant, often have alterations in shape, size, and proportions which are related to flight (and are considered under principle 17 below). Reptiles offer particularly good examples of change in form and size, and the review by Mertens (1934) of island reptiles is a landmark.

Gigantism is common among insular animals as compared with their mainland relatives (Berland, 1924; Mertens, 1934; Steven, 1953; Hill, 1959; Cook, 1961; Berry, 1964). The reasons for gigantism are rather speculative at present, and well-designed studies would be very welcome. Among the explanations for insular gigantism which can be offered at present are the following:

(1) Lack of predators. Larger sizes may be achieved if predator pressure is reduced. Increased longevity and thereby increased size are possible under these circumstances.

(2) A new diet. Especially for herbivorous and to some extent insectivorous animals, food supply may be more abundant. This abundance may not take the form of a greater quantity, for an animal population would soon enlarge to take advantage of the supply. On an island, however, three or four food items might be taken by one animal species, whereas on a continental area, several animal species might compete for them. On some islands, food supplies might be present throughout the year, owing to milder climatic conditions. More likely, however, an animal can adapt to new, and in particular to larger, articles of diet. The quantity and types of nutrition available might be expected to be correlated with body

size, and a species faced with increase in nutrition could be "released" from some factor limiting size and could evolve into a larger race.

(3) Lack of competitors except for members of their own species. If competition for food is *within* a species rather than between or among species, one might expect gigantism to have a selective advantage. Moreover, mating struggles might favor larger individuals; this would be true on mainland areas, too, but predation and food supply might cancel out this trend on the continents.

Dwarfism is also a notable tendency on islands. The following may be the reasons:

(1) Smaller forms on islands may reflect the small size of immigrant species, a fact related to their greater ease in dispersal.

(2) Smaller size may be an adaptation to pressures of predators, if greater on a particular island (Hecht, 1952).

(3) Smaller size may be an adaptation to smaller food articles or smaller food supplies, and thus is the reverse of (1) under gigantism above. A smaller animal could maintain a viable population size in a situation where food is scarce.

Changes in proportion which are evident on islands include:

(1) Fatter bodies, fatter tails, and thicker limbs (Mertens, 1934). These changes, shown especially well by lizards, may be forms of gigantism, and to that extent they are explained above. Lack of need for locomotion may also underlie these trends, as may need for storage during dry seasons.

(2) Shorter limbs and tails are characteristic of many island reptiles. A good instance of this is reported in a well-designed study by Kramer (1951). Stubby legs and clumsy habits characterize some island insects, such as certain ones in Hawaii (Perkins, 1913) or the New Zealand wetas. Adaptation to a terrestrial way of life where food supplies are secured easily by crawling may be responsible. Change in location of available foods may also explain alteration of body proportions in reptiles. The instances studied by Kramer suggest that lack of predators and smaller spaces on small islets lower the selective value of long, agile limbs suited to evasive tactics.

(3) Change to new habits may result in leglessness. This trend is shown independently in two genera of skinks: *Brachymeles* (Philippines) and *Grandidierina* (Madagascar). These genera show adaptation to life underground or in forest litter.

Melanism is widespread in island reptiles (Mertens, 1934). This is not a protective color except in a few cases. Among the most appealing of the explanations offered by Mertens is that of thermoregulation. Cooler maritime climates of islands might render heat-absorptive coloration valuable, especially for reptiles whose size is greater owing to gigantism. Coloration in the Galápagos ground finches is related to the proportion of time spent on or near the ground in feeding (Bowman, 1963), and may be related to protection from predators.

16. *Dispersal mechanisms and dispersal ability may be lost during the evolution of plants on oceanic islands.*

Autochthonous loss or alteration of dispersal mechanisms on islands seems not to have been recognized. Study of floras of oceanic islands — particularly in the Pacific — has convinced me that it is just as real a phenomenon as flightlessness in insular birds and insects. Reasons for this tendency are as follows:

(1) As noted above (under principle 12), islands which can support a forest must, to a greater or lesser extent, reconstitute a forest from a waif flora, which consists mostly of nonforest species. Large fruit and seed size characterizes many true forest species, a fact related to the requirement of seedlings in deep forest for greater food supplies as they advance to upper, better-lighted levels of the forest. Such fruits and seeds are poorly suited to dispersal, whereas the best-dispersed seeds and fruits are usually small — a condition antithetical to an abundance of storage materials. Increase of seed and fruit volume, an evolutionary trend on many oceanic islands, has the net effect of reducing dispersal ability.

(2) Dispersibility may acquire a neutral or negative value in island situations. A plant with excellent dispersal ability — as with plants typical of pioneering habitats — disperses its seeds widely. If such a species reaches an island and adapts to an ecological situation of limited geographical extent (as have many island species), good dispersibility actually acquires a negative value. The area favorable for a

particular island species is usually much smaller than the island itself — often only a ridge or valley. Although some persons have noted that a dispersal mechanism which permits disseminules to be swept off an island is unfavorable, the limits beyond which disseminules are "wasted" are, in fact, much narrower than the island itself. Precinctiveness is thus linked to poor dispersal; this may operate on mainland areas, but it does so to a greater extent on islands.

(3) In some cases, a dispersal mechanism takes the form of an appendage or some other special formation. Economy would dictate that such structures be gradually lost if they no longer have any selective value. Even if it is assumed that a dispersal mechanism has a neutral value, it may disappear as a result of changes within the fruit — by means of pleiotropic gene action, for example. Island plants still need a certain dispersal ability, although it may be much less than that of continental plants. A dispersal mechanism may dwindle to the point where it is equal to the dispersal required for success of a species.

Among the more salient examples of loss of dispersal on oceanic islands are *Bidens* (Polynesia, including Hawaii) and *Dendroseris* (Juan Fernandez Islands), both Compositae. Loss or alteration of dispersal mechanisms is especially prominent in Polynesian floras and will be detailed in a forthcoming paper by the writer.

Another change which may occur is the tendency for seeds of island species to lose prolonged viability. One would expect that as pioneer species develop into forest species, the shorter viability typical of seeds of rain-forest trees might be acquired. Data on this point are very much needed.

17. *Flightlessness may evolve in volant groups of animals in response to insular conditions.*

The number of flightless birds and insects among waif faunas on islands is quite startling. Early noted by Darwin (1855), it has received comment from various authors such as Perkins (1913), Darlington (1943), Brinck (1948), Zimmerman (1948, 1957), Hagen (1952), Gressitt, Leech, and Wise (1963), Holloway (1963), and Gressitt (1964). A listing of flightless insular birds has been assembled (Carlquist, 1965).

Loss of flight occurs most frequently in groups which normally are airborne only a small proportion of the time, such as rails (Rallidae), a family that is exceptionally well represented by non-flying as well as flying species on islands (Hagen, 1952; Carlquist, 1965). An explanation for the frequency of rails on islands might be that because they are infrequent and perhaps poor fliers, they are easily swept out to sea, cannot fight against storm winds, and thus cannot return home as easily as birds which are stronger fliers. Because of limited flying ability, some birds seem more likely to stay on islands than others, even before loss of flight.

Flightlessnes probably does not have a single cause (Darlington, 1943), but one or more of the following may operate in particular cases:

(1) Absence on islands of ground-feeding animals — such as most mammals — permits birds and insects to enter a terrestrial way of life, where flight becomes unnecessary as an adjunct to food-getting. As flight becomes infrequent, a bird or insect species easily and imperceptibly crosses the threshold from ability to inability to fly. Volant species which have a near-terrestrial mode of life (such as rails) would cross this threshold more easily.

(2) Entry into the ground-feeding habit is associated with winglessness in insects, and stable forests of tropical islands have an abundance of flightless species (Darlington, 1943). In birds, a mimicking of the habits of some mammals may be accompanied by increase in body size without increase in wing size and musculature. Change in feeding habits may be accompanied by increased precinctiveness if food sources occur within a limited area; in this case, restriction of flight pattern might acquire a positive selective value. In New Zealand species of Lucanidae (Coleoptera), flightless species occupy smaller ranges than do volant species (Holloway, 1963). Entry into new ecological situations is related to winglessness in certain non-insular situations also: insects of mountaintops (Darlington, 1943), caves (May, 1963), and some groups of parasitic insects, such as those flies that parasitize bats (Streblidae, Nycteribiidae).

(3) Increase in leg size and musculature may force a decline in size of other body parts. If wings are no longer used, they are the most expendable structures. In this concept, the body would be viewed as a closed economy or budget, in which increase in one item forces decrease in another. Of the rails native to Tasmania, the best at running is the native hen (*Tribonyx mortieri*), which is also the only one unable to fly (Sharland, 1958).

(4) Ability to fly does not continue without maintenance by positive selective pressure. If this pressure lessens or vanishes, flight will, in time, disappear. Flight is an ability dependent on a complex of components, just as is flight of an aircraft, and decrease in selective pressure will permit mutation of only one or a few genes to cancel flying ability.

(5) Lack of predators or enemies lowers the value of flight as an evasive tactic.

(6) Flight becomes unfavorable if an appreciable proportion of a population could be blown away or straggle away from an island or even away from suitable portions of an island. This is the most likely explanation among the smaller volant animals and on locations where wind pressure is often high, as on the subantarctic islands. Experimental evidence that wind, and possibly also straggling, are selective factors in flightlessness has been obtained in *Drosophila* by L'Heritier, Neefs, and *Teissier* (1937). Gressitt (1964) has shown that in the insect fauna of Campbell Island, at least 40 per cent which belong to normally winged groups' show a reduction in wing size. This reduction varies from moderate to complete absence of wings. Subantarctic islands are particularly notable for their high proportion of flightless moths (Enderlein, 1909; Viette, 1948, 1952a,b, 1954, 1959; Salmon and Bradley, 1956; Gressitt, 1964). On the basis of this explanation, one can also understand why males are more fully winged than females (which would be less expendable) within many of these moth species. The flightless moths of subantarctic islands seemingly have compensated for lack of flight by developing grasshopper-like springing ability (Salmon and Bradley, 1956), as have flightless flies of these islands (Gressitt, 1964). This development may have contributed correlatively to wing reduction.

(7) Development of winglessness may be permitted on islands which are relatively free from flooding (Darlington, 1943).

Darlington (1943) views flightlessness as a habit controlled by a number of factors, and predominance of one or more of these may shift the proportion of winged to wingless. Clearly, wingless species are not restricted to islands, and thus these factors operate in many situations.

As soon as the threshold to flightlessness has been crossed, wings seem to be rapidly reduced phylogenetically. At various stages in their reduction, wings may function for climbing or as brakes during hopping (Hagen, 1952). Because insect wings are less complex than bird wings and are governed by fewer genes, one may expect wingless insects to evolve more frequently and rapidly on islands than do wingless birds. Of the flightless birds on oceanic islands, all have some wing vestiges; later stages in wing loss are shown on old islands such as New Zealand (e.g., *Apteryx*, the kiwi). Selective pressure for loss of wings would be maximal at the time of and immediately following the loss of flying ability, and would decrease as wings become mere vestiges that neither have any function nor require the expenditure of much energy in formation or maintenance. Darlington (1943) offers an alternative explanation, that pleiotropic genes are responsible for retention of wing vestiges.

Flightlessness may be a matter of habit, as well as morphology. According to Gressitt and Weber (1959), wingless or partially winged antarctic and subantarctic insects are active, whereas winged species are "sluggish." When these two groups are added together, the insect fauna of far-southern islands has a strongly sedentary aspect.

18. *Competitive ability is often decreased slightly to markedly among endemics of oceanic islands.*

This statement has an intentional vagueness which hinges on the inexactness of the concept "competition." The phenomenon is real enough, certainly, and aspects have been noticed by many biologists who have witnessed the rapidity with which indigenous island species yield to continental species introduced by man (cf. Elton, 1958). Competitive ability would seem to depend upon constant selective pressure, and is thus abundantly represented on continents, where numerous aggressive groups are evolving simultaneously. This pressure vanishes or is lowered when a species migrates to an island where there are fewer species, and where many ecological opportunities which are not preempted exist. Each immigrant group would, in this view, lose competitive ability following arrival, so that the total flora or fauna at any time would be less competitive.

In the Hawaiian Islands, almost any introduced continental species of plant seems capable of replacing autochthonous species of comparable ecological requirements. Even if it is admitted that soils have been disturbed by man and his domesticates, native island species show poorer self-replacement after disturbance than do native species in a comparably disturbed continental area. The rain forests of Kauai now host a remarkable variety of weeds, including many garden flowers, few of which would be noxious — if they were weedy at all — in continental areas. Even high bogs are not exempt from weeds (e.g., *Rubus* is now covering the bogs of Mt. Kaala, Oahu). This situation augurs poorly for attempts at conservation of island endemics. Not only are weeds well entrenched in many areas of the Hawaiian Islands, but also efforts to remove them would very likely only renew and widen the areas of disturbance and encourage more weedy growth than before. Many plants which are now weeds in the Hawaiian Islands can hardly be kept out of areas because of their good dispersal mechanisms (e.g., *Schinus* and *Psidium* are spread by frugivorous birds). Only a few native Hawaiian plants, such as *Scaevola, Pipturus,* and *Acacia,* seem capable of occupying disturbed sites.

Loss of competitive ability may in part be due to genetic depauperation, a fate which seems common to most island autochthones. One might expect that even in prehuman times, there would have been genera that "lost momentum." In fact, there do seem to be such genera in the Hawaiian biota. These include the genera of land shells *Carelia* (Cooke, 1931) and (to a lesser extent) *Achatinella* (Cooke and Kondo, 1960). Among plant genera, the lobeliad *Delissea* has been labelled "decadent" by Rock (1962), and other Hawaiian genera which could be so described include *Hesperomannia, Hibiscadelphus, Isodendrion, Kokia, Munroidendron, Pteralyxia, Remya, Rollandia,* and, to some extent, *Cyanea* and *Clermontia.*

Irreversible adaptation to excessively specialized locations may be a key to these vanishing genera. These specializations would be irreversible if loss of variability occurred. An insular phylad would be expected to be either in a state of expansion and speciation as it draws on genetic variability, retained or acquired; or in a state of decadence, as adaptability to new situations dwindles. The upgrade groups would be expected to replace the downgrade taxa, so that groups in both categories could be found at any given time. Paucity of individuals would seem to play a key role in loss of genetic variability. Adaptation to an ecological zone of limited extent (and on oceanic islands, any zone would be limited in extent) would result in a smaller number of individuals per species. Excessive specialization is exemplified among Hawaiian animals by the land shell *Achatinella,* which is capable of eating, not foliage, but only epiphytic algae. The Hawaiian drosophilids seem to subsist only on leaves of the endemic arborescent Araliaceae and on rotting lobeliads (Elmo Hardy, pers. commun.), an unusual diet in this family of flies. Some Hawaiian insect species may be so restricted that they occur only on a single tree (Zimmerman, 1948).

An interesting manifestation of loss of competitiveness is seen in genera and even families which are widespread on islands but which have, with few exceptions, not managed to gain or retain a foothold on continents. Such genera of land shells as *Tornatellides* and *Elasmias* (Cooke and Kondo, 1960) or *Partula* (Germain, 1934) have almost unbelievable distributions which span wide stretches of the Pacific, even reaching offshore islands of continents but not the continents themselves. Such distributions would suggest a kind of relictism, except that the genera and the islands they occupy are doubtless relatively recent in geological terms. Possibly these genera range the Pacific by means of good dispersal, establishing themselves only in situations which are both suitable ecologically and in which competitiveness is rather low. Further observational and, if possible, experimental evidence is needed to demonstrate the nature and causes of "incompetent" insular species.

19. *Means for outcrossing become highly developed in waif floras. Species without potential for outcrossing are probably doomed to a short tenure.*

Baker (1955) hypothesized that self-compatibility is advantageous for the establishment of plant immigrants. The obvious advantages of this habit for initial establishment may well be overwhelmingly outweighed by the long-term disadvantages of inbreeding. So disadvantageous is inbreeding on islands that self-pollinated species do not bulk large in insular floras, and, where they are present, one often suspects that they are declining species. Where population size is limited, as it necessarily is on islands, and where inflow of new genetic material is cut off by the sea barrier, maximizing of outcrossing seems a necessity. All genetic variability can be dispersed throughout a population by means of outcrossing. A species with flowers that will self-pollinate if cross-pollination does not occur within the first day or two after opening, would possess an advantage. This habit characterizes the Compositae, a family notable for its success on islands. The long-term mode toward which insular groups evolve is cross-pollination, however. Baker (1955) has claimed that the characteristics of the Plumbaginaceae offer evidence of a relationship between island habitats and the occurrence of self-pollination, but calculations based on his data on one genus from this family, *Limonum* (Baker, 1953), proves the reverse. In the genus *Limonium* as a whole, 79.6 per cent have dimorphic flowers, a condition which would make outcrossing a virtual necessity. Of the species of *Limonium* endemic to small or medium-sized oceanic islands, 94.5 per cent have dimorphic flowers. There are, however, instances reported in which speciation on islands is accompanied by selfing, as in the Galápagos tomatoes, *Lycopersicon* (Rick, 1963). Autogamy may be expected more in the strand flora, less in the montane flora of islands. Re-introduction of new genetic material is possible in the strand flora, whereas the montane flora is more effectively cut off from source areas. Autogamy may also be expected in relatively recent, upgrade groups on islands, less in the older species of the forest flora. Many species capable of autogamy may experience sufficient outcrossing to maintain genetic variability.

The importance of some means for outcrossing on islands has not been generally appreciated. Outcrossing may be enforced simply by one or several gene pairs, or it may be required by deep-seated and visible means, such as unisexual flowers. Dioecism makes outcrossing mandatory. In the New Zealand flora, 14.5 per cent of the species are dioecious, whereas in a continental flora, such as that of the British Isles, only 2 per cent are dioecious (Rattenbury, 1962). New Zealand may not seem a small enough island for the limitation of population size to make outcrossing highly valuable. In the Pleistocene, however, many New Zealand species were doubtless very much restricted by the advance of ice sheets. Families which elsewhere are represented mostly by normal bisexual flowers have dimorphic or unisexual flowers in their New Zealand representatives (Godley, 1955; Franklin, 1962; Dawson, 1964).

Flowers suited for outcrossing by the various means listed below are particularly abundant in the floras of the Juan Fernandez Islands (Skottsberg, 1928, 1938), the Desventuradas Islands (Skottsberg, 1963), and the Hawaiian Islands (Hillebrand, 1888; Skottsberg, 1936a,b, 1944a,b, 1945; Fosberg, 1956; St. John and Frederick, 1949; Carlquist, 1965). Because this phenomenon has been insufficiently appreciated, the writer is preparing an account of outcrossing mechanisms in the Hawaiian flora.

Mechanisms which aid or insure outcrossing in the floras of the above islands are as follows: (a) dioecism; (b) gynodioecism; (c) monoecism; (d) heterostyly, floral dimorphism, and trimorphism; (e) wind pollination; (f) pollen sterile on some plants, ovules infertile on others; (g) protandry or protogyny; and (h) massing of flowers into large, conspicuous inflorescences.

20. *Natural hybridization acquires a positive value in evolution of the waif biota.*

In a sense, this is merely an extension of outcrossing, for exchange of genetic material is involved. With hybridization, however, a greater degree of difference between, or a barrier between, species (or other taxa) is implied.

Species on oceanic islands are notoriously "unstable" or "variable." This condition does not seem to be wholly the result of the lack of extinction of intermediates. A variable species is probably a successful species on an island, and as long as it can retain or attain a degree of polymorphism, it would seem to have an evolutionary future.

Does hybridization play an important role on islands? Only a few cases of variability in island species have so far been traced to hybridization. There has been a tendency to overlook hybridization, however, partly because taxonomic studies of island organisms are often based upon museum specimens rather than field studies. One can safely say that hybrids would prove to be more frequent if students of particular groups would entertain this possibility. The Hawaiian species of *Scaevola* (Goodeniaceae), hitherto regarded as a series of easily defined endemics, now prove to be highly polymorphic, mostly linked to each other by a series of hybridizations, current and old (George W. Gillett, pers. commun.). "Cylic hybridization" has been claimed as a mechanism by which many species in the New Zealand flora survived radical climatic changes of the Pleistocene (Rattenbury, 1962).

Reports of hybridization among waif floras include those of Rock (1919a) in *Clermontia,* Skottsberg (1939) in *Viola,* Fosberg (1956) in *Gouldia,* Lems (1958) in *Adenocarpus,* Dawson (1960) in *Acaena,* and Franklin (1962, 1964) in *Gaultheria* and *Pernettya.* Many reports of hybrids in the New Zealand flora are summarized by Cockayne and Allen (1934) and Allan (1961).

Hybrids might be said to occur between races (although some will argue that this violates the meaning of the term "hybrid") as well as between species on islands. A successful curriculum (at least in plants) would seem to be that of a population which takes advantage of reproductive isolation in exploring (speciating into) new ecological territory, but which retains fertility with other populations. As conditions change, gene flow among a series of semi-separate populations could maintain a high level of adaptability. Instances, modes, and extent of natural hybridization remain rewarding avenues for investigation by students of insular botany. These investigations are particularly urgent, because they can be pursued only while insular floras are relatively intact.

21. *Pollination relationships correspond to and change with respect to availability of insects and other pollinating agents on islands.*

Wallace (1895) noted the paucity of conspicuous flowers in the floras of New Zealand and the Galápagos Islands, a fact he correlated with poverty of insects on those islands. This insect poverty is best described, however, in terms of the absence or scarcity of particular groups, such as butterflies in the Galápagos (Wallace, 1895) or long-tongued bees in New Zealand (Rattenbury, 1962). The Hawaiian forest flora is also abundant in small green or white flowers which are poor in scent. Smaller flowers have probably established preferentially or evolved in these islands to suit the smaller size, and the habits and preferences of available pollinators. As will be noted, the waif insect fauna consits of immigrants belonging to smaller size classes, and this may have promoted the evolution of smaller floral sizes. That island conditions do influence pollination mechanisms is suggested by Hagerup (1950a,b, 1951). Flowers in floras of oceanic islands often have simple open forms, suitable to entry by a wide variety of potential pollinators.

Massing of flowers may serve to attract pollinators, and is theoretically advantageous if pollinators are scarce. This factor might or might not help to explain the occurrence of insular monocarpic rosette trees, such as *Wilkesia* and *Trematolobelia* (Hawaiian Islands) or *Centaurodendron, Yunquea,* and *Phoenicoseris* (Juan Fernandez Islands). Other plants on these islands with massive inflorescences could easily be cited. Wallace (1895) has claimed that the perennial habit aids in securing pollinators. The value of this habit seems questionable, because a few additional flowering seasons will probably not serve to secure pollination if suitable pollinators are not present in sufficient numbers during any one season. Probability seems to favor either the presence of a suitable insect in sufficient numbers during any given year, or else its complete absence from an island. The high proportion of perennials on oceanic islands probably is primarily related to climatic factors (see principle 14, 2).

The attractiveness of Compositae to a variety of insects is alleged by Wallace (1895) as a reason for the abundance of Compositae on islands. If operative, this reason is probably subsidiary to the good dispersibility, weediness, and adaptability characteristic of this family. Compositae, by congestion of flowers into a head, may be said to fulfil the floral aggregation cited above as a possible advantage in securing pollination.

Change partly or wholly to wind-pollination solves the problem of a scarcity of suitable insect pollinators. Autochthonous evolution into anemophily may have occurred on a few islands (e.g., *Rhetinodendron* on the Juan Fernandez Islands; Skottsberg, 1928). The proportion of anemophilous flowers may be higher in waif floras, but calculations are apparently not yet available.

Speculations such as the above suggest that a study of pollination relationships in the waif biota is very much needed. Few definite statements can be made or particular flower-insect relationships cited.

22. *Some mutations which would be lethal or disadvantageous in continental environments have a more nearly neutral value in the less competitive environment of an oceanic island.*

This statement, easy to make, is difficult to demonstrate, although many of the changes described under headings above might qualify as examples. One feature which clearly does qualify is the fearlessness of island animals. Many descriptions of fearlessness in island animal — particularly birds — have been offered (Lönnberg, 1920; Beebe, 1924; Rand, 1938; Greenway, 1958; Rice, 1964). Where predators are absent, evasive action would seem to be wasteful, because it would interfere with other activities, such as feeding.

Development of conspicuous color patterns may be a visual equivalent of fearlessness, reflecting, as does fearless behavior, the absence of predators. This characteristic occurs prominently among certain lizards (Mertens, 1934; Carlquist, 1965).

Various forms of reproductive inefficiency characterize some island animals, although this subject is as yet poorly explored. Possibly, careful field studies would reveal more instances of the sort reported by Hagen (1952) on Tristan da Cunha: birds with smaller clutches of eggs than characteristic of mainland relatives, and with prolonged sexual immaturity. Vivipary, as in New Zealand geckos, and abundance of intersexes, as in the viper *Bothrops insularis* on the Brazilian island, Queimada Grande (Anon., 1959), would probably be disadvantageous on continental areas. Natural selection might favor a low rate of reproduction in a species with restriction to a small land area, as would such factors as lack of competitors, or greater longevity, all of which conditions do occur on islands.

23. *Endemism, although high on oceanic islands, is not of itself a criterion for identification of an island as oceanic; the nature of the endemism may be indicative, however.*

Oceanic islands tend to have endemism restricted to lower categories, particularly species; to a lesser extent, genera. Old continental islands may be likely to possess endemic families, even orders, as relicts from continents. Setchell (1928) hints at this.

Endemism is a constant byproduct of evolutionary change, and the percentage of endemics is more a measure of degree of isolation in time and space than of mode of origin of islands. If island biotas contain phylogenetically primitive forms with poor dispersal ability, a continental origin for the island may be suspected. For example, the presence of araucarias strongly suggests that New Caledonia is an old, continental-like island.

24. *Evolutionarily plastic groups will be sensitive indicators of directions of evolution in the biota of long-distance dispersal.*

Groups such as insects or composites may be expected to fit themselves rapidly and closely to the templates provided by the island environment. As one example of the usefulness of this concept, one can discount Skottsberg's (1956) claim that peculiar growth forms on the Juan Fernandez Islands are relicts. One would expect such growth forms, if they are relicts, to be representatives of relatively primitive or slowly evolving groups. Instead, the Juan Fernandez rossette-trees and rosette-shrubs occur in upgrade, predominantly herbaceous groups, characterized by weediness and rapid evolution: the Plantaginaceae, the Umbelliferae, and three tribes of the Compositae.

LIST OF LITERATURE

ALLAN, H. H. 1961. *Flora of New Zealand.* Vol. I. R. E. Owen, Gov't Printer, Wellington.

AMADON, DEAN. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). *Bull. Amer. Mus. Natur. Hist.*, 95:151–262.

ANDREWS, E. C. 1940. Origin of the Pacific insular floras. *Proc. 6 Pacific Sci. Congr.*, 4:613–620.

ANONYMOUS 1959. Queer vipers. *Time,* October 19, 1959: 53.

BAILEY, D. W. 1956. Re-examination of the diversity in *Partula taeniata. Evolution,* 10:360–366.

BAKER, H. G. 1953. Dimorphism and monomorphism in the Plumbaginaceae. II. Pollen and stigmata in the genus *Limonium. Ann. Bot.*, 17:433–445.

——. 1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution,* 9: 347–349.

BEEBE, W. 1924. *Galápagos: World's End.* G. P. Putnam's Sons, New York.

BERLAND, L. 1924. Araignées de l'île de Pâques et des îles Juan Fernandez. *Natur. Hist. Juan Fernandez and Easter I.*, 3:419–437.

BERRY, R. J. 1964. The evolution of an island population of the house mouse. *Evolution,* 18:468–483.

BLAKE, S. F., and A. C. ATWOOD. 1942. *Geographical Guide to Floras of the World. Part. I.* U. S. Dept. Agr. Misc. Pub. 401, Washington, D.C.

BØRGESEN, F. 1924. Contributions to the knowledge of the vegetation of the Canary Islands. *Mém. Acad. Roy. Sci. Danemark, Sect. Sci.*, Ser. 8, 6:285–398.

BOWMAN, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Pub. Zool.*, 58:1–302.

——. 1963. Evolutionary patterns in Darwin's finches. *Occasional Papers Calif. Acad. Sci.*, 44:107–140.

BRINCK, P. 1948. Coleoptera of Tristan da Cunha. *Results Norwegian Sci. Exp. Tristan da Cunha,* 17:1–121.

CARLQUIST, S. 1959. Studies on Madinae: anatomy, cytology, and evolutionary relationships. *Aliso,* 4:171–236.

——. 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology,* 12:30–45.

——. 1964. Morphology and relationships of Lactoridaceae. *Aliso,* 5:421–435.

——. 1965. *Island Life.* Natural History Press, New York.

CLOUD, P. E., JR. 1956. Provisional correlation of selected Cenozoic sequences in the western and central Pacific. *Proc. 8. Pacific Sci. Congr.*, 2:555-573.

CLOUD, P. E. JR., R. G. SCHMIDT, and H. W. BURKE. 1956. Geology of Saipen, Mariana Islands. Part 1. General Geology. *U. S. Geol. Surv. Profess. Papers,* 208A:1–126.

COCKAYNE, L., and H. H. ALLAN. 1934. An annotated list of groups of wild hybrids in the New Zealand flora. *Ann. Bot.*, 48:1–55.

CONSTANCE, L., L. HECKARD, K. L. CHAMBERS, R. ORNDUFF, and P. R. RAVEN. 1963. Amphitropical relations in the herbaceous flora of the Pacific coast of North and South America: a symposium. *Quart. Rev. Biol.*, 38:109–177.

COOK, L. M. 1961. The edge effect in population genetics. *Amer. Natur.* 95:295–307.

COOKE, C. M., Jr. 1931. The land snail genus *Carelia. Bishop Mus. Bull.*, 85:1–97.

COOKE, C. M., and Y. KONDO. 1960. Revision of Tornatellidae and Achatinellidae (Gastropoda, Pulmonata). *Bishop Mus. Bull.*, 221:1–303.

CRAMPTON, H. E. 1916. Studies on the variation, distribution and evolution of the genus *Partula. Carnegie Inst. Wash. Pub.*, 228:1–311.

——. 1925. Contemporaneous differentiation in the species of *Partula* living on Moorea, Society Islands. *Amer. Natur.* 59:5–35.

——. 1932. Studies on the variation, distribution and evolution of the genus *Partula.* The species inhabiting Moorea. *Carnegie Inst Wash. Pub.*, 410:1–335.

DAMMERMANN, K. W. 1948. The fauna of Krakatau 1883–1933. *Verh. kon. Ned. Akad. Wetensch. Afd. Natuurk.*, Ser. 2, 44:1–594.

DARLINGTON, P. J., JR. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. *Quart. Rev. Biol.*, 13:274–300.

——. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas and on atrophy of wings. *Ecol. Monogr.*, 13:37–61.

——. 1957. *Zoogeography.* John Wiley & Sons, New York.

DARWIN, C. 1855. Letter to J. D. Hooker, March 7, 1855. *In* F. Darwin (ed.), *Life and Letters of Charles Darwin.* Basic Books, New York.

——. 1859. *On the Origin of Species by Means of Natural Selection.* (Reprint of first edition, 1950.) Watts & Co., London.

DAWSON, J. W. 1958. Interrelationships of the Australasian and South American floras. *Tuatara,* 7:1–6.

——. 1960. Natural *Acaena* hybrids growing in the vicinity of Wellington. *Trans. Roy. Soc. N. Z.,* 88:13–27.

——. 1963. Origins of the New Zealand alpine flora. *Proc. N. Z. Ecol. Soc.,* 10:1–4.

——. 1964. Unisexuality in the New Zealand Umbelliferae. *Tuatara,* 12:67–68.

DOBZHANSKY, T. 1957. Genetics of natural populations. XXVI. Chromosomal variability in island and continental populations of *Drosophila willistoni* from Central America and the West Indies. *Evolution,* 11:280–293.

DOCTERS VAN LEEUWEN, W. M. 1936. Krakatau, 1883–1933. *Ann. Jard. Bot. Buitenzorg,* 46–47: xii + 506.

DURHAM, J. W. 1963. Paleogeographic conclusions in light of biological data. *In,* J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 355–365. Bishop Museum Press, Honolulu.

ELTON, C. S. 1958. *The Ecology of Invasions by Animals and Plants.* John Wiley & Sons, New York.

ENDERLEIN, G. 1909. Die Insektfauna der Insel St. Paul. Die Insektfauna der Insel Neu-Amsterdam. *Deut. Südpolar-Exped., Zool.,* 2 (4) :481–492.

FALLA, R. A. 1960. Oceanic birds as dispersal agents. *Proc. Roy. Soc., Lond.,* B, 152:655–659.

FLEMING, C. A. 1963. Paleontology and southern biogeography. *In* J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 369-382. Bishop Museum Press, Honolulu.

FOSBERG, F. R. 1948. Derivation of the flora of the Hawaiian Islands. *In* E. C. Zimmerman (ed.), *Insects of Hawaii. Introduction,* p. 107–119. Univ. of Hawaii Press, Honolulu.

——. 1956. Studies in Pacific Rubiaceae: I–IV. *Brittonia,* 8:165–178.

——. 1963. Plant dispersal in the Pacific. *In* J. L. Gressitt, (ed.), *Pacific Basin Biogeography,* p. 273–281. Bishop Museum Press, Honolulu.

FRANKLIN, D. A. 1962. The Ericaceae in New Zealand (*Gaultheria* and *Pernettya*). *Trans. Roy. Soc. N. Z. (Bot.),* 1:155–173.

——. 1964. *Gaultheria* hybrids on Rainbow Mountain. *N. Z. J. Bot.,* 2:34–43.

GERMAIN, L. 1934. Études sur les faunes malacologiques de l'océan Pacifique. *Mém. Soc. Biogéogr.,* 4:89–153.

GODLEY, E. J. 1955. Breeding systems in New Zealand plants. I. *Fuchsia. Ann. Bot.,* 19:549–559.

GREENWAY, J. C., JR. 1958. *Extinct and Vanishing Birds of the World.* Amer. Com. Int. Wild Life Protection, New York.

GRESSITT, J. L. 1956. Some distribution patterns of Pacific Island faunas. *Syst. Zool.,* 5:11–32, 47.

——. 1961a. Problems in the Zoogeography of Pacific and Antarctic Insects. *Pacific Insects Monogr.,* 2:1–94.

——, 1961b. Zoogeography of Pacific Coleoptera. *Verh. XI. Int. Kong. Entomol. (Wien),* 1:463–465.

——. 1964. Insects of Campbell Island. Summary. *Pacific Insects Monogr.,* 7:531–600.

GRESSITT, J. L., R. E. LEECH, and K. A. WISE. 1963. Entomological investigations in Antarctica. *Pacific Insects,* 5:287–304.

GRESSITT, J. L., and S. NAKATA. 1958. Trapping of air-borne insects on ships on the Pacific. *Proc. Hawaiian Entomol. Soc.,* 16:363–365.

GRESSITT, J. L., J. SEDLACEK, K. A. J. WISE, and C. M. YOSHIMOTO. 1961. A high speed airplane trap for air-borne organisms. *Pacific Insects,* 3:549–555.

GRESSITT, J. L., and N. A. WEBER. 1959. Bibliographic introduction to Antarctic-Subantarctic entomology. *Pacific Insects,* 1:441–480.

GRESSITT, J. L., and C. M. YOSHIMOTO. 1963. Dispersal of animals in the Pacific. *In* J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 283–292. Bishop Museum Press, Honolulu.

GULICK, A. 1932. Biological peculiarities of oceanic islands. *Quart. Rev. Biol.,* 7:405-427.

HAGEN, Y. 1952. Birds of Tristan da Cunha. *Results Norweg. Sci. Exped. Tristan da Cunha,* 20:1–248.

HAGERUP, O. 1950a. Thrips pollination in *Calluna. Kong. Danske Videnskab. Selskab. Biol. Medd.,* 18 (4):1–16.

——. 1950b. Rain pollination. *Kong. Danske Videnskab. Selskab. Biol. Medd.,* 18 (5):1–19.

——. 1951. Pollination in the Faroes—in spite of rain and poverty of insects. *Kgl. Danske Videnskab. Selskab, Biol. Medd.,* 18 (15) :1–48, HAMILTON, E. L. 1953. Upper Cretaceous, Tertiary, and Recent planktonic Foraminifera from mid-Pacific flat-topped seamounts. *J. Paleontol.*, 27:204–237.

——. 1956. Sunken island of the mid-Pacific mountains. *Geol. Soc. Amer., Mem.*, 64:1–97.

HAMILTON, T., and I. RUBINOFF. 1963. Isolation, endemism and multiplication of species in the Darwin finches. *Evolution*, 17:388–403.

HARLING, G. 1962. On some Compositae endemic to the Galápagos Islands. *Acta Horti Bergiani*, 20:63–120.

HECHT, M. K. 1952. Natural selection in the lizard genus *Aristelliger*. *Evolution*, 6: 122–124.

HEMSLEY, W. B. 1885. Endemic and arborescent Compositae in oceanic islands. *Rep. Sci. Results Voyage H. M. S. Challenger, Bot.*, 1:19–24.

HILL, J. E. 1959. Rats and mice from the islands of Tristan da Cunha and Gough, South Atlantic Ocean. *Results Norweg. Sci. Exped. Tristan da Cunha*, 46:1–5.

HILLEBRAND, W. 1888. *Flora of the Hawaiian Islands.* Privately published, Heidelberg.

HOLDGATE, M. W. 1960. The fauna of the mid-Atlantic islands. *Proc. Roy. Soc., Lond.*, B. 152:550–567.

HOLLOWAY, B. A. 1963. Wing development and evolution of New Zealand Lucanidae (Insecta: Coleoptera). *Trans. Roy. Soc. N. Z., Zool.*, 3:99–116.

JOHNSON, C. G. 1960a. A basis for a genera system of insect migration and dispersal by flight. *Nature*, 186:348–350.

——. 1960b. Present position in the study of insect dispersal and migration. *Rep. 7. Commonw. Entomol. Conf., Lond.*: 140–145.

JOHNSTON, I. M. 1953. Studies in the Boraginaceae. A revaluation of some genera in the Lithospermeae. *J. Arnold Arboretum*, 34:258–299.

KECK, D. D. 1936. The Hawaiian silverswords: systematics, affinities and phytogeographic problems of the genus *Argyroxiphium*. *Occasional Papers Bishop Mus.*, 11 (19):1–38.

KOZHOV, M. 1963. *Lake Baikal and Its Life.* Dr. W. Junk, The Hague.

KRAMER, G. 1951. Body proportions in mainland and island lizards. *Evolution*, 5:193–206.

LACK, D. 1945. The Galápagos finches (Geospizinae). *Occasional Papers. Calif. Acad. Sci.*, 21:1–151.

—— 1947. *Darwin's Finches.* Cambridge University Press, Cambridge.

LADD, H. S. 1958. Fossil land shells from western Pacific atolls. *J. Paleontol.*, 32:183–198.

LADD, H. S., E. INGERSON, R. C. TOWNSEND, M. RUSSELL, and H. K. STEPHENSON. 1953. Drilling on Eniwetok Atoll, Marshall Islands. *Bull. Amer. Asso. Petrol. Geol.*, 37:2257–2280.

LEMS, K. 1958. Botanical notes on the Canary Islands. I. Introgression among the species of *Adenocarpus*, and their role in the vegetation of the islands. *Bol. Inst. Nac. Invest. Agron. (Madrid)*, 39:351–360.

——. 1960a. Botanical notes on the Canary Islands. II. The evolution of plant forms in the islands: *Aeonium*. *Ecology*, 41:1–17.

——. 1960b. Floristic botany of the Canary Islands. *Sarracenia*, 5:1–94.

——. 1961. Botanical notes on the Canary Islands. III. The life form spectrum and its interpretation. *Ecology*, 42:569–572.

L'HERITIER, P., Y. NEEFS, and G. TEISSIER. 1937. Aptérisme des insectes et selection naturelle. *Compt. Rend. Acad. Sci. Paris*, 204:907–909.

LÖNNBERG, E. 1920. The birds of the Juan Fernandez Islands. *Natur. Hist. Juan Fernandez and Easter I.*, 3:1–17.

MACARTHUR, R. H., and E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. *Evolution*, 17:373–387.

MASON, R. 1961. Dispersal of tropical seeds by ocean currents. *Nature*, 191:408–409.

MATTHEW, W. D. 1915. Climate and evolution. *Ann. N. Y. Acad. Sci.*, 24:171–318.

MAY, B. M. 1963. New Zealand Cave Fauna. II. The limestone caves between Port Waikato and Piopio Districts. *Trans. Roy. Soc. N. Z. Zool.*, 3: 181-204.

MCCANN, C. 1953. Distribution of the Gekkonidae in the Pacific area. *Proc. 7. Pacific Sci. Congr.* 4:27–32.

MCDOWALL, R. M. 1964. The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara*, 12:59–67.

MCDOWELL, S. B., JR. 1958. The Greater Antillean insectivores. *Bull. Amer. Mus. Natur. Hist.*, 115:113–214.

MELLISS, J. C. 1875. *St. Helena.* L. Reeve & Co., London.

MENARD, H. W. 1956. Recent discoveries bearing on linear tectonics and seamounts in the Pacific basin. *Proc. 8. Pac. Sci. Cong.*, 2a:809.

MENARD, H. W., and E. L. HAMILTON. 1963. Paleogeography of the tropical Pacific. *In* J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 193–217. Bishop Museum Press, Honolulu.

MERTENS, R. 1934. Die Insel-reptilien, ihre Ausbreitung, Variation, und Artbildung. *Zoologica,* 32:1–209.

MUNRO, G. C. 1960. *Birds of Hawaii.* Ed. 2. The Ridgeway Press, Rutland, Vermont.

MYERS, G. S. 1953. Ability of amphibians to cross sea barriers, with especial reference to Pacific zoogeography. *Proc. 7. Pacific Sci. Congr.,* 4:19–26.

——. 1960. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. *Evolution,* 14:232–333.

PERKINS, R.C. L. 1913. *Fauna Hawaiiensis. Introduction.* Cambridge University Press, Cambridge.

RAND, A. L. 1938. Results of the Archbold Expedition No. 22. On the breeding habits of some birds of paradise in the wild. *Amer. Mus. Natur. Hist. Novit.,* 993:1–8.

——. 1955. The origin of the land birds of Tristan da Cunha. *Fieldiana, Zool.,* 37:139–163.

RATTENBURY, J. A. 1962. Cyclic hybridization as a survival mechanism in the New Zealand forest flora. *Evolution,* 16:348–363.

RICE, D. W. 1964. The Hawaiian monk seal. *Natur. Hist.,* 73 (2):48–55.

RICK, C. M. 1963. Biosystematic studies on Galápagos tomatoes. *Occasional Papers. Calif. Acad. Sci.,* 44:59–77.

RIDLEY, H. N. 1930. *The Dispersal of Plants Throughout the World.* L. Reeve & Co., Ashford, Kent.

RIKLI, M. 1912. *Lebensbedingungen und Vegetationsverhältnisse der Mittelmerländer und der Atlantischen Inseln.* Verlag Kramer, Jena.

ROBYNS, W., and S. H. LAMB. 1939. Preliminary ecological survey of the Island of Hawaii. *Bull. Jard. Bot. Bruxelles,* 15:241–293.

ROCK, J. F. 1913. *The Indigenous Trees of the Hawaiian Islands.* Privately published, Honolulu.

——. 1917. The ohia lehua trees of Hawaii. *Terr. Hawaii Bd. Agr. Forest. Bull.,* 4:1–76.

——. 1919a. A monographic study of the Hawaiian species of the tribe Lobelioideae, family Companulaceae. *Mem. Bishop Mus.,* 7 (2):1–394.

——. 1919b. The arborescent indigenous legumes of Hawaii. *Terr. Hawaii Bd. Agr. Forest. Bot. Bull.,* 5:1–153.

——. 1962. Hawaiian lobelioids. *Occasional Papers Bishop Mus.,* 23:65–75.

ST. JOHN, H. 1966. Monograph of *Cyrtandra* (Gesneriaceae) on Oahu, Hawaiian Islands. *Bishop Mus. Bull.,* 229:1–466.

ST. JOHN, H., and L. FREDERICK. 1949. A second species of *Alectryon* (Sapindaceae): Hawaiian plant studies 17. *Pacific Sci.,* 3: 296–301.

SALMON, J. T., and J. D. BRADLEY. 1956. Lepidoptera from the Cape Expedition and Antipodes Islands. *Rec. Dominion Mus. (N. Z.)*,3:61–81.

SCHENCK, H. 1907. Beiträge zur Kenntniss der Vegetation der Kanarischen Inseln. *Wiss. Ergebn. deut. Tiefsee-Exped. "Valdivia",* 2 (1: 2):225–406.

SETCHELL, W. A. 1926. Les migrations des oiseaux et la dissemination des plantes. *Compt. Rend. Soc. Biogéogr.,* 3:54–57.

——. 1928. Migration and endemism with reference to Pacific insular floras. *Proc. 3. Pan-Pacific Sci. Congr.,* 1:869–875.

——. 1935. Pacific insular floras and Pacific paleogeography. *Amer. Natur.,* 69:289–310.

SHARLAND, M. 1958. *Tasmanian Birds.* Ed. 3. Angus & Robertson, Sydney.

SIMPSON, G. C. 1952. Probabilities of dispersal in geologic time. *Bull. Amer. Mus. Natur. Hist.,* 99:163–176.

SKOTTSBERG, C. 1928. Pollinationsbiologie und Samenverbreitung auf den Jan Fernandez Inseln. *Natur. Hist. Juan Fernandez and Easter I.,* 2:503–547.

——. 1936a. The arboreous Nyctaginaceae of Hawaii. *Svensk Bot. Tidskr.* 30:722–743.

——. 1936b. Vascular plants from the Hawaiian Islands. II. *Medd. Göteborgs Bot. Trädg.,* 10:97–193.

——. 1938. On Mr. C. Bock's collection of plants from Masatierra (Juan Fernandez), with remarks on the flowers of *Centaurodendron. Medd. Göteborgs Bot. Trädg.,* 12:361–373.

——. 1939. A hybrid violet from the Hawaiian Islands. *Bot. Notis.,* 1939:805–812.

——. 1941. Plant succession on recent lava flows in the island of Hawaii. *Göteborgs Kgl. Vetenskaps. Vitterhets-Samhäll Handl.,* Ser. b, 1 (8):1–32.

——. 1944a. On the flower dimorphism in Hawaiian Rubiaceae. *Ark. Bot.,* 31a (4):1–28.

——. 1944b. Vascular plants from the Hawaiian Islands. IV. *Medd. Göteborgs Bot. Trädg.,* 15:275–531.

——. 1945. The flower of *Canthium. Ark. Bot.,* 32a (5) :1–12.

——. 1953. The vegetation of the Juan Fernandez Islands. *Natur. Hist. Juan Fernandez and Easter I.,* 2:793–960.

——. 1956. Derivation of the flora and fauna of Juan Fernandez and Easter Island. *Natur. Hist. Juan Fernandez and Easter I.,* 1:193–438.

——. 1963. Zur Naturgeschichte der Insel San Ambrosio (Islas Desventuradas, Chile). 2. Blütenpflanzen. *Ark. Bot.,* 4:465–488.

Smith, A. C. 1955. Phanerogam genera with distributions terminating in Fiji. *J. Arnold Arboretum,* 36:273–292.

Stark, J. T., and S. O. Schlanger. 1956. Stratigraphic succession on Guam. *Proc. 8. Pacific Sci. Congr.,* 2:262–266.

Stephens, S. G. 1958a. Factors affecting seed dispersal in *Gossypium. N. Carolina Agr. Exp. Sta. Tech. Bull.,* 131:1–32.

——. 1958b. Salt water tolerance of seeds of *Gossypium* species as a possible factor in seed dispersal. *Amer. Natur.,* 92:83–92.

——. 1963. Polynesian cottons. *Ann. Missouri Bot. Gard.,* 50:1–22.

——. 1964. Native Hawaiian cotton (*Gossypium tomentosum* Nutt. *Pacific Sci.,* 18:385–398.

Steven, D. M. 1953. Recent evolution in the genus *Clethrionomys. Symp. Soc. Exp. Biol.,* 7:310–319.

Thorne, R. F. 1963. Biotic distribution patterns in the tropical Pacific. *In* J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 311–354. Bishop Museum Press, Honolulu.

Van Zwaluwenburg, R. H. 1942. Notes on the temporary establishment of insect and plant species on Canton Island. *Hawaiian Planter's Rec.,* 46:49–52.

Viette, P. 1948. Croisière du Bougainville aux îles australes Françaises. 20. Lepidoptera. *Mus. Nat. Hist. Natur. (Paris), Mém.,* n.s., 27 (1) :1–28.

—— 1952a. Lepidoptera. *Results Norweg. Sci. Exped. Tristan da Cunha,* 23:1–19.

——. 1952b. Lepidoptera. *Sci. Res. Norweg. Antarctic Exped.,* 33:1–4.

——. 1954. Une nouvelle éspèce de Lépidoptère de l'île Campbell. *Entomol. Med., Copenhagen,* 27:19–22.

——. 1959. Lépidoptères de l'île d'Amsterdam (récoltes de Patrice Paulian, 1955–1956). *Bull. Soc. Entomol. France,* 64:22–29.

Visher, S. S. 1925. Tropical cyclones and the dispersal of life from island to island in the Pacific. *Amer. Natur.,* 59:70–78.

Wace, N. M. 1960. The botany of the southern oceanic islands. *Proc. Roy. Soc. Lond.,* B, 152:475–490.

Wallace, A. R. 1880. *Island Life.* Macmillan & Co., London.

——. 1895. *Natural Selection and Tropical Nature.* Macmillan & Co., London.

Wheeler, W. N. 1916. Ants carried in a floating log from the Brazilian coast to San Sebastian Island. *Psyche,* 28:180.

Whitaker, T. W., and G. F. Carter. 1954. Oceanic drift of gourds—experimental observations. *Amer. J. Bot.,* 41:697–700.

—— and ——. 1961. A note on the longevity of seed of *Lagenaria siceraria* (Mol.) Standl. after floating in sea water. *Bull. Torrey Bot. Club,* 88:104–106.

Wilson, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution,* 13:122–144.

Yoshimoto, C. M., and J. L. Gressitt. 1959. Trapping of air-borne insects on ships on the Pacific. II. *Proc. Hawaiian Entomol. Soc.,* 17:150–155.

——, and ——. 1960. Trapping of air-borne insects on ships on the Pacific. III. *Pacific Insects,* 2:239–243.

——, and ——. 1961. Trapping of air-borne insects on the Pacific. IV. *Pacific Insects,* 3:556–558.

——, and ——. 1963. Trapping of air-borne insects in the Pacific-Antarctic area, 2. *Pacific Insects,* 5:873–883.

——, and ——. 1964. Dispersal studies in Aphididae, Agromyzidae and Cynipoidea. *Pacific Insects,* 6:525–531.

Yoshimoto, C. M., J. L. Gressitt, and C. J. Mitchell. 1962. Trapping of air-borne insects in the Pacific area, 1. *Pacific Insects,* 4:847–858.

Zimmerman, E. C. 1948. *Insects of Hawaii. Introduction.* University of Hawaii Press, Honolulu.

——. 1957. *Insects of Hawaii. 6. Ephemeroptera — Neuroptera — Trichoptera.* University of Hawaii Press, Honolulu.

——. 1960. Possible evidence of rapid evolution in Hawaiian moths. *Evolution,* 14:137–138.