

Colonization of Islands by Humans: A Biogeographical Perspective

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INTRODUCTION

When European navigators began to explore the Atlantic and Indian oceans in the fifteenth century, they discovered remote uninhabited islands. The absence of people from these islands was only to be expected, since Europeans themselves had had such difficulty reaching and finding them. It was therefore a surprise when the navigators entered the Pacific and found its most remote islands inhabited by Neolithic peoples, ignorant of writing and lacking anything that Europeans could recognize as instruments of

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celestial navigation. While some of these peoples, like the Tongans, had large and fast sailing vessels, others, such as the Easter Islanders, possessed no more visible means of reaching their islands than did flightless insular birds, like the dodo. Ever since those discoveries, scientists have labored to understand how preindustrial peoples did reach some islands, and why they failed to reach other islands.

Today, this specific interest in island colonialization is joined to interest in broader issues raised by island populations. Islands are often viewed as "laboratories" for the study of cultural and ecological processes (MacArthur and Wilson 1967; Evans 1973, 1977; Terrell 1977). This perspective is based partly on the conveniently definite borders of island ecosystems, in contrast to the connections among most of the world's "continents." In addition, islands differ from each other in variables likely to be important to populations of humans and other species, such as climate, geology, area, and isolation. Thus, islands offer "natural experiments": comparisons of islands differing in a certain variable may help us understand the effect of that variable on island populations. For example, one can compare societies that have developed from the same cultural stock on different islands, as in Kirch's (1984) study of how social stratification in Polynesian societies differs between large high tropical islands, small low tropical islands, and temperate-zone islands in the Pacific. Alternatively, one can compare similar island systems occupied by peoples who are very different culturally (e.g., the stepping-stone archipelagoes of the Caribbean and Mediterranean). Finally, when the cultural history is known for the mainland area from which an island was colonized, the comparison of cultural developments on the mainland and island(s) can provide evidence for the effects of insularity.

In this review we are interested in questions of when, how, and why preindustrial human populations reached oceanic islands, and what happened to the populations after arrival. There have been many outstanding studies of human populations on particular island groups, such as Pacific islands (Jennings 1979; Kirch 1984; Terrell 1986b); Mediterranean islands (Cherry 1981; Waldren *et al.* 1984; Knapp and Stech 1985); Australia, New Guinea, Indonesia, and Sahul (Allen *et al.* 1977; Jones 1979; White and O'Connell 1982; Bellwood 1985); Caribbean islands (Rouse 1970, 1986; Rouse and Allaire 1978; Keegan 1985); and Bass Straits islands (Jones 1977). Our review takes a worldwide perspective because we found many issues that were brought more sharply into focus by comparisons of the world's islands (see Hallam 1977).

We also make some use of the extensive literature on colonization of islands by animals and plants. Obviously, human colonization poses unique problems of its own, and "humans aren't just animals." However, problems of island colonization vary enormously among plants and animals: islands

and sea barriers mean very different things to marine birds, rhinoceroses, freshwater fish, and coconut palms. Zoogeographers and phytogeographers have had to develop an overall framework for understanding the diverse solutions that species have found to problems faced by any colonizing species, such as overwater dispersal, intergroup competition, and demographic bottlenecks. Colonizing humans face these same problems. Thus, while no other species serves as a good model for the unique features of human colonization, the overall framework of island biogeography may nevertheless afford useful perspectives (see Terrell 1974, 1976).

The chapter begins with a worldwide summary of island colonization by preindustrial peoples, a history of who colonized what and when. Three geometrical properties of islands that effect the probability of settlement are then described: island distance, configuration, and area (MacArthur and Wilson 1967). This leads to the question of whether islands were reached accidentally or on purpose, and to the theory of autocatalysis as a suggested key to waves of island colonization. From that discussion it can be deduced that island distributions in the world's various oceans affected the degree to which the people living around those oceans developed maritime skills (Diamond and Keegan 1984; Diamond 1985). Next, some consequences of competition between human populations occupying islands are examined. Finally, three phenomena that may develop as an island is colonized are considered: niche shifts, beachhead bottlenecks, and degradation of island environments. The chapter concludes with some reflections on the relevance of biogeography to archaeological studies of islands.

Due to limitations of space, this chapter is necessarily selective. Examples were chosen to illustrate uses of biogeographical concepts and to facilitate comparisons in a generalized context. Thus, the diversity apparent in specific cases is sometimes obscured. Since the study of variation and diversity in island population is the emphasis of much current research, attention is directed to the literature cited for specific cases. As for what constitutes an "island," there is a virtual continuum between the world's conventionally termed "continents," its "islands," and its habitat patches isolated from each other by alien habitat. An extended definition that includes "habitat islands" as well as true islands might read: "a piece of habitat with fairly distinct boundaries, separated from other pieces of similar habitat by water or other alien habitats in which the organism of interest is not resident." In practice, this chapter will not discuss human colonization of "habitat islands" such as deserts and mountains, although they pose interesting questions. Instead, only islands in the conventional sense of land surrounded by water will be considered, and Australia will be included in the discussion.

THE WORLDWIDE HISTORY OF ISLAND COLONIZATION BY HUMANS

If nothing were known about the actual history of island colonization by people, it might logically be assumed to have proceeded as follows:

1. Close islands were colonized before distant islands.
2. Big islands were colonized before small islands.
3. Islands were colonized by the peoples closest to them, or at least by the peoples with easiest access, taking winds and currents into account.
4. Technologically more advanced peoples reached islands earlier, or reached more distant islands, than technologically less advanced peoples.

Compared to these simple expectations, reality is riddled with paradoxes. Why was Samoa colonized 1500 years earlier than the much larger and less remote Madagascar? Why was Easter, which is among the world's most remote scraps of land, colonized 500 years before the much larger and less remote scraps of land, colonized 500 years before the much larger and less remote Iceland? Why was Madagascar settled by people from remote Indonesia, rather than from nearby Africa? Why were Hawaii and Easter settled by people stemming ultimately from Southeast Asia, rather than from the nearer Americas? Why had the Greater Antilles been settled by hunter-gatherers about 3000 B.C., and Fiji by Neolithic horticulturalists about 1200 to 1300 B.C., while the Madeiras and Azores remained empty for thousands of years after Iron Age civilizations had spread over Europe?

To place paradoxes in context, let us summarize the worldwide history of island colonization (Figures 2.1–2.4). Recent archaeological, linguistic, and experimental studies have done much to clarify the dates at which prehistoric human groups colonized islands, the feasibility of alternative colonization routes, and the identities and economies of the colonizers.

The earliest evidence for hominid water-crossing is provided by Paleolithic tools on the eastern Indonesian islands of Flores and Timor, possibly dating from 100,000 to 200,000 B.P. (White and O'Connell 1982). Reaching these islands from the Asian continental shelf required the crossing of at least four (Flores) or nine (Timor) water gaps of up to 29 km (Birdsell 1977). The Paleolithic occupations of Japan (Aikens and Higuchi 1982; Akazawa 1982) and Java do not indicate water-crossing ability, as these two "islands" were colonized while still attached to the Asian continent by land bridges.

The next advance was the colonization of Australia and New Guinea (a single landmass until around 10,000 B.P.) perhaps 50,000 years ago (Jones 1979; White and Allen 1980; White and O'Connell 1982). This continent was reached from either Timor or the Moluccas, necessitating the crossing of 70- to 90-km water gaps (Birdsell 1977).

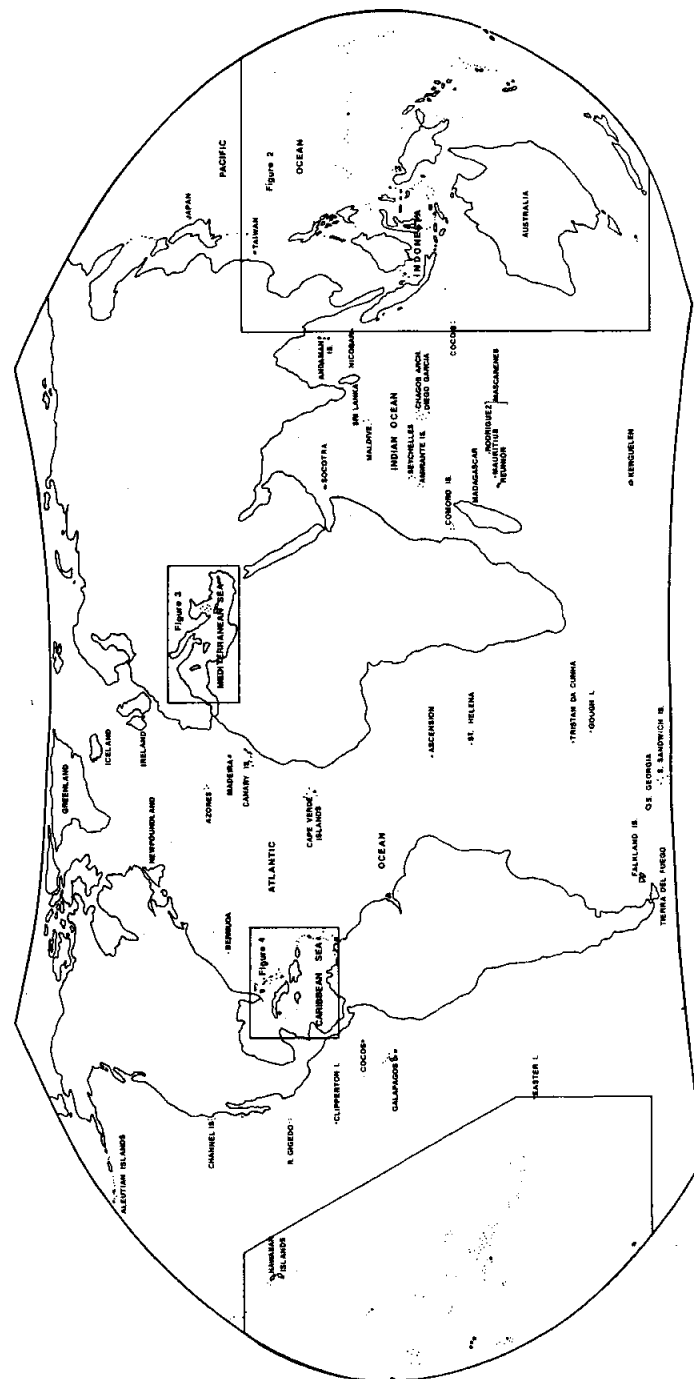


Figure 2.1. Map of the world's major islands.

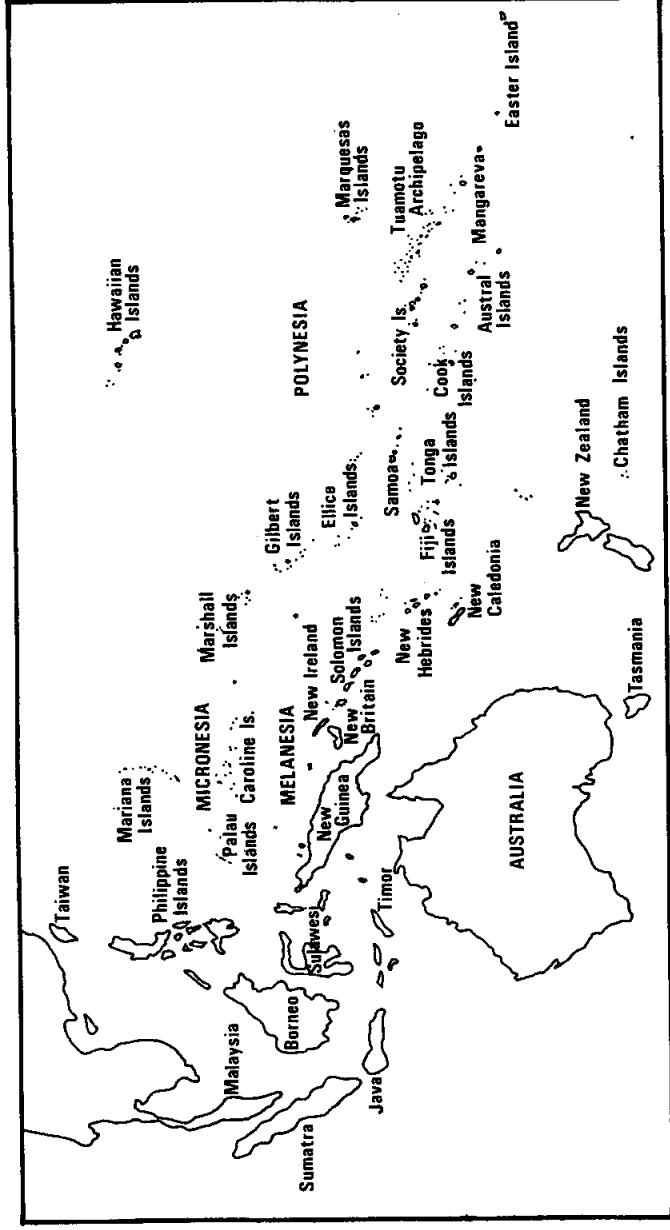


Figure 2.2. Map of the Pacific islands.

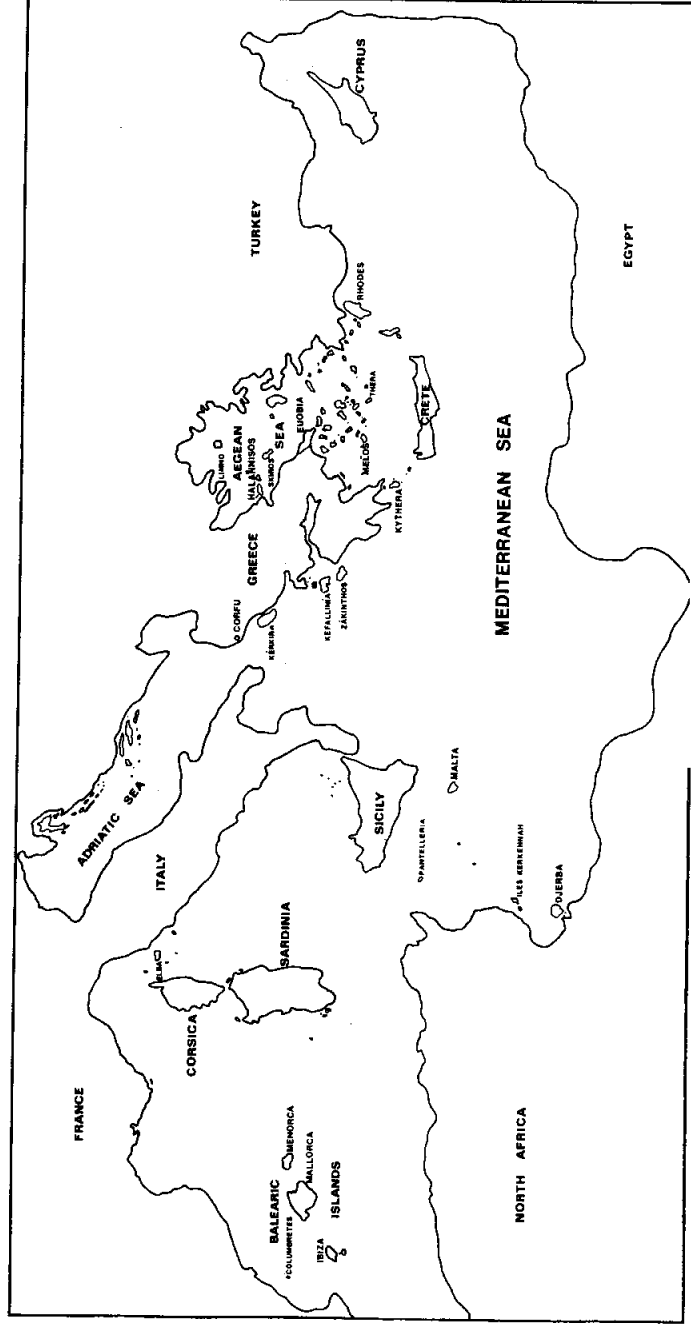


Figure 2.3. Map of the Mediterranean islands.

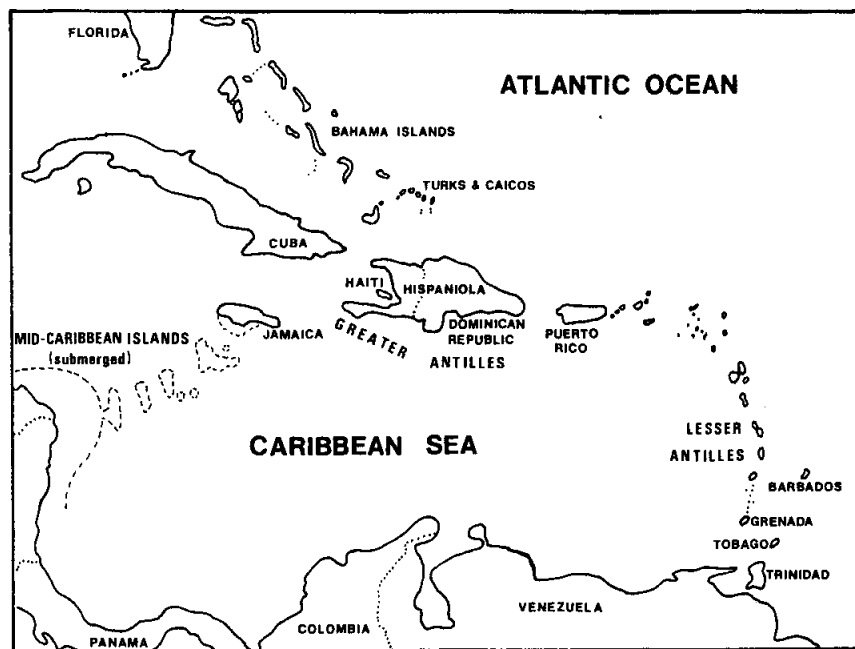


Figure 2.4. Map of the Caribbean islands.

By 11,000 B.P. and probably even earlier, the 88-km gap between New Guinea and New Britain had been breached (Specht *et al.* 1983). Around the same time, coastal populations began colonizing the Aleutian Islands (Aigner and Del Bene 1982), and the first evidence for water-crossing in the Mediterranean is provided by the appearance of obsidian from the island of Melos on the Greek mainland (Cherry 1981). Despite this evidence of water-crossing for obsidian procurement, there is no evidence of settled populations living on Mediterranean islands until around 8000 B.P. (Evans 1977; Cherry 1981). The introduction of ceramics from the Asian mainland to Japan around the same time, following the submergence of Japan's Pleistocene land bridges to the mainland, also provides evidence of early water-crossing ability (Aikens and Higuchi 1982).

Some of the Channel Islands off California may or may not (Junger and Johnson 1980) have had Pleistocene land connections to the mainland, but evidence for Native American overwater exploitation of these islands begins after the Pleistocene (about 7000 B.P.) and continues to historic contact times (Glassow 1985). By 5000 B.P. Native Americans had reached the Greater Antilles across stepping-stone archipelagoes from Central America (via mid-Caribbean islands) or from South America (via the Lesser Antilles)

(Cruexent and Rouse 1969; Rouse and Allaire 1978; Veloz and Vega 1982). By 4000 B.P. the commencement of shellfish exploitation on Martha's Vineyard Island off Massachusetts indicates water-crossing by northeastern Native Americans (Ritchie 1969). Also by 4000 B.P., the high islands of western Micronesia had been settled, probably from the direction of Southeast Asia (Craib 1983). At some undated time in the European-North African Neolithic, the Canary Islands, the sole eastern Atlantic islands other than Britain and Ireland to be settled by this time, were reached across the 100-km water gap from North Africa by the ancestors of the Guanches. The widest gap breached anywhere in the world by 3000 B.P. was in the Pacific, where the Lapita potters crossed the 900 km separating Fiji and western Polynesia from Vanuatu (formerly New Hebrides) (Green 1979; Kirch 1984).

About the time of Christ, Taino colonists entered the Lesser Antilles (Rouse and Allaire 1978; Rouse 1982, 1986), and Pacific peoples continued to set records as the Polynesian descendants of the Lapita people crossed the 2000-3200-km gap separating Tahiti and the Marquesas from Tonga and Samoa. Within the next 800-1000 years, the Polynesians had reached their most remote outposts on Hawaii, New Zealand, and Easter Island. During the same period, Indonesian seafarers crossed the 400-km-wide channel separating Madagascar from Africa at the end of a much longer push of about 8000 km from Indonesia.

We enter the historic period with the Norse colonization of Iceland in A.D. 874, followed by their colonization of Greenland (already reached by two groups of Eskimos) and Newfoundland (Tuck 1971; McGhee 1984). These feats left but a few remote scraps of previously uninhabited land to be colonized by Europeans whose explorations commenced in the fifteenth century A.D.: the Azores, Madeiras, and Bermuda in the North Atlantic; Tristan da Cunha, Ascension, and the Falklands in the South Atlantic; and the Seychelles and Mascarenes in the Indian Ocean.

The overall pattern revealed by this history is that peoples originating from the western flank of the Pacific colonized earlier, farther, and at a lower overall level of technology than did other peoples. The Mediterranean also stands out, though less strikingly, as a site of early water-crossing. At the opposite extreme, the failure of western Europeans to colonize the Madeiras and Azores until about five centuries ago, and of Africans to colonize Madagascar until transported with Indonesians, are notable. We shall argue that these patterns reflect different overwater colonizing abilities of the peoples involved, stimulated by differences in the distribution of islands available to them for colonization. Before we can explore this interpretation, we must first consider what properties of islands determine their accessibility to colonists.

ISLAND GEOMETRICAL PROPERTIES RELEVANT TO COLONIZATION

The physical properties of islands differ in numerous respects. Climatic differences are an obvious first source of variability. For instance, Cuba and Greenland have different environments, which required radically different cultural adaptations. Less dramatic differences characterize all island systems, and, although the configuration of land areas is a convenient starting point for interpreting distributional differences, the marine environments that surround islands may also significantly influence patterns of settlement (Kirch and Yen 1982; Wing and Reitz 1982). Environmental influences are considered in the discussion of phases of a colonization.

Islands also differ as a result of geological processes. For example, cultural development has followed different trajectories on coral atolls and volcanic islands in the Caribbean and Pacific (Watters 1982; Kirch 1984). Furthermore, the initial colonization of islands in a number of areas occurred during periods of lower sea level (e.g., White and O'Connell 1982). Geomorphic changes reflect a variety of continuous processes: sea level changes, tectonic uplifting and subsidence, and the erosion and accretion of coastal sediments (Watters 1982; Kirch and Yen 1982; Butzer 1982; Mitchell and Keegan 1986). Attention must therefore be directed to the reconstruction of coastal geomorphology at the time of island colonization.

Although the physical properties of islands exert specific influences over colonizing efforts, a general understanding of distributional problems also requires examining differences in island distance, configuration, and area. These geometrical properties need consideration because they affect the likelihood that an island with a given climate and geology will be reached and settled. Discussion of these geometrical effects was greatly stimulated by MacArthur's and Wilson's (1967) book *The theory of island biogeography* and has been continued by many subsequent authors (e.g., Simberloff 1974; Williamson 1981; Diamond and May 1981; Diamond and Gilpin 1983).

Distance Effects

Island biogeographers have identified at least four effects of distance on plant and animal colonization (Figure 2.5). The first, emphasized by MacArthur and Wilson (1967) and most subsequent authors, is that the likelihood of immigration decreases with increasing distance between the source and the target. The reason is simply that colonists setting out from the source are exposed to the risk of death en route; the greater the distance, the fewer surviving colonists are left. The second effect, recognized by Brown and Kodric-Brown (1977), is the "rescue effect": the closer an island is to a source, the less likely is an existing population on the island to go extinct, because the

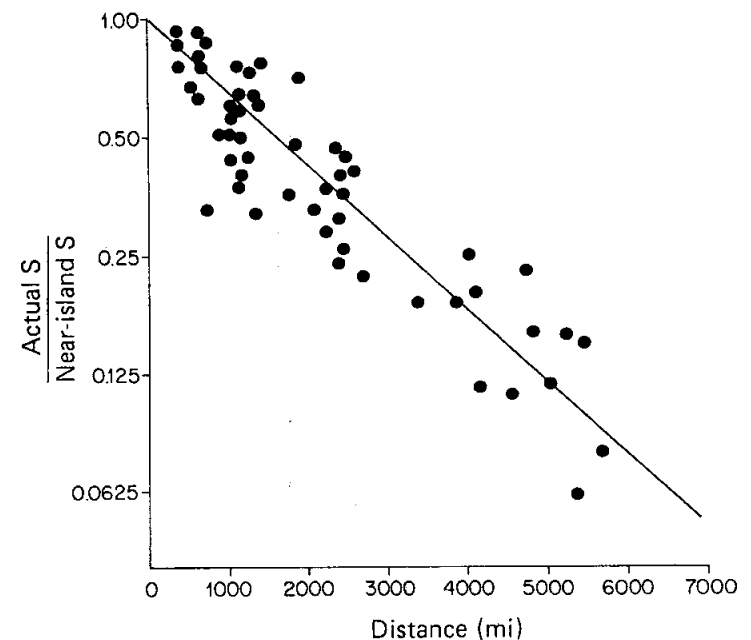


Figure 2.5. Island birds illustrate that islands remote from a large land mass tend to have fewer species than islands nearby do. Each point is based on the number of land bird species breeding on a tropical southwestern Pacific island. The abscissa is the island's distance from New Guinea, the main source of colonists for southwestern Pacific birds. To eliminate effects of area, the ordinate depicts the number of species (S) on the given island, divided by the number of species on an island of the same area within 300 miles of New Guinea. Note that species number declines logarithmically with distance (declines by a factor of two every 1620 mi), until the most remote tropical Pacific islands, Pitcairn and its neighbors, have only 1/10th as many species as similar-sized islands near New Guinea. (From Diamond 1972.)

The third effect is the "commuter effect": islands that are too small to support a self-sustaining population may nevertheless be habitable if the island is within commuting distance of another island or mainland offering additional resources. For example, many small Solomon islands are occupied by eagles, fruit pigeons, and hornbills that regularly fly among the islands, although each individual island alone could not support these species. A fourth effect, emphasized by Lack (1976), is that reduced diversity of species used as food resources on remote islands makes it harder for consumer species to survive.

Distance effects on human colonization are obvious. In the Mediterranean and Pacific, close islands were colonized before distant islands. Pitcairn and some other small remote islands of the Pacific were formerly occupied by Polynesians but were unoccupied at the time of European discovery, possibly because the small populations that developed on these

small islands went extinct and the remoteness of these islands made population rescues by further colonists unlikely or infrequent.

Human equivalents of bird "commuters" include people who make seasonal use of small islands or who rely on trade with larger islands or the mainland for essential resources (e.g., Cherry 1985). The former pattern characterizes the Taino exploitation of the southern Bahama Archipelago from Hispaniola. Saline ponds, which produce salt through solar distillation during the summer months, apparently attracted seasonal salt-collecting expeditions prior to the establishment of a permanent village (Sullivan 1981). An extreme example of year-round commuting is provided by Malai, a small (0.8 km²) island in the Siassi group off New Guinea. Malai supports hundreds of people who live by fishing and trading but who commute to gardens on the nearby much larger island of Umboi, where they also obtain trees for their canoes (Harding 1967). Similar "commuter islands" off the southeast coast of New Guinea include Motupore (Allen 1977) and Mailu (Irwin 1978).

Distance effects are modified by wind and ocean current patterns between the source and the target island. These variables may either favor or inhibit dispersal along a particular vector, depending on the means and timing of dispersal. In their computer simulations of drift voyages in Polynesia, Levison *et al.* (1973) concluded from information about daily wind and current patterns and typhoon probabilities that drift voyages had essentially no chance of reaching eastern Polynesia from the west. Finney (1985) strengthened this conclusion by a more refined analysis that considered in detail the capabilities of Polynesian sailing canoes, the effects of wind direction and ocean currents on the actual distance traveled (i.e., to make one good nautical mile against the true wind, a double canoe must tack for 3.9 mi), and the possible influences of nonprevailing winds and currents (e.g., westerly winds associated with El Niño). In the Bahamas (Figure 2.6), even though the Turks and Caicos Islands present a larger target than Great Inagua, wind and current patterns favor travel from Ft. Liberte, Haiti, to the latter on 281 days of the year, while travel to the former is favored only on 91 days of the year (Keegan 1985). Great Inagua does in fact appear to have been colonized before the Turks and Caicos, presumably due to its effectively greater accessibility (Keegan 1985).

Configurational Effects

Distance effects may be mitigated by the presence of intervening island "stepping stones" (MacArthur and Wilson 1967:29; Gilpin 1980). For example, relationships of Pacific birds make it clear that many bird populations spread progressively from New Guinea to the Bismarcks to the Solomons to Vanuatu to Fiji (Diamond and Marshall 1976). Similarly,

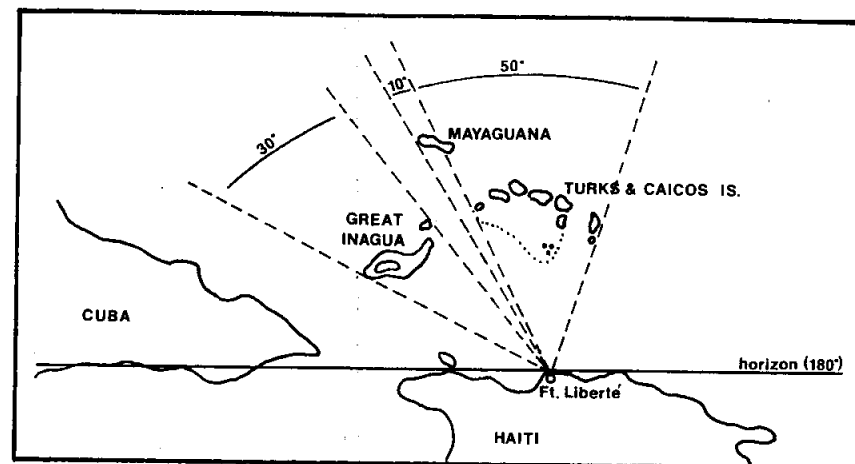


Figure 2.6. The configuration of islands in the southern Bahama Archipelago illustrates the "target effect." Using Ft. Liberte, Haiti, as the embarkation point, the horizon is divided into arc segments that define the probabilities for contact with those islands when the direction of travel is selected at random and when winds and currents are not considered. Under these conditions, the Turks and Caicos Islands present a unified target that subtends 50° of the 180° horizon, which yields a 20% probability for contact. Similarly, Great Inagua presents a target of 30° (16% probability for contact), and Mayaguana presents a target of less than 10° (6% probability for contact). When, in addition, winds and currents are taken into consideration, Great Inagua is calculated to be the most accessible target. In agreement with this reasoning, Great Inagua appears to have been the first island colonized. (After Keegan 1985.)

exceeded their maritime abilities because intervening islands reduced the crossings to a series of feasibly shorter steps. Examples include the colonization of Alaska by Bering Sea Mongoloids from Kamchatka via the Aleutians (Aigner and Del Bene 1982); the colonization of the Greater Antilles by Native Americans from Venezuela via the chain of Lesser Antilles (Rouse 1970); and the colonization of Samoa by Lapita potters (Ancestral Polynesians) from the Bismarcks via the Solomons, Vanuatu, and Fiji.

Another configurational effect is that an island chain arrayed perpendicular to one's axis of travel offers a more easily located target than does a single island (Figure 2.6). Each island can be detected by means of its surrounding "screen" of clouds, seabirds, and altered wave patterns, so that an island chain may effectively contribute a virtually continuous target (Lewis 1972; Levison *et al.* 1973). Thus, although Hawaii was more distant from the next inhabited Polynesian island than was Pitcairn or Easter, the Hawaiian chain offered an easier target than did the latter isolated islands. This difference may help explain why Hawaii, but not Pitcairn or Easter, affords evidence of further visits after the initial settlement

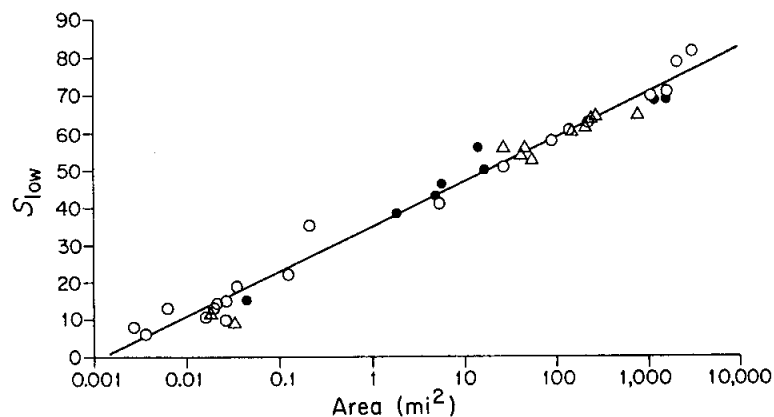


Figure 2.7. Birds of the Solomon Islands illustrate that larger islands tend to have more species than smaller islands. Each point refers to one island, and the ordinate is the number of species resident in the lowlands (S_{low}), while the abscissa is island area. Different symbols identify different groups of islands. Note the very regular increase in species number with island area. (From Diamond and Mayr 1976.)

Area Effects

Like the effects of distance on colonization, those of area are severalfold (Figure 2.7). First, a larger island presents a more visible target and is more likely to be seen by colonists. Second, a colonizing group is more likely to choose to remain on a larger island than a smaller island (rather than abandon it), because the larger island offers a greater quantity and variety of habitats and resources, and more *Lebensraum*. [Even colonizing lizards and birds have been seen to abandon small islands (Schoener and Schoener 1983).] Third, smaller islands support smaller populations in the steady state, so that the population is more likely to go extinct (MacArthur and Wilson 1967; Cawte 1978; Brady 1978; Williamson and Sabath 1982). Finally, populations living on small islands experience higher levels of "risk" because small islands are susceptible to catastrophic disturbances and have an impoverished variety of plants and animals (Fosberg 1963; Williamson 1981; Kirch 1983). Cherry (1985) has suggested that selectively favored adaptations to the risks of island life should include: very small dispersed groups, a broad-spectrum exploitation of resources, and a high level of mobility on the part of at least some members of the group.

An especially clear example of the second effect of area on human colonization, together with the effect of distance, comes from studies of the earliest colonization of the Mediterranean islands (Cherry 1981, 1985; Lewthwaite 1981; Waldren *et al.* 1984). Not surprisingly, settlement proceeded from nearer to more remote islands and required thousands of years

obsidian from Melos Island implies human ability to cross 150-km water gaps *circa* 11,000 B.C., there is no evidence of actual settlement on any island of the eastern Mediterranean for a further 5000 years. Earlier settlements may have been obliterated by sea level changes, but the more likely reason is that no island in the eastern Mediterranean is large enough to have supported a self-sustaining population at the level of hunter-gatherers or early Neolithic herdsman-farmers. By the sixth millennium B.C., only the two largest of the eastern Mediterranean islands, Crete and Cyprus (*ca.* 10,000 km² in area and 100 km from the mainland), had been occupied. By 4000 B.C. occupation had extended to a dozen other eastern Mediterranean islands, most of them larger than 100 km² and less than 40 km from the mainland. Finally, by 2000 B.C. practically all islands larger than 50 km² had been occupied.

A further effect of area and distance is illustrated in Figure 2.8 by the settlement of islands in the western Mediterranean before those of the eastern Mediterranean (Cherry 1981, 1985). The probable reason is the presence of larger islands in the western Mediterranean (Sicily, Sardinia, Corsica) which could support self-sustaining human populations earlier and thus served as stepping stones. Thus, although Neolithic Europeans were clearly capable of reaching most Mediterranean islands by 11,000 B.C., it was not until much later that they chose to settle these islands (Cherry 1985). As improved farming and animal domestication permitted denser human populations, smaller and smaller islands were settled.

A similar pattern obtains in the Caribbean islands. At least two distinct groups of prehistoric hunter-gatherers colonized the larger islands of the Greater Antilles, but they apparently established only temporary settlements on the smaller, intervening islands of the Lesser Antilles. The earliest settlements are dated to 5000 B.P. on Hispaniola (*ca.* 76,000 km²) (Cruxent and Rouse 1969; Rouse and Allaire 1978; Sanoja and Vargas 1983; Rouse 1986). There is no evidence for this initial group in the Lesser Antilles, and it has been suggested that the now submerged mid-Caribbean islands were the route of migration or that early settlements were submerged by the rise in sea level (Nicholson 1976; Watters 1982). In either case, those smaller islands, separated by distances of less than 50 km, would have acted as stepping stones from the Central or South American mainlands, and they would have facilitated the crossing of gaps adding up to 700 to 1000 km. A second migration apparently began about 2000 B.C. and proceeded from northeastern Venezuela through the Lesser Antilles to the Greater Antilles (Veloz and Vega 1982). The Greater Antilles were occupied permanently, with hunter-gatherer populations surviving in western Cuba and southwestern Haiti at Spanish contact. The smaller islands of the Lesser Antilles also were settled during this migration, but they apparently were abandoned at least 1000 years prior to the arrival of the Island Arawak colonists about A.D. 1 (Goodwin 1978; Nicholson 1983). The largest of these Lesser An-

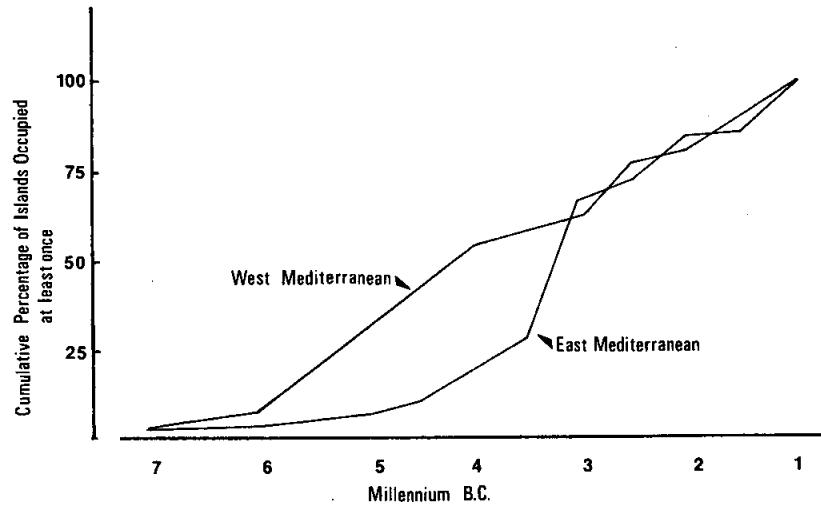


Figure 2.8. The chronological patterns of island colonization in the West and East Mediterranean. The difference in the rate of colonization is attributed to the fact that western islands are larger and are closer to the mainland or to large stepping-stone islands than are eastern islands. (From Cherry 1985.)

availability of marine organisms, resource distributions on these small islands have been interpreted as insufficient to support a hunter-gatherer economy permanently (Goodwin 1978).

The abandonment of the Lesser Antilles leads into the third effect of area: reducing the risk of population extinction. Our clearest examples of area's effect on extinction rates come from the Pacific. Off the southeast coast of Australia, Tasmania and the Bass Straits islands were settled at least 20,000 years ago by people who walked to them from Australia during Pleistocene times of low sea level, when the Bass Straits were dry land. As sea level rose at the end of the Pleistocene, these islands (Tasmania, King, Flinders, and Cape Barren) were converted to their modern configuration. Jones (1977) has shown that on all of the Bass Straits islands except the largest, Tasmania, the human population went extinct or abandoned the islands shortly after insularization. Jones calculated that even the second largest island could have supported only 300–400 people at the Tasmanian subsistence level. This number was evidently insufficient to maintain an isolated human population for thousands of years (cf. Livi 1949; MacCluer and Dyke 1976).

Tasmania and the Bass Straits islands exemplify what biographers term *land-bridge* islands: islands lying on continental shelves and hence connected to the nearby mainland at Pleistocene times of lower sea level. Lampert (1981) has argued that on Kangaroo Island, a land-bridge island off south Australia, a human population survived for thousands of years

after the land bridge was submerged but eventually disappeared. For the world's other land-bridge islands that were already settled at the time of first written records, we can similarly ask whether their populations are derived from the people who walked out to these islands during the Pleistocene Epoch, or whether these Pleistocene populations became extinct following insularization and were replaced by overwater colonists. In the Mediterranean, the first colonists of Corfu, Euboia, and Halannisos in the east, and Sicily and Egadi in the west, apparently reached these islands by crossing land bridges (Cherry 1984). Other land-bridge islands whose archaeological records might reveal evidence for extinction and replacement include Ireland, Fernando Po, Ceylon, Bali, Andaman, Taiwan, and Trinidad.

In addition to land-bridge extinctions, at least 13 Polynesian islands provide evidence for local extinctions of human populations that arrived over water (Bellwood 1979; Kirch 1984). When the mutineers of H.M.S. *Bounty* reached Pitcairn Island in 1790, it was uninhabited. However, stone platforms and statues and excavated archaeological remains (e.g., pig bones, fishhooks, adzes) attest to the prior presence and extinction of a Polynesian group. Tiny Anuta Island (0.4 km²), which supported 180 Polynesians when discovered by Europeans, exhibits a similar sequence of colonization, extinction, and recolonization (Yen and Gordon 1973; Kirch 1982b). Other Polynesian islands that were unoccupied on European discovery, but for which there is archaeological evidence of vanished Polynesians, are Christmas, Fanning, Henderson, Howland, Malden, Necker, Nihoa, Norfolk, Palmerston, Raoul, Suvarrow, and Washington. All of these islands are isolated, all except Christmas are small (mostly 10 km² or less), and fresh water is scarce on almost all. The small size and aridity of these islands made their populations prone to extinction, while their isolation meant that dwindling populations were unlikely to be rescued, or that new populations would soon be founded by immigrants.

Effects of area and distance even operated on the plants and animals carried by the Polynesians (Kirch 1982a). While Polynesians on most of the larger islands had three domestic animals (dog, pig, and chicken), certain of these animals were lacking on the more remote or smaller islands. For example, Easter Island lacked dog and pig, the Tuamotus lacked dog and chicken, and New Zealand lacked chicken and pig. The number of cultigens decreased from 23 or 24 in the Polynesian homelands of Tonga, Futuna, and Uvea, to 18 or 19 in the Societies and Marquesas, 13 in remote Hawaii, 9 in remote and small Easter Island, and 4 in the tiny and scattered Tuamotus. Some of the losses may be due to ecological unsuitability of the colonized island for certain domesticates, but the progressive impoverishment with distance suggests that some domestic plant and animal species simply failed to survive colonizing voyages or to propagate after colonization.

COLONIZATION: ACCIDENTAL OR PURPOSEFUL?

Modern Westerners have tended to assume that they alone were capable of purposeful exploration. Thus, the colonization of islands by technologically simple societies is often attributed to accidental dispersal of small groups swept to sea while exploiting coastal resources from rafts or other simple watercraft. Archaeologists still guess this scenario to hold for the initial settlement of Australia-New Guinea from Indonesia (White and O'Connell 1982). After the first securely dated human colonization (*ca.* 35,000 B.P., actual arrival probably earlier), there is no evidence that a second group of people reached Australia-New Guinea until pigs of undoubted Asian origin and taro of questionably Asian origin appear in New Guinea about 10,000 B.P. or somewhat later, and dogs appear in Australia around 5000 B.P. The most parsimonious assumption is that one raft-load of people from Timor or the Moluccas survived after being swept to Australia or New Guinea, and that this unlikely accident was not repeated for tens of thousands of years. The probability that a single raft-load of people could have successfully colonized an isolated landmass is discussed below.

Accidental colonization was formerly argued vigorously for Polynesia (Sharp 1956). However, it has become clear during the past decade that the initial settlement of East Polynesia, and the settlement of Hawaii, Easter, New Zealand, and other remote outposts, could only have been achieved by purposeful voyages of exploration. Computer simulations of accidental drift voyages (Levison *et al.* 1973), and records of such voyages (Denning 1963), show them to have essentially no chance of reaching East Polynesia and the remote outposts. Finney (1985) has argued that Polynesian mariners did not sail directly into the prevailing winds and currents but consciously waited for occasional periods of westerly winds before voyaging to the east. The distributions of several dozen species of cultigens and domesticated animals throughout Polynesia attest to planned voyages of settlement (Kirch 1982a). Oral traditions concerning navigation, tests of surviving nonliterate Oceanic navigators (Lewis 1972), and the Hawaii-to-Tahiti sea trial of the reconstructed Polynesian sailing canoe *Hokule'a* (Finney 1977) all testify to Polynesian navigational capabilities.

All this is not to say that prehistoric navigational skills were sufficient to eliminate risk and accident. Historically recorded Polynesian canoe voyages in recent centuries, over distances much less than those involved in reaching Hawaii, incurred considerable mortality. It has been estimated that the settlement of Polynesia was accomplished at the cost of 500,000 Polynesians dead at sea, a number equal to the standing population of Polynesia once settled (Jennings 1979). One of us (JMD) visited the Siassi Islands in 1972, shortly after a series of fatal canoe accidents had brought to an end a tradition of interisland voyaging that had lasted for thousands of years. The Siassi canoe

voyages were not abandoned voluntarily by the native population, who considered such accidents to be an acceptable risk of trading expeditions, but were instead discontinued by orders of the Australian administrators on humanitarian grounds.

To modern Westerners, who refuse to board a boat without 99.9% certainty of safe arrival, such risk-taking is utterly incomprehensible. Why did the Polynesians explore and colonize in the face of such risks? Obviously, the answers to questions about motivations of peoples who lived millennia ago must be speculative, but one can draw some inferences that lead to testable predictions. Our explanation is a process we term *autocatalysis* (Diamond and Keegan 1984; Diamond 1985): the discovery of some islands led to the expectation of more islands to be discovered (*cf.* Levison *et al.* 1973; Irwin 1980). The clearest examples of autocatalytically motivated exploration, because the explorers recorded their motives in writing, are the European voyages of exploration that began in the fifteenth century (Sauer 1966; Morison 1971, 1974). When Columbus sailed westward across the Atlantic in 1492, he had no valid evidence whatsoever that lands awaited him within the reach of his ships. Instead, the earlier Portuguese discoveries of the Azores, Madeiras, and Canaries had led him to *expect* undiscovered islands en route to Asia. His discoveries triggered waves of other explorers, and the finds of wealth by Hernan Cortes and Francisco Pizarro triggered floods. Eventually, explorers consciously set out in directions untravelled previously, in the hope of finding new lands. These explorers set out fully aware of the high death tolls among their predecessors: John Cabot, Giovanni da Verrazzano, and thousands of others failed to return alive; so did Captain James Cook, who was the first European to explore Polynesia (Sahlins 1985), and Magellan and 174 of his 210 crew members who entered the Pacific. Of those explorers who did return alive, few had found wealth or new lands worth settling, but those few who did survive and struck it rich told their tales, and new waves of greedy listeners continued to set out with high hopes in an autocatalytic cycle that lasted for centuries.

If autocatalysis is similarly the key to the Polynesian expansion, it explains several otherwise puzzling facts: that Pacific peoples colonized earlier, farther, and at a lower overall level of technology than other peoples; the mysterious "Long Pause" on Samoa and Tonga, if it indeed was real; and the even more mysterious cessation of long distance voyaging after about A.D. 1000 (Irwin 1980, 1981). The Pacific is unique among the world's oceans in that an island chain extends virtually across it. To reach Australia-New Guinea from Southeast Asia involves crossing up to 18 straits, but no strait exceeds 100 km, and almost every island is visible from the previous island. The same is true for the jump from New Guinea to the Bismarcks and for jumps within the Bismarcks and within the Solomons. Thus, explorers could either see their target or could reach it within a few

days, and could thus (for most jumps) maintain contact with the people of the previous island. *We thus suggest that it was the configuration of islands in the Pacific that rewarded Pacific peoples, more than peoples of other oceans, for developing maritime skills.* Other oceans offer fewer accessible targets (see Figures 2.1 and 2.2), and voyagers could not have returned with tales of new lands to justify the risk of voyaging.

The earliest radiocarbon date for Lapita potters in the Bismarcks is about 1850 B.C. By about 1200 to 1300 B.C. the Lapita potters had reached Fiji, Samoa, and Tonga, where seaways of 2000 to 3200 km separated them from the next large islands eastward, the Marquesas and Societies (Tahiti). The earliest radiocarbon date for settlement of these eastern Polynesian islands is not until around 100 B.C. (Kirch 1984). This settlement was quickly followed by an explosion of colonization that carried Polynesians all the way to Easter and Hawaii by A.D. 300–500, and to New Zealand around A.D. 800–1000. Shortly after A.D. 1000, long-distance voyaging within Polynesia ceased and was only a memory by the time that Europeans arrived. Unless the 1000-yr “Long Pause” on Fiji, Samoa, and Tonga proves to be an artifact of available radiocarbon dates, we suggest that it may indicate a period of stasis in long-distance voyaging due to the lack of readily accessible targets. When a lucky voyage finally did reach the Societies or Marquesas and returned with the news of these verdant islands with now-extinct, easily hunted flightless birds, the effect must have been electrifying. It would have ended the Long Pause and stimulated new explorations, just as did Columbus’s voyage. By A.D. 1000, all habitable islands had been settled, canoes failed to return with tales of uninhabited islands, and the motivation for the hazardous long-distance journeys disappeared.

We postulate that occupation of Mediterranean and Caribbean islands was achieved by similar but smaller scale waves of autocatalytic expansion. In the Mediterranean, islands are visible from the European mainland or from other islands that are close to shore. Furthermore, the European shore has a narrow coastal plain backed by mountains that discouraged overland transportation, while good harbors distributed along an extensive coastline favored overwater communications. Colonization took place from the northern Mediterranean because the southern shore along the north coast of Africa had far less coastline, few natural harbors, and a more accessible hinterland and thus provided less incentive to pursue seafaring (Evans 1977). In the Caribbean, the discovery of Grenada (120 km from Trinidad) opened the Lesser Antilles. From Grenada, the Lesser Antilles form a linear archipelago of islands with volcanic peaks that make subsequent islands visible from their predecessor; the islands are separated by 40 to 60 km (Sleight 1965). The continued discovery of islands to the north and west would have encouraged the crossing of wider gaps from Hispaniola to Jamaica and to the Bahamas (150 and 90–140 km, respectively).

Thus, the presence of island stepping-stones extending in several directions across the Pacific, but not across the Atlantic and Indian Oceans, played a two-fold role in human colonization. First and most obviously, for a given width of water gap and a given level of maritime skills, stepping-stones make colonization easier. Even if the Polynesians had been no better seafarers than Native Americans or Africans, many more islands were accessible to the Polynesians by a series of short steps. But this is not the whole story. The gaps that the Polynesians crossed to reach the Marquesas, Easter, and Hawaii dwarf those that prevented Native Americans and Africans from reaching Bermuda and Madagascar by themselves or that prevented Europeans from reaching the Azores and Madeiras until much later. Thus, the Pacific’s configuration of islands had an additional effect, that of stimulating development of maritime skills among Pacific peoples. This positive feedback relationship is especially apparent during later periods when improved vessels and maritime skills were developed to improve the efficiency of overwater exchange in the Mediterranean and West Polynesia (Tonga) (Kirch 1984; Knapp and Stech 1985).

This argument in its simplest form assumes feedback of information from derived populations to source populations. That is, it assumes that people on source islands learned from returning voyagers about at least some cases of new islands successfully reached and were thereby motivated to explore further. For Polynesia’s three remotest outposts (Hawaii, New Zealand, Easter) return voyaging is unproven, though the *Hokule’a* trial supports the possibility for Hawaii. However, Polynesians’ geographical knowledge indicates return voyages among the other Polynesian islands. For example, when first encountered by Europeans in the eighteenth century, Tahitians knew of the existence, name, and approximate bearing of Fiji, Tonga, Samoa, and the Cooks, Australs, Tuamotus, and Marquesas (Lewis 1972). There is also an alternative form of the autocatalysis theory that does not depend on return voyaging. Instead, colonist populations know that they were derived from overwater voyagers, and that knowledge may have stimulated the derived populations (rather than the source populations) to undertake further exploration.

The motivation for voyaging was presumably some combination of trade, search for prized resources, search for unoccupied lands to relieve overpopulation, and curiosity. For instance, Cherry (1985) suggested that the development of Mediterranean economic exchange networks under conditions of increasing population density during the third millennium B.C. *permitted* the settlement of small islands rather than vice versa. In a similar vein, Kirch (1986) examined long-distance trade in the southwestern Pacific as a strategy for initial island colonization. Population expansion in the Bahama Archipelago has been shown to conform to the predictions of an economic optimization model (Keegan 1985): colonization of the next

unoccupied island occurred when a higher rate of return from subsistence production (including transportation costs) could be obtained (cf. DaVanzo 1981). The result was a rapid expansion of population at low densities, rather than the intuitively expected increase in population density to an island's "carrying capacity" prior to the colonization of the next unoccupied island. Other motives cited for particular cases include expulsion of one group by a competing neighbor, opposition between senior and junior siblings or between branches of a descent group, and "wanderlust" or the "spirit of discovery" (e.g., Levison *et al.* 1973; Kirch 1984).

COMPETITION

Attributing the end of Polynesian long-distance voyaging to the filling up of all habitable islands, recognizes that established colonists may prevent colonization by subsequent arrivals. Let us consider this phenomenon in more detail and on a worldwide basis.

On very large islands, different human groups may coexist by occupying different habitats or by employing different subsistence technologies. Examples include coastal and highland populations in New Guinea (White and O'Connell 1982), coastal and mountain peoples (often, speakers of Austronesian and non-Austronesian languages, respectively) on the larger Bismarck and Solomon Islands, and the coexistence of horticultural Taino and hunter-gatherer Archaic populations in the Greater Antilles. In the latter case, the Taino arrived in the Greater Antilles between 7000 and 2000 years after Archaic hunter-gatherers (Rouse and Allaire 1978; Rouse 1986). The expanding Taino population displaced the indigenous hunter-gatherer populations in the Antilles to the point at which only a small population, known as the Guanahabateys, survived in western Cuba at the time of Spanish contact. Direct interaction between the Taino and Antillean hunter-gatherers is apparent in the Taino adoption of Archaic age artifacts and is suggested by similarities in certain decorative motifs (Rouse 1986). Although the Antillean hunter-gatherers were pushed into a small fraction of their original range, they succeeded in coexisting with the expanding Taino for about 600 to 1000 years. To contrast with these cases of coexistence, three cases of competitive exclusion among human groups will now be considered: Norse-Native American-Eskimo relations, Taino-Florida Native American relations, and Polynesian-Melanesian-Australian relations.

After settling Iceland (*ca.* A.D. 874), the Norse settled southwest Greenland around A.D. 986 and began to explore the opposite North American coast of Newfoundland, Labrador, and Baffin Island. A settlement was briefly established on Newfoundland. The Iceland colony survives

today; the Greenland colony failed after 500 years; and the Newfoundland settlement, whose existence has been documented archaeologically, apparently survived only a few years (McGhee 1984). Norse accounts of the Newfoundland colony state explicitly that the land was fruitful but that it was abandoned because of attacks by Native Americans. The decline of the Greenland colony was due partly to deteriorating climate and the end of supply voyages from Europe, but hostilities with Eskimos may also have been a factor.

These Norse examples illustrate the interacting effects of distance, climate, and competition. The Norse might have displaced the Newfoundland Native Americans and the Greenland Eskimos if the distances to Iceland and Norway had not been so great, or if Norse had been better mariners and found the voyages easier, or if the Little Ice Age had not altered Greenland's climate to the advantage of the Eskimo and disadvantage of the Norse. As colder conditions prevailed in Greenland, the Norse increasingly had to rely on imported European products that eventually stopped arriving (McGhee 1984). There is little reason to doubt that Newfoundland's Norse colony would have survived had it not been for the established presence of Native Americans.

The Taino spread more than 1600 km through the Caribbean islands from South America, passing up the chain of Lesser Antilles through the Greater Antilles to reach the Bahama archipelago. Difficulties of overwater dispersal therefore could not have been the reason why the Taino failed to make the final 70-km jump from the Bahamas or the 150-km crossing from Cuba to colonize Florida as well, particularly since there was regular long-distance exchange in the northern Caribbean over greater distances (Sullivan 1981; Keegan 1985). We assume that the Taino did on occasion reach Florida, but that established Native American populations prevented their establishing settlements. Artifactual evidence for contact between the islands and southern Florida is limited, due perhaps to the limited number of archaeological excavations in both areas and to the modern paving over of the Florida coast. However, historic reports do indicate that Native Americans in south Florida permitted the settlement of Cuban Taino who fled from the Spanish (Carr and Riley 1982). This permission apparently was something of a special dispensation, because a specific location was assigned to the Arawaks.

At the beginning of the contact period, the Windward islands of the Lesser Antilles were occupied by a population that has come to be known as the Island Carib (Allaire 1980; Rouse 1986). Proceeding from oral traditions collected among the Island Carib in the seventeenth century, which identified their homeland as northeastern South America, and combining these traditions with ethnohistoric reports of their warlike behavior and cannibalism, archaeologists attempted to identify artifactual evidence for a

late prehistoric or protohistoric migration into the Antilles by Cariban-speaking people from northeastern South America (Gullick 1980; Harris 1980; Allaire 1980; Rouse 1986; Davis n.d.). Yet, recent linguistic studies indicate that the Island Carib were Arawakan speakers, and archaeological deposits reflect a long sequence of local development. It is therefore apparent that the presence of the Island Carib in the Windward islands can no longer be explained as resulting from a Cariban migration from the mainland.

During the historic period the island Carib interacted with both Cariban and Arawakan groups on the mainland (Davis n.d.; Boomert 1985). They were also raiding and encroaching upon the territories of their Taino neighbors to the north (Rouse 1986). Efforts to explain the predatory expansion of the Island Carib will require the examination of the demographic and biogeographic stresses that contributed to their reputation as fierce cannibals (see Davis n.d.).

The Pacific islands provide our third and most illustrative case of complementary distributions among island peoples. The spatial arrangements of Polynesians, Melanesians, Micronesians, and Australians in the Pacific are striking. [While such general classifications of Pacific island peoples are a gross oversimplification of reality (Terrell 1981, 1986a), the following argument can be restated in terms of finer classifications.] Polynesians have the eastern part of the Pacific realm entirely to themselves. As one proceeds westward, the first non-Polynesian peoples encountered are the Fijians, who exhibit a complex mixture of Melanesian and Polynesian traits. In the next archipelago to the west, Vanuatu, Polynesians are confined to three small outlying islands (Aniwa, Mele, and Futuna), plus three villages on the central islands of Emae and Efate. In the New Caledonia group to the south and the Santa Cruz group to the north, the Polynesians are again confined to small outliers (Ouvea in the former; the Reef and Duff islands, Tikopia, and Anuta in the latter). The situation is even more striking in the Solomons, where Polynesians are confined to the outlying islands of Rennell and Bellona plus five small outlying atolls (Sikaiana, Ontong Java, Nukumanu, Takuu, and Nuguria). In Micronesia, the Polynesians are confined to two atolls at the southern fringe, Kapingamarangi and Nukuoro. The remaining islands of Vanuatu, New Caledonia, the Santa Cruz group, the Solomons, and Micronesia are inhabited by Melanesians or Micronesians, though there has obviously been some mixing of the groups, especially in Vanuatu and the Santa Cruz Islands.

It seems paradoxical that Polynesians traversed thousands of kilometers to reach New Zealand and other islands but failed to make the last 1600-km jump from New Zealand to Australia, or the 100-km jumps from Rennell and Bellona and the other Solomon outliers to the central Solomon islands. The difference, of course, is that New Zealand was uninhabited when the Polynesians arrived, but Australia and the central Solomons were not. It is

likely that Polynesians did reach Australia and the central Solomons but were killed on arrival, prevented from settling by the already established Australians and Melanesians, or assimilated into existing populations. Archaeological evidence suggests that Polynesians did reach Norfolk Island between New Zealand and Australia (Specht 1984). Finds of Polynesian-type stone adzes in coastal eastern Australia may suggest occasional arrivals of Polynesians there too, unless the finds are due to post-European contact. In the case of the Solomons, the reasons that the Polynesians failed to make those last jumps to the central Solomons are still vivid in living memory. When one of us (JMD) visited Rennell in 1976, its inhabitants could still recall incidents early in the twentieth century when canoes from Rennell or Bellona drifted to the nearest large islands of Guadalcanal or San Cristobal and the canoe occupants were killed and eaten.

The biogeographic literature on animal and plant distributions offers numerous instances in which closely related species or subspecies occupy different islands within traveling distance and exclude each other competitively. The boundaries between the taxa may be maintained by overt aggression and fighting, or as a result of each taxon being more effective at harvesting resources within a different area or habitat (e.g., Brown 1971; Diamond 1975; Järvinen and Väisänen 1979). The resulting distributional patterns depend on the ecologies and life histories of the two taxa. For example, some taxa are sedentary and rarely found on islands but maintain themselves well in mainland environments in the presence of many competing taxa. *Tramp species* are adapted for overwater colonization and reach many islands. Some tramps are also widespread on the mainland, but others are restricted on the mainland to marginal habitats, such as seacoasts or ecologically disturbed areas. Finally, *supertramps* are taxa that have specialized so heavily in overwater colonizing ability that they occupy most available small or remote islands but are excluded from mainlands and larger islands near colonization sources by more sedentary species (Diamond 1974, 1975). For instance, in the Solomon and Bismarck archipelagoes there are supertramp species of pigeons, starlings, flycatchers, and honey-eaters that occupy small outlying atolls and remote larger islands but are absent from all the large central islands (Diamond 1975).

Those life-history strategies are not fixed forever; they can evolve in a given evolutionary lineage. For example, supertramps often evolve a more sedentary life history after colonizing a large remote island. The most dramatic examples are the large flightless birds that occupied islands in eastern Polynesia prior to the arrival of humans. They are descended from flying species and apparently evolved flightlessness quickly by neoteny (Olson 1973). In the absence of terrestrial competitors and predators, flightless birds survived and reproduced, then diverged into distinct species.

The Taino and especially the Polynesians can be considered to approach

the human equivalent of supertramps: initially mobile populations on islands, excluded from mainlands by other populations. The Tainos' failure to colonize Florida is paralleled by the similar failure of the bananaquit (*Coereba flaveola*) and numerous other Caribbean birds, which occasionally reach Florida as vagrants. Distributions of Melanesians and Polynesians, as already summarized, parallel those of tramp and supertramp bird species, and the parallels extend in some cases down to details of the islands occupied (Diamond 1977b). For example, the atoll starling, *Aplonis insularis*, is a supertramp that occupies the "Polynesian islands" of Rennell, Bellona, Ontong Java, Takuu, and Nuguria in the Solomons, but none of the large or central Solomon Islands. The reason is the same as that for the absence of Polynesians from the central Solomons: the established presence of related starlings (or humans). Obviously, in the human case one is discussing differences between populations of the same species, while in plant and animal cases one is usually discussing separate species. However, this distinction is not critical: similar considerations apply to both cases, and some plant and animal examples involve populations of the same species. For instance, the fruit pigeon, *Ptilinopus rivoli*, is represented in the New Guinea region both by tramp and supertramp populations [respectively, the races *bellus* and *miquelii* on New Guinea and a large island, races *prasinorrhous* and *strophium* on small islets (Mayr 1941)].

THE PHASES OF A COLONIZATION

Any colonization of an island, whether by humans or by other species, confronts a series of demographic and ecological problems. First, the colonized island's environment will generally not be identical to the colonist's source environment. To exploit the new environment, the colonists must begin to make ecological adjustments or niche shifts. Second, the initial group of colonists is generally few in number and exposed to a high stochastic risk of extinction. If the colonists survive this crucial *beachhead bottleneck*, their numbers may grow exponentially until a saturating population density is approached. At that point several alternative outcomes are possible: the colonists may achieve and remain at that saturating density; they may develop improved or intensified methods of harvesting resources and may increase in numbers to a still higher density; or they may exploit resources to a level beyond that at which the resources can renew themselves, leading to resource decline (environmental degradation) and consequent decline in colonist numbers. Kirch (1984) has discussed these themes for Polynesia. We shall consider three aspects of them for island peoples.

Niche Shifts

When a colonizing animal or plant individual reaches a new island, it may encounter a new climate, array of resources, and constellation of competitors and predators. Foods and habitats available in the source region may be lacking; potentially suitable but unfamiliar foods and habitats may be present; competing populations that preempted certain habitats in the source region may be absent. There is a large biogeographic literature on the resulting niche shifts and life history changes of colonists populations (e.g., Diamond 1970; Diamond and Marshall 1977). Many of the niche shifts can be crudely dichotomized as either spatial or dietary.

Typical spatial niche shifts are in altitudinal range or habitat occupied. For example, large mountainous islands have species confined to the mountains, but species that colonize by floating over the sea are necessarily coastal species. Thus, the mountain lizards of colonized islands are not related to the mountain lizards of the mainland or source island but are instead rederived anew on each colonized island by evolving from coastal colonists. Other common spatial niche shifts are the spread of coastal or second-growth species into lowland rain forest, on islands initially lacking a native rain forest biota. For instance, the reef heron, *Egretta sacra*, is, as its name implies, strictly coastal in New Guinea, the Bismarcks, and Solomons, where several other heron species occupy rivers. On Santa Cruz, Vanuatu, Fiji, and Tahiti these competing herons are absent, and the reef heron occurs inland along rivers as well as on the coast (Diamond and Marshall 1977).

Typical dietary niche shifts are in type of food item selected, range of food items selected, or foraging technique employed to capture food. For example, on New Guinea the aerial catching of insects over lakes is the specialty of swifts or swallows, while fantail flycatchers of genus *Rhipidura* specialize in brief short sallies within the forest. On New Zealand, however, where there is no widespread swift or swallow species, the flycatcher *Rhipidura fuliginosa* may be seen spinning in the air over lakes for long periods to catch insects (Diamond 1970). On different Pacific islands the finches of genus *Erythrura* specialize on either bamboo seeds, figs, fig seeds, or grass seeds, depending on what other competing finch species are present (Diamond and Marshall 1977).

Niche shifts operate on various time scales. The most rapid are immediate behavioral responses by an individual colonizing animal confronted with new food resources harvestable by a foraging technique already practiced by the animal. Slower are niche shifts that require learning or "culturally" transmitted information and that take years or generations. Slowest of all are niche shifts requiring genetic change, such as new digestive enzymes or digestive anatomy to process new foods (Ziswiler *et al.* 1972), or altered body size or proportions suitable for a new habitat.

Examples of similar niche shifts abound for human populations colonizing islands. Habitat shifts must have been dramatic for Australia's first settlers, who originated as coastal people on tropical islands with monsoon forest and who spread out to occupy the deserts of central Australia and the cold temperate rainforests of Tasmania and montane New Guinea (White and O'Connell 1982). The mountain peoples of Bougainville, Guadalcanal, and New Britain, like the mountain lizards of these same islands, must have been derived from coastal lowlanders. A sequence of four distinct adaptations has been defined for Archaic Native American populations of the Caribbean (Veloz and Vega 1982), and the horticultural Taino shifted from initial riverine settlements, at which land crabs were the major prey, to coastal settlements, at which marine fish and shellfish predominate (Veloz *et al.* 1976, 1977; Goodwin 1980; Carbone 1980; Wing and Reitz 1982; Jones 1985). At the time of Spanish contact, the Taino of the Greater Antilles practiced intensive marine fishing and agriculture (with incipient irrigation and mound cultivations), and the population had expanded from the coasts into the mountainous interior.

Niche shifts are especially conspicuous for Polynesians, who occupied a greater diversity of habitats than any other people in the world until the recent expansions of industrialized societies. Although the Polynesians originated as coastal peoples on wet tropical islands fringed by coral reefs, they came to occupy not only many similar islands but also high volcanic islands such as Hawaii and Tahiti, islands with rocky shores and few reefs such as Easter Island and the Marquesas, and the cold temperate zone of New Zealand and the Chathams (see Jennings 1979; Kirch 1984). On each island they had to learn a new set of plant and animal species, whose utility and palatability had to be discovered. Although farmers and fishermen by background, some of the Polynesians who colonized New Zealand became hunters for a few centuries until they had exterminated the large flightless birds that they found. These niche shifts can be traced through time in the archaeological record as Polynesian colonists became hunters, exterminated their prey, increased in population density, occupied increasing areas of the island's surface, and modified their agricultural practices in response to new habitats and increasing population densities (Davidson 1979, 1984; Anderson 1983). Those Polynesians who colonized the subantarctic Chatham islands had to learn to survive without agriculture. The settlement history of Tikopia also provides ample documentation of niche shifts by Polynesians (Kirch and Yen 1982).

Such changes in subsistence practices are amenable to analysis with optimal foraging and other marginal cost models (Earle and Christenson 1980; Winterhalder 1981; Smith 1983; Keegan 1986a). For example, the shift from terrestrial animals to marine organisms in Caribbean diets has been shown to reflect the predicted direction of diet breadth expansion based on retrodicted

values for the average and marginal return rates for prey types in those categories (Keegan 1985).

We know little about the time scale needed for these human niche shifts. For the colonizing individuals to survive at all, they must have made some behavioral adaptations within a few days. (When Polynesians reached New Zealand from the Cook or Society Islands, where they could never have seen a land animal larger than a pig or chicken, how many days elapsed before they killed their first moa?) After a tidal wave from the eruption of Ritter Island in 1888 drowned the lowland people of West New Britain, mountaineers moved down to the coast of New Britain, but by 1969 the descendants of those mountaineers were still unskilled at using canoes. The consistently smaller stature of New Guinea's mountain peoples than its lowlanders surely implies genetic change. We assume that the first Polynesian settlers of New Zealand and the Chatham Islands suffered a high death rate from cold-related respiratory illness; comparisons of modern Maoris and tropical Polynesians might indicate whether the resulting severe natural selection caused genetic changes that adapted Maoris physiologically to cold. The Polynesians' large body size and tendency towards obesity, compared to the wiry Melanesians, have often been noted. Is this difference a genetic legacy of the fact that all modern Polynesians are descendants of survivors of long canoe voyages, of which most passengers died of starvation and only the fittest may have lived to reach shore (Diamond 1977b)?

A factor that may contribute to observed niche shifts between parent and daughter communities occupying different islands is the *founder effect*. This concept was originally developed in genetics to describe one outcome of genetic drift, but it has since been applied to cultural-behavioral variability in recognition of the probability that a small colonizing group may be "unable to reproduce in full the culture from which they derived" (Vayda and Rappaport 1963: 134-135). Founder effects are, therefore, potentially immediate causes of differences between parent and colonizing groups. Terrell (1986a) has argued that such incomplete sampling of the parent population, followed by local differentiation, can explain the observed and often overstated differences between Melanesians and Polynesians. In Terrell's (1986a: 12) words, it may be that "Polynesians are Melanesians of a slightly different shade of brown . . ."

The Beachhead Bottleneck

The riskiest stage in colonization, that is, the stage at which the population runs the greatest risk of extinction, is the first, when a small number of individuals reaches an uninhabited island. From demographic models (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1981) one can calculate a population's expected lifetime, which depends on such parameters as

the number and sex of individuals, their ages, and age-specific birth and death rates. Naturally, the risk of extinction is minimized by large colonizing group size, high birth rates, low death rates, and colonists at early prime reproduction age (Black 1978). McArthur *et al.* (1976) estimated likely demographic parameters for Polynesians and calculated survival probabilities of groups composed of three, five, or seven couples obeying an incest taboo. The risk of population extinction declined from 77% to 19% as the number of original couples increased from three to seven. Such calculations are very sensitive to details of the assumptions about demographic parameters and mating practices (Black 1978). They do, however, provide a baseline for evaluating the viability of small, colonizing groups. For instance, White and O'Connell (1982: 48) have used the results of demographic simulations to reconstruct a "suitable picture" of the initial settlement of Australia-New Guinea as comprising a large family consisting of one male, two or three women, and some male and female juveniles.

The *Bounty* mutineers exemplify a colonist population that almost failed to survive the beachhead bottleneck. A group of 15 men and 12 women landed on Pitcairn Island in 1790. Within a decade a series of murders left only 1 of the men and about 10 women, but there were about 25 children by then. The earlier Polynesian settlements of Pitcairn and of the 12 other islands mentioned earlier failed to survive. In Bass Straits, initially populated islands with an estimated carrying capacity of 300 to 400 people failed to retain human populations throughout the Holocene Epoch, but the largest island population, of about 5000, did survive (Jones 1977).

Degradation of Island Environments

If a founding population survives the beachhead bottleneck, it is likely to grow until it reaches some maximum value that depends on island area, resource levels, and the level of technology (Keegan *et al.* 1985). For example, on western Hawaii, where the first permanent settlements date from around A.D. 800, densities of dated residential sites suggest that a population ceiling was reached around A.D. 1600-1700 (Kirch 1984; cf. Cordy 1984). What happens thereafter to population levels, and how does the human population affect the island environment?

Two prevalent and related assumptions are that island populations, after growing to a peak value, fluctuate about that level; and that hunter-gatherers and early farmers-herders practiced a conservation ethic and carefully refrained from overhunting prey species or damaging the environment. Evidence to assess the first assumption is scanty, while evidence permitting rejection of the second assumption is abundant.

Regarding the first assumption, estimates of population change through time are available for some Hawaiian sites (Kirch 1984; but cf. Cordy 1984).

may have been slightly below the peak value reached in the previous century, but this is not certain. On Kahoolawe the population apparently peaked in the 1500s and crashed during the next two centuries to about one-seventh of the peak level. At four sites on Molokai and Oahu the population was apparently still increasing at the time of European discovery. Thus, information for many more sites will be needed to assess the first assumption.

Regarding the second assumption, evidence of habitat degradation is available for many Polynesian sites. The population crash on Kahoolawe was due to destruction of the island's fragile, semi-desert plant cover, consequent soil erosion, and forced retreat of the human population to the coast. On Easter the felling of the original forest (Flenley and King 1984) exposed the soil to desiccation and wind erosion, leading probably to a drop in agricultural yields, while the loss for wood for canoes would have led to a decline in deep-sea fishing yields. Extensive degradation of forests into fern savanna unsuitable for agriculture took place on Uvea, Futuna, Mangaia, Mangareva, the Societies, the Marquesas, and New Zealand (Kirch 1982a, 1984). Naturally, human activities do not automatically lead to habitat degradation: they can also increase an island's human carrying capacity, either intentionally (e.g., by construction of terraced fields, irrigation systems, and fishponds) or unintentionally [e.g., by expansion of Tikopia's lowland agricultural area due to upslope erosion (Kirch and Yen 1982)].

The most striking evidence of man's impact on island ecosystems has come from recent studies of large insular species of mammals, birds, and reptiles exterminated by the first humans who reached islands. The former presence of moas on New Zealand has long been known, but the relative contributions of man's impact and climatic change on the moas have been debated, and the wealth of New Zealand's extinct fauna was in any case believed to be unique. After all, the number of species of mammals and flightless birds on oceanic islands today is modest. Within the past few years it has become clear that most habitable oceanic islands probably had endemic species of flightless birds that were exterminated by the first human colonists within the first few centuries of settlement at most, and within the first few decades in some cases. Much greater numbers of large mammal species became extinct around the time that humans first reached Australia and the Americas, but it remains controversial whether these continental extinctions were wrought by man or by climatic changes (Martin and Klein 1984). The catalog of islands and possible victims includes: Madagascar [a dozen species of giant lemurs, three other large mammals, a dozen species of flightless elephant birds, and giant tortoises (Dewar 1984)], Mediterranean islands [pygmy elephants and hippos, dwarf deer, large rodents, antelope, small macaque, and others (Burleigh and Clutton-Brock 1981; Davis 1985)], Caribbean islands [ground sloths, a bear-sized rodent, a monkey, a large rock iguana, and various other mammals and birds (Campa-

Islands [the flightless duck *Chendytes lawi*: (Steadman and Martin 1984)], New Zealand [moas and many other flightless birds (Trotter and McCullough 1984; Anderson 1984; Cassels 1984)], Hawaii [seven flightless geese and many other birds (Olsen and James 1982)], Tikopia [a megapode (Kirch and Yen 1982)], plus the Chathams, Cooks, Fiji, Henderson, the Marquesas, and New Caledonia [mostly seabirds and large flightless land birds (Cassels 1984; Steadman 1985; Steadman and Olson 1985)].

The extinction of several bird species on Henderson Island is noteworthy (Steadman and Olson 1985). Lying in a remote and rarely visited location east of Pitcairn, Henderson was uninhabited on European discovery, has remained uninhabited through historic times, and is sometimes cited as an example of a pristine habitat untouched by man. Polynesians occupied Henderson for only about 300 years, from A.D. 1100 to 1400, but this brief settlement sufficed to exterminate two large pigeon species and some breeding seabird colonies. Steadman and Olson speculate that the Polynesian settlers of Henderson depended heavily on its birds for food and had to abandon the island when these were exhausted, and that a similar fate may have overtaken the former populations of the 12 other Polynesian islands settled prehistorically but uninhabited when discovered by Europeans.

Many or most of these extinct insular species were examples of large or flightless organisms that would have been easy to kill and that were probably exterminated through overhunting food. However, on one of the few archipelagoes where paleontologists have bothered to study bones of small birds (Hawaii), at least 31 populations of small land birds capable of flight were also exterminated by the first Polynesian arrivals, probably due to clearing of the lowland forest for agriculture (Olson and James 1982). Other exterminations reflect predation or competition from the numerous adventive species (e.g., pigs, dogs, rats, terrestrial snails, cockroaches, weeds) that people introduced to islands, whether intentionally or as accidental stowaways on canoes.

Human colonists also affected the marine environment. For instance, midden analyses show that settlement of Tikopia led within a few years to marked declines in turtle, fish, and shellfish yields and to elimination of the largest size classes of shellfish (Kirch and Yen 1982). Similar results have been reported for New Zealand, Tonga, the Marquesas, and the Reef Islands (Swadling 1976; Anderson 1981; Kirch 1984).

ARCHAEOLOGICAL APPLICATIONS OF BIOGEOGRAPHICAL PRINCIPLES

In their introduction to their classic book, *The theory of island biogeography*, MacArthur and Wilson (1967: 3) describe the importance of islands

"The Zoology of Archipelagoes," Charles Darwin wrote at an early moment in his career, "will be well worth examination." And so it has proved. The study of insular biogeography has contributed a major part of evolutionary theory and much of its clearest documentaton. An island is certainly an intrinsically appealing study object. It is simpler than a continent or an ocean, a visibly discrete object that can be labelled with a name and its resident populations identified thereby. In the science of biogeography, the island is the first unit that the mind can pick out and begin to comprehend. By studying clusters of islands, biologists view a simpler microcosm of the seemingly infinite complexity of continental and oceanic biogeography. Islands offer an additional advantage in being more numerous than continents and oceans. By their very multiplicity, and variation in shape, size, degree of isolation, and ecology, islands provide the necessary replications in natural "experiments" by which evolutionary hypotheses can be tested. [From MacArthur and Edward (1967). Copyright © 1967 Princeton University Press.]

MacArthur and Wilson (1976: 3) go on to point out that although "insularity is . . . a universal feature of biogeography . . . many of the principles . . . apply in lesser or greater degree to all natural habitats." In other words, insularity is a property of geographical boundaries, and while islands are obviously bounded ecosystems, this property is not restricted to oceanic islands. A biogeographical perspective is useful for the study of most distributional questions (MacArthur 1972).

Scientific models aim at generality, precision, and realism (see Winterhalder 1981), but these model qualities cannot be maximized simultaneously (Levins 1966). Thus, scientists must develop models at successively more detailed and particular, less general, levels and must integrate this hierarchy of models so that each model yields the parameters used in the next higher level model. The place of biogeographical concepts with respect to these hierarchical levels of analysis is briefly reviewed in this concluding section.

Understanding and explaining human spatial distributions are significant archaeological concerns. As this chapter has demonstrated, biogeographical principles provide a useful framework for addressing *general* principles underlying human colonization of islands. This emphasis on general patterns prompts worldwide comparisons of human colonization, and comparisons of human colonization with related problems for plants and animals, which help to focus attention on the intellectual issues that archaeological investigations can address. In this regard, the examination of distributional patterns in a generalized context may offer fresh insights (Cherry 1984). Furthermore, a geographical perspective on biological and cultural variability can provide nonobvious and counterintuitive interpretations of cultural diversity (Terrell 1976, 1981, 1986b).

The chapter began with some paradoxes that contradict intuitively logical assumptions about how island colonization should have proceeded. Despite what one might initially have assumed, it is not consistently true that people colonized the world's near-shore islands before its remote islands, or big islands before small islands, or that technologically more advanced peoples or peoples closest to islands colonized first.

or more distant peoples. Many of these paradoxes conformed to the pattern that people from the Pacific's western flank colonized islands earlier, farther, and at a lower overall level of technology than did peoples elsewhere. The recognition and solution of these paradoxes required a worldwide, comparative perspective. The solution proved to be a biogeographical one: the area, distribution, and configuration of the earth's surface has molded the behavior (and possibly, in the case of Polynesians, the anatomy) of humans as of other species. The effect of successful colonization on human behavior involves the positive feedback that we term autocatalysis.

With general patterns thus identified, one can proceed in the next, finer level of analysis to study the processes that account for how geography conditions culture (Cherry 1981; Williamson and Sabath 1982; Kirch 1984; Keegan 1985). Most such studies have been structured using Neo-Darwinian evolutionary principles (e.g., Kirch 1985; Hunt 1985; Terrell 1986a). For instance, Terrell (1986a) has recently suggested a framework for studying the evolution of human diversity. His framework views patterns as a snapshot of variation in a space at a single instant in time, pathways as a temporal series of patterns, and processes as predictable kinds of pathways. This approach focuses attention on the processes that produced patterns at particular times during an evolutionary sequence (Terrell 1986b). Kirch (1984, 1985) has adopted a similar perspective in his study of evolutionary divergence in Polynesia, in which he has examined the interactive processes of dispersal, demography, production, and competition.

A still finer level of refinement involves developing mathematical models that predict the effects of particular processes. For example, life history strategies (e.g., the tramp or supertramp strategy, K-selected or r-selected strategies) can be analyzed in economic terms as potentially optimal solutions to the problems of allocating scarce means (time, energy, and space) among the competing biological demands of maintenance, growth, and reproduction (Gadgil and Bossert 1970; Keegan 1986b). Competition can be analyzed with respect to the impact of shared resource use on the costs of procuring that resource (Tilman 1982). Analysis in terms of game theory has been shown to illuminate the reasons for particular behavioral responses to intergroup competition (Gumerman 1986). Finally, niche shifts can be analyzed with marginal cost models of procurement decision making (Earle and Christenson 1980; Smith 1983; Keegan 1986a). One recent use of microeconomic/ecological models to predict the timing of island colonization is the study of population growth, dispersal, and subsistence change in the prehistoric Bahama Archipelago (Keegan 1985).

In conclusion, biogeographical principles can be used to identify significant patterns in the spatial distributions of insular cultures. The present chapter emphasized some general patterns that would be surprising if one

neglected a biogeographical perspective. Pattern recognition is, however, but the first step in developing and testing models that explain and predict diversity in island populations. Explanations for those patterns will require specific attention to the historical, adaptational, and random processes that generated the identified patterns. Such models are the focus of current efforts in the archaeological study of island biogeography.

ACKNOWLEDGMENTS

It is a pleasure to record our debt to Tim Earle, Patrick Kirch, David Watters, Irving Rouse, and Peter White for valuable suggestions or discussion; and to John Cherry, George Gumerman, and John Terrell, who provided prepublication copies of manuscripts and drew our attention to recent publications.

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Shellfish Gathering and Shell Midden Archaeology

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*"Oysters, come and walk with us!"
 The Walrus did beseech.
 "A pleasant walk, a pleasant talk,
 Along the briny beach;
 We cannot do with more than four
 To give a hand to each."*

Lewis Carroll *Through the Looking Glass*, 1872

INTRODUCTION

Many a seduction, it is said, has begun with oysters. Explorers and travelers have long pondered and speculated on the origins of the massive shell accumulations that line the world's coasts. Bleached and decaying molluscan exoskeletons of many species, in the aggregate of their inconceivable numbers, furnished ample food for antiquarian thought and, indeed, were the subject of some of the earliest scientific archaeology. Their nacreous allurements has not waned; rather the attraction has grown more profound with the understanding gained as archaeology passes from adolescent naivete to the slightly insecure self-satisfaction of its early maturity.