

Chapter 5

From the Vagile to the Sedentary: Disease Implications and New Host Relationships on Islands

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Abstract How species come to be established on islands and their consequent adaptations and evolution are subjects that lie at the heart of much of ecology and evolutionary and conservation biology. On islands, small populations, limited gene diversity and flow, and simpler ecosystems facilitate our understanding of how species arrive and then adapt and evolve in new locations. One component of this is understanding how the transition from arrival to establishment may affect species and their parasites and diseases. Colonizing species may arrive without the full burdens of parasites weighing on their source populations, allowing them to reduce their energetic investments in immune defenses. However, reduced genetic diversity may also reduce populations through inbreeding depression or diminish capacity to evolve. Loss of genes and adaptation to novel environments may over time reduce the capacity of insular species to deal with new parasites or old ones that “catch up.” With increasing anthropogenic introduction of novel biotas, including parasites, to islands, the conservation of insular biodiversity becomes increasingly challenging, which in turn reduces our ability to study and understand both islands and diseases.

Keywords Arrival • Establishment • Parasites • Flightlessness • Adaptive radiation • Extinction

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5.1 Introduction

Islands have been the anvil upon which much of our theoretical understanding of evolution and ecology has been hammered out. They have a similar promise for our understanding of diseases, especially emerging ones.

Did species arrive on islands over past or present land bridges (Hooker 1844; Gregory 1928)? Did they follow successive island “stepping stones” generated over “hot spots” or islands exposed by changes in sea level (Simpson 1940; Wagner and Funk 1995; Gillespie and Roderick 2002; Parent et al. 2008)? Or did they arrive through the lottery of long-distance dispersal (Darwin 1860)? The theories of island biogeography (MacArthur and Wilson 1967; Whittaker et al. 2008), taxon cycles (Wilson 1961; Ricklefs and Bermingham 2002) and Darwin’s naturalization hypothesis that new species most dissimilar to those already present are most likely to be successful (Darwin 1860; Elton 1958; Daehler 2001) have been used to explain arrival, establishment, and subsequent fates of species. The theories of assembly rules and unified neutral theory of biodiversity and biogeography provide contrasting views of how subsequent communities are organized: the former, deterministic; the latter, random (Diamond 1975; Hubbell 2001; Götzenberger et al. 2011). The metapopulation theory of island habitats has focused on the behavior and persistence of species populations across discontinuous island-like landscapes (Hanski and Gaggiotti 2004). Island theory has also helped shape the design and management of natural areas to protect diversity (Simberloff and Abele 1976, 1982). More recently, understanding the establishment and ecological impacts of alien invasive species has also focused on islands, whether true islands or habitat remnants, both for conservation and to provide insights into continental systems (e.g., Mack et al. 2000).

Islands have given us a wealth of examples of evolution and the adaptive radiation of founder species (Darwin 1839; Carlquist 1965; Schluter 2000; Carlquist et al. 2003; Grant and Grant 2014) that laid the foundation and furthered the development of one of the central theories of biological science, evolution through natural selection (Darwin 1860; Wallace 1870).

This chapter provides an overview of how arriving and becoming established and sedentary on islands interact with the population biology and parasite ecology of island species. What makes a species a good colonizer may make it unsuitable for longer-term persistence on an island. On the other hand, adapting to an island and becoming sedentary may make species vulnerable to novel changes in their environment, including the arrival of new parasites and diseases. Other chapters focus more specifically on the ecology and evolution of disease in Galapagos.

Our focus is on terrestrial species on Pacific oceanic islands, those beyond continental shelves that have never been connected to the mainland. Colonization of these islands is different from that of islands closer to species sources and the challenges of establishment and persistence may be different.

The topics covered here have generated an extensive, distinguished, and often contentious literature. This chapter can at best serve as a modest introduction to the

various lines of thought and research. We have tried to combine both the “classic” literature and newer papers to reflect the diversity of approaches, subjects, and geographic areas. The chapter is divided into three main units: how species get to islands, the consequences of becoming established on islands, and the subsequent effect of disease.

5.2 Getting There

Islands are not static in geological time. The geodynamics of islands affect how species reach islands and which species persist and diversify over time (Darwin 1860; Lim and Marshall 2017). Islands may rise from the ocean as volcanoes over “hot spots.” They may disappear as their own weight, erosion, landslides, or changes in sea level sink them or link them to continents (e.g., Darwin 1842). New and old islands may be smaller and lower with fewer habitats and geographic discontinuities, while “middle aged” islands may be high, with variations in topography, climate, and environments (e.g., Whittaker et al. 2008) (Fig. 5.1) leading to changes in colonization, speciation, and extinction (Fig. 5.2). Changes in sea level, atmospheric circulation, and ocean currents may also affect accessibility of islands (Ali and Huber 2010; Claridge et al. 2017).

For islands close to continents, colonization may be by rafting or by dispersal across a land bridge during periods of lower sea level or by being stranded with a rising sea level (Matthew 1918; Simpson 1940). For oceanic islands, successful settlement may be by successive moves down a chain of past or present islands, by “sweepstakes” long-distance dispersal, landing in a suitable spot in a sea of hostile habitats, or by repeated colonizations of islands within an archipelago

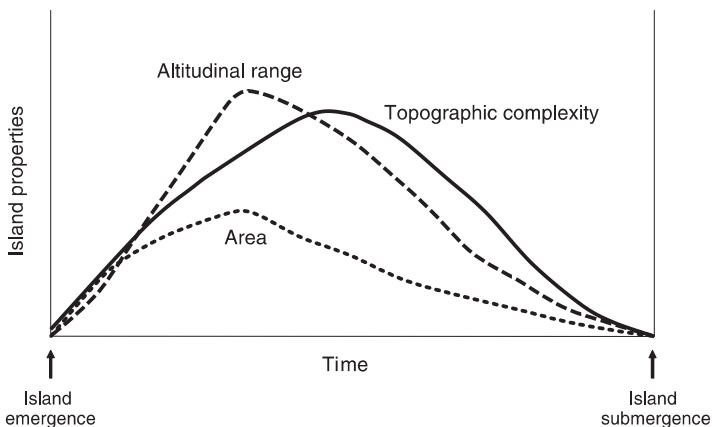


Fig. 5.1 Simplified oceanic island geodynamics over time. Altitude and area accumulate over time, followed by topographic complexity, then all diminish with erosion, land slides and subsidence (Figure 3 from Whittaker et al. 2008)

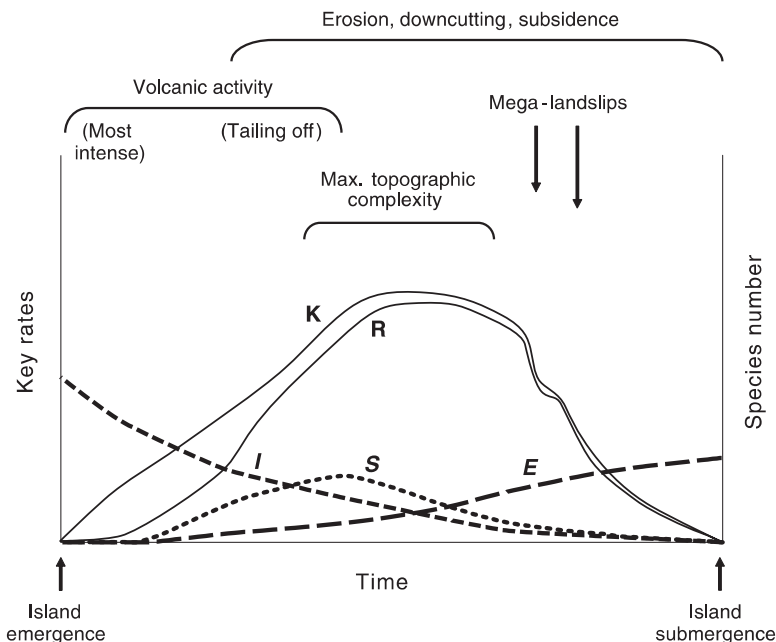


Fig. 5.2 Idealized model of biological change and oceanic island dynamics. I is immigration rate, S is speciation rate, E is extinction rate, K is the carrying capacity, and R is the number of species. Species and speciation increase after the island rises from the sea because of volcanic activity. As the island reaches a plateau in topographic complexity volcanism diminishes, and K and R reach their maxima, with I declining. As erosion and landslides eventually reduce the island to sea level, K and R decrease and E rises (Figure 4 from Whittaker et al. 2008)

(Fig. 5.3) (Darwin 1860; Simpson 1940; Wagner and Funk 1995; Shaw and Gillespie 2016).

Colonizing species of oceanic islands tend to have characteristics often identified in the literature with “invasive species,” “supertramps,” and weediness that predispose them to vagrancy and establishment. Characteristics include small size, wide habitat tolerances, high fecundity, early age of reproduction, and a willingness and ability to cross water gaps (Carlquist 1966a; Diamond 1974). For plants, good dispersers tend to be self-fertilizing with propagules that are small or have winglets and are wind-dispersed, with barbs and fruits that attach to or pass through birds, or float for water dispersal (Carr 1987; Aoyama et al. 2012), a range that can be described as taking advantage of “wind, waves, wings.” In addition, for anything from seeds to medium-sized animals, rafting may transport flightless species to isolated islands (Simpson 1940; Claridge et al. 2017). Even the most improbable species undertake unlikely dispersals (Hansen et al. 2016), such as the recent record of an Aldabra giant tortoise *Dipsochelys dussumieri* that reached the African mainland almost 750 km away (Gerlach et al. 2006). Table 5.1 shows the estimated contributions of wind, sea, and birds to the arrival of different components of the Hawaiian biota. Arrivals are not frequent and vary between taxa. Ziegler (2002) estimated the

Fig. 5.3 Different types of colonization and speciation on islands. (1) “Jackpot” dispersal to an isolated island. (2) “Stepping stone” colonization and speciation down an island chain, (3) Colonization of an archipelago and subsequent allopatric speciation within the archipelago, (4) Colonization of a single island and consequent allopatric speciation within the island

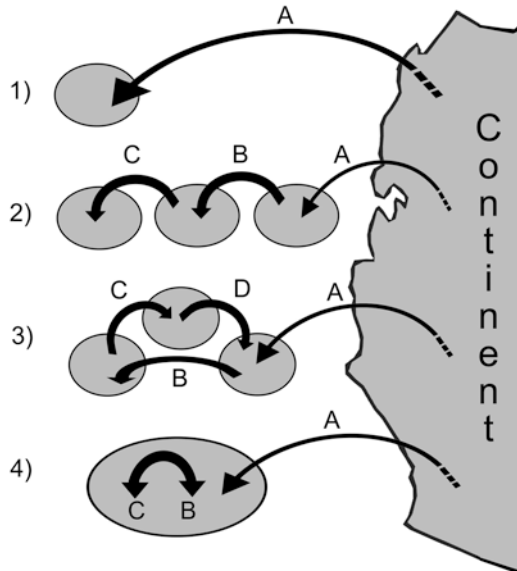


Table 5.1 The estimated percentage importance of various means of transport for species reaching the Hawaiian Islands (after Ziegler 2002)

Group	Sea	Wind	Birds
Ferns		95	5
Flowering plants	23	2	75
Insects	**	***	*
Spiders	**	***	*
Snails	**	*	***
Fishes	100		
Birds		100	
Mammals		100	

*** = most important, ** = important, * = least important

average interval between arrival of founding species of different taxa, ranging from 70K years for insects to 15M years for mammals (Table 5.2).

Not all species get to oceanic islands, so the resulting biota is termed “disharmonic” in that whole groups are rare or absent or over-represented compared to the mainland, depending on their dispersal ability (Carlquist 1966a). Species that fail to become established may have factors that limit them, such as requiring forests or freshwater habitats or specific pollinators or dispersers. Parasites typically need to be transported by their hosts, unless the parasite has catholic tastes or can switch to other hosts upon arrival (Solarz and Najberek 2017; Blackburn and Ewen 2016).

Table 5.2 The estimated average number of years (1000 \times) between arrivals of successful founding species in Hawaii (after Ziegler 2002)

Marine	
Seaweed	175
Stony Coral	1800
Molluscs	115
Inshore Fish	175
Terrestrial	
Ferns and Allies	265
Flowering Plants	105
Insects	70
Siders	2310
Snails	1035
Freshwater Fish	6000
Birds	1155
Mammals	15,000

5.3 Being There

5.3.1 *Becoming Sedentary*

There are various definitions of being sedentary. At one extreme are plant and marine invertebrate species that are sessile, fixed in one spot, dispersing only through seeds or larval stages. At the other extreme are ruderal or pioneer plants and animals that live in unstable environments and are dependent on dispersal to find new suitable habitats as the old ones become unsuitable (Shelford 1914). If there is only limited colonization, there may be a lower probability that the full complement of a species' baggage of predators, parasites, and diseases will accompany it, leading to predator or parasite "release" (Liu and Stiling 2006), although the effects are neither universal nor clear cut (Colautti et al. 2004; Lester et al. 2015).

Adaptation to an island, decreased gene flow, and an increase in sedentariness can have genetic, physiological, morphological, behavioral, ecological, and evolutionary consequences. These are considered below.

5.3.1.1 Genetic

The smaller or more distant the island from a source, the greater the selection for a species to become sedentary once it colonizes. Further dispersal beyond the island would have a reduced probability of survival. The more distant the island, the lower the probability of gene flow from outside and the greater the probability that only a reduced genetic diversity reaches the island, producing a "founder effect" (Templeton 1980). The smaller the island, the smaller the sustainable carrying capacity "K" for a population and the greater the probability that genetic diversity will become reduced over time with less chance of mutations that might facilitate selection for

adaptation to the new environment. Inbreeding and genetic drift in such small populations may also allow the accumulation of lethal and other deleterious genes that may reduce population viability (e.g., Kennedy et al. 2014). Frankham (1997) reported lower genetic diversity for island endemics than for nonendemic birds and mammals. García-Verdugo et al. (2015) reported that while neutral genetic diversity in plants did not differ between island and mainland populations, island endemics with narrow distributions did have lower genetic diversity. While the genetics of colonization would seem likely to set the stage for decreasing dispersal, movement, and survival in new populations, on the other hand, they could produce rapid adaptation and novel responses to the new environment (Darwin 1860).

5.3.1.2 Morphological

Among the most famous adaptive responses of organisms to islands are extreme changes in morphology in endemic species (Carlquist 1965). Changes may include gigantism, producing the giant tortoises of Galapagos and Aldabra (Geotestudinae), elephant birds and rodents of several hundred kilograms (Biknevicius et al. 1993; Murray and Vickers-Rich 2004), dwarfism such as in deer, elephants, and humans (Lister 1996; Brown et al. 2004). Such changes are not universal and the causes of such extremes may be complex and phylogenetically or climatically constrained, suggesting caution in generalization (Lomolino 2005; Meiri et al. 2008; van den Hoek Ostende et al. 2016).

There may also be changes in body proportions and sexual dimorphism (Losos et al. 2003; Wright et al. 2016). Flightlessness has evolved repeatedly in island birds, such as rails (Rallidae) across the Pacific (Ripley and Lansdowne 1977), kiwis (*Apteryx* spp.) in New Zealand, the Flightless Cormorant (*Phalacrocorax harrisi*) in Galapagos (e.g., Slikas et al. 2002; Burga et al. 2017) and geese (*Branta* spp.) and ducks (*Thambetochea* spp.) in Hawaii (Sorenson et al. 1999). Wright et al. (2016) found that volant island birds tend toward reduced flight muscle mass and longer legs, reducing the potential for dispersal. Island beetles also tend to flightlessness (Darwin 1860, Zimmerman 2017) and Carlquist (1966b, c) noted reduced dispersal in the Hawaiian flora.

Reduction or loss of flight may reduce energetic requirements. In New Zealand the lesser short-tailed bat (*Mystacina tuberculata*) walks and even burrows through substrate, expanding its diet and reducing energetic demands while foraging (Hand et al. 2009). Flightlessness in extinct Hawaiian birds may have allowed them to exploit lower value food such as ferns as important, if not primary, dietary items (James and Burney 1997). The flightless New Zealand Takahe (*Notornis mantelli*) feeds on fern rhizomes in winter (Mills et al. 1980).

Species can also evolve to exploit “empty niches,” as suggested here for Hawaiian bird species (Fig. 5.4). Filling the “woodpecker niche,” extracting insects from below the bark of trees, the woodpecker finch (*Camarhynchus pallidus*) in Galapagos uses thorns to probe crevices in bark for insects. In Hawaii, Maui Parrotbills (*Pseudonestor xanthophrys*) have “can opener” bills to pry open bark. The now

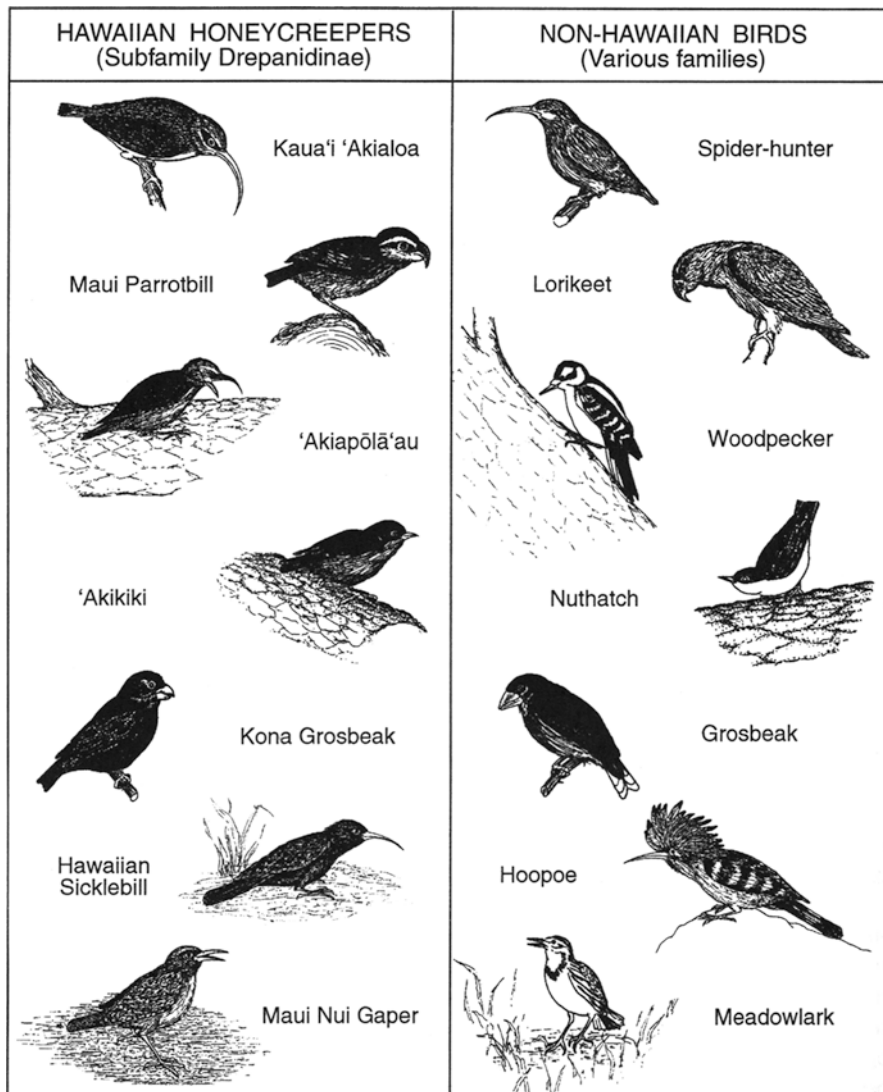


Fig. 5.4 Convergence of Hawaiian honeycreepers to occupy various “empty niches” or ecotypes found in birds elsewhere (reproduced from Ziegler 2002, Figure 10.4, with permission of the University of Hawaii Press)

extinct Hawaiian nukupu'u (*Hemignathus lucidus*) had a lower mandible used as a wedge and an upper bill to use as a probe. In New Zealand, sexual dimorphism in beak morphology of the now extinct Huia (*Heterolocha acutirostris*) allowed pairs to extract food from different parts of a branch and perhaps to feed cooperatively (Buller 1871; Jamieson and Spencer 1996).

Plants exhibit a variety of adaptations to islands. They may lose chemical and morphological defenses against herbivorous mammals (Rhoades 1979; Bowen and Van Vuren 1997). Because birds lack the cutting ability of mammalian teeth, plants may use other strategies such as divaricating growth forms, spines, mimicry, defensive coloration, heteroblasty: changing morphology between juvenile and adult plants, and “playing dead” to reduce herbivory by large herbivorous birds such as flightless moas in New Zealand, elephant birds in Madagascar, and flightless geese in Hawaii (Greenwood and Atkinson 1977; Givnish et al. 1994; Bond and Silander 2007; Fadzly et al. 2009; Berentson 2012). Island plants may acquire secondary woodiness and attendant longevity, allowing them to grow above herbaceous competitors (Darwin 1860; Carlquist 1970; Böhle et al. 1996) and to be pollinated where insects are rare (Wallace 1878).

Plant species may co-evolve with pollinators or seed dispersers, changing seed and flower shape, size, and color, making them dependent on the new pollinators. For example, in New Zealand, the parasitic wood rose (*Dactylanthus taylorii*) is pollinated by the ground-foraging lesser short-tailed bat (*Mystacina tuberculata*) (Ecroyd 1996). In Hawaii, a variety of plants appear to have co-evolved with endemic honeycreeper pollinators (Drepanidini) (Carlquist 1965). Unfortunately, many of the birds are now extinct and the plant species are endangered so we can only infer relationships based on beak and flower morphology (Cory et al. 2015).

5.3.1.3 Behavioral

Behavior may change, such as increasing tameness (Darwin 1839; Cooper et al. 2014), reduced flocking in birds, presumably a reduction in antipredator defenses (Beauchamp 2004), “unwillingness to disperse” or to cross water or other habitat gaps (Darwin 1839; Diamond 1974, 1984; Komdeur et al. 2004) and loss of migratory behavior (Ferrer et al. 2011) as in the Hawaiian Nene (*Branta sandvicensis*) which in turn can lead to flightlessness and speciation (Ripley and Lansdowne 1977).

5.3.1.4 Ecological and Evolutionary

Island birds may be selected for life history strategies with longer life spans, reduced reproductive effort, and later age of sexual maturity, perhaps as a response to limited resources and space (Diamond 1974; Ferrer et al. 2011). To reduce competition or to better exploit resources, species may diverge in how they use such habitats at the macro or micro levels. Divergence might take place in isolation, allopatry, on larger islands or on different islands of an archipelago (e.g., Parent et al. 2016, Fig. 5.3). Species may further diversify within islands as barriers arise following landscape erosion, landslides, or desiccation and consequent separation of once contiguous habitats (Whittaker et al. 2008). This may have occurred among Hawaiian land snails where separate species occupy adjacent ridges (Holland and Hadfield 2002).

All these factors may combine to produce rapid evolution of diverse, endemic species, and “adaptive radiation,” found in Galapagos finches, mockingbirds and tortoises, Hawaiian land snails, silverswords and honeycreepers, and Gulf of Guinea white eyes (*Zosteropidae*) (Darwin 1860; Schluter 2000; Barrier et al. 2001; Carlquist et al. 2003; Melo et al. 2011). While charismatic tortoises, finches, and honeycreepers have been the popular exemplars of adaptive radiation, smaller organisms such as land snails and *Hyposmocoma* moths in Hawaii are much more diverse and are deepening our understanding of species evolution on islands (e.g., Cowie and Holland 2008, Rubinoff 2008; Fig. 5.5).

Speciation and habitat specialization may lead to smaller populations and greater vulnerability to environmental change, arrival of competitors or disease, or increased population variability. This may increase the possibility of extinction over time unless a species can once again expand its habitat and range and become an effective colonist, a concept known as the taxon cycle (Wilson 1961; Ricklefs and Bermingham 2002).



Fig. 5.5 An emerging exemplar of adaptive radiation in invertebrates on islands. Fancy-cased moths *Hyposmocoma* moths in Hawaii have evolved more than 350 species from a single colonizing ancestor. The species manufacture a diverse array of larval protective covers or cases for a range of habitats from freshwater to shoreline to 3000 m (Rubinoff and Haines 2005; Rubinoff 2008) (published with permission of D. Rubinoff https://www.ctahr.hawaii.edu/rubinoff/rubinoff_lab/projects/Hyposmocoma/hyposmocoma.htm)

5.4 Disease Implications and New Hosts

5.4.1 *Consequences of Small Founder Populations*

Island colonization tends to be by small groups or individuals, resulting in reduced genetic diversity, more likelihood of inbreeding and genetic drift, and less scope for mutations (Schrieber and Lachmuth 2017). If only a few individuals colonize, they may be less likely to be accompanied by the full suite of parasites that the species hosted on the mainland because not all potential host individuals are parasitized and there may be selection against parasitized individuals being able to successfully disperse (Dobson and McCallum 1997).

Successful colonists may not be exposed to continuing challenges that would strengthen their immune systems against such lost parasites or other challenges, should these subsequently arrive (Spencer and Zuk 2016). The genetic diversity of the parasites that do accompany their hosts may be similarly reduced (e.g., Gage and Kosoy 2005; Minard et al. 2015) but still more genetically diverse than the host species because parasites can escape post-colonization population bottlenecks more rapidly through their shorter lifespans and faster population growth. Finally, single-strand RNA viruses are capable of rapid evolution through genetic drift so they could play roles in species establishment and survival that remain largely unexplored (Chen and Holmes 2006; Holmes and Grenfell 2009; Faillace et al. 2017).

5.4.2 *Host and Habitat Switching*

At the community level, parasite species may require the same range of suitable conditions as do host species if they are to become established (Blackburn and Ewen 2016). Parasite species that require multiple hosts to complete their life cycles are less likely to be effective colonists. The alternate host has to already be there or the parasite has to adapt to a new one as it arrives (Lymbery et al. 2014).

Parasites may be generalists across their ranges, but specialize on hosts locally (McCoy et al. 2013), potentially priming them to adapt to new hosts after colonization. Ewen et al. (2012) found that *Plasmodium* spp. which successfully established in New Zealand tended to be generalists with a wide range of host species. In contrast, Levin et al. (2016) found that *Plasmodium* in Galapagos did not have a greater host range than on the mainland. Filarial worms, a nematode parasite not uncommon in cormorant relatives worldwide, thus likely arriving to the Galapagos Islands in cormorants, have jumped to the Galapagos Penguin *Spheniscus mendiculus* (Merkel et al. 2007). This jump was probably facilitated by the sedentariness of the Flightless Cormorant *Phalacrocorax harrisi* sharing the same breeding habitat with penguins in the western part of the archipelago (see Chap. 7, this volume).

Parasites may switch habitats and associated hosts. For example, the mosquito *Aedes taeniorhynchus* in Galapagos, having spread inland from its “traditional”

brackish water habitat, switched to reptiles from its usual avian and mammalian diet (Bataille et al. 2009; 2012). The Rock Dove protozoan *Trichomonas gallinae* switched to the Galapagos Dove *Zenaida galapogensis* (Harmon et al. 1987). Some apparent parasite switches may actually reflect the arrival of additional parasite strains that can attack new hosts that were resistant to previous strains. In Hawaii, new strains of *Toxoplasma gondii* were associated with mortality of Nene, although the wider demographic consequences need to be investigated (Work et al. 2016).

5.4.3 Migrants

Islands on regular migration routes may be exposed to a regular rain of potential diseases and parasites carried by migrants such that over time the indigenous hosts go extinct, or they evolve to co-exist with the parasites (Laird 1960). Bobolink (*Dolichonyx oryzivorus*) migrating through Galapagos may have served as a pathway for the introduction of *Plasmodium* sp. (Levin et al. 2016). Similarly, migratory birds may have a greater parasite diversity than do more sedentary populations (Jenkins et al. 2012, but see Ricklefs et al. 2016).

Host population structure may also be important on islands, as variable response among multiple small populations may produce rapid selection for resistance that might be slower or impossible in larger, panmictic populations (e.g., Foster et al. 2007).

5.4.4 Ecological Triggers

The arrival of humans with their commensals has frequently unleashed new pathogens and parasites into island ecosystems (Goodman 1995; Cheke 2010). This may have occurred so far in the past that we cannot tell immigrant parasite from indigene, even if the initial arrivals triggered drastic “virgin soil” epidemics or even extinctions (Crosby 1976). There are, however, numerous recent or contemporaneous anthropogenic introductions from which to draw insights (Cliff et al. 2000) and the threat remains from future introductions (Dethier 1945; Lounibos 2002; Gottdenker et al. 2005).

Diseases and parasites may invade repeatedly but fail to be established until a vector or alternate host arrives, the invader switches to an alternative host, or until vector populations expand sufficiently to come into contact with potential native hosts. Parasites may also be too virulent in endemic species to become established until more resistant host species arrive that serve as reservoirs, allowing the parasite to persist and spill over in a density-independent manner on the declining native populations (McCallum and Dobson 1995; Woodworth et al. 2005; Sturrock and Tompkins 2008; Lymbery et al. 2014). Alternately, the parasite may evolve reduced virulence over time, although the endemic hosts may not persist during the transition, as may be occurring with the parasitic fly, *Philornis downsi* in Galapagos (Kleinendorfer and Dudaniec 2016).

In Hawaii, the arrival of the mosquito *Culex quinquefasciatus* in 1826 provided a potentially effective disease vector that awaited the arrival of poxviruses in the last decade or so of the nineteenth century and introductions of reservoir bird hosts from elsewhere in the early twentieth century to support avian malaria *Plasmodium relictum* (van Riper et al. 1986). These species triggered major mortality and extinctions in native forest birds in Hawaii, eventually restricting many species to elevations above the limits of the mosquito vector (van Riper et al. 1986; Atkinson et al. 2014). The recent arrival (circa 1985) of the same mosquito species in Galapagos may provide an unfortunate opportunity to replicate the Hawaiian experiment, if this mosquito proves a more effective vector than is *Aedes taeniorhynchus* for avian malaria or poxvirus (Whiteman et al. 2005; Parker et al. 2011; Meile et al. 2013). More widely, further arrivals of *C. quinquefasciatus* genotypes on islands may introduce new genes, expanding the distribution of this species from its present peridomestic habitat (Bataille et al. 2009).

Similarly, the arrival of cats (*Felis catus*) across the Pacific allowed the establishment of toxoplasmosis, felids being the definitive host. In island ecosystems such as Hawaii, toxoplasmosis is associated with morbidity and mortality of a range of land and seabirds and marine mammals (Work et al. 2000, 2002, 2016; Honnold et al. 2005; Duffy and Capece 2012). Rats, transported on ships, have brought a wide range of zoonotic pathogens to islands (Gage and Kosoy 2005; Kosoy et al. 2015). They may exchange pathogens with island endemic rodents, leading to emerging diseases for humans (Mumford 1942; Wilkinson et al. 2014). More recently, habitat destruction, whether direct or caused by introduced herbivores, has brought endemic zoonoses into contact with humans and other animals (e.g., Halpin et al. 2007).

5.4.5 *Reduced Immunity*

Species may change investment in their amounts or types of immunological defenses, depending on the level of parasite challenge (Schmid-Hempel and Ebert 2003). General immune responses may be less costly than the production of specific antibodies (Frank 2000). Beadell et al. (2007) compared the immunology of pairs of endemic and introduced bird species in the Pacific islands with mainland counterparts. Parasite and genetic diversity were reduced in the island species but there was no consistent immunological response. Similarly, Matson (2006) compared pairs of mainland, Hawaii, Bermuda and Galapagos bird species and found no reduction in immunological defenses.

In contrast, within-species comparisons across islands may reveal more consistent patterns. Lindström et al. (2004) found that Galapagos small ground finch (*Geospiza fuliginosa*) on larger islands in the archipelago, where parasitism was heavier, had “standing” immune systems that generally mounted nonspecific but faster responses than did the immune systems of finches on smaller islands. Whiteman et al. (2006) found that Galapagos hawks (*Buteo galapagoensis*) had lower genetic diversity, reduced natural antibody response, and higher parasite load

on small islands than on large islands. Huber et al. (2010) found that antibody levels in the Medium Ground Finch (*Geospiza fortis*) were higher where poxvirus was observed in birds than where it was apparently absent. Behavior can also play a role. Antibody levels against the parasitic nest fly (*Philornis downsi*) were higher in the finches during the breeding season and higher in females, which do the brooding on the nest (Huber et al. 2010) (Fig. 5.6).

Genetically bottlenecked populations on islands may have lower immune responses to challenges, even if their parasite loads are similar to those in outbred populations (e.g., New Zealand Robin *Petroica australis*; Hale and Briskie 2007), but the consequences may vary between species. For example, absence of particular alleles did not significantly affect vulnerability to malaria in a small population of North Island Saddleback *Philesturnus carunculatus* on Mokoia Island, New Zealand (Sutton et al. 2016).

Overall, the relation between immunity and islands appears complex. Past genetic and parasite history and evolution, tradeoffs in resource allocation, differences between susceptibility and resistance, and difficulties in measurement

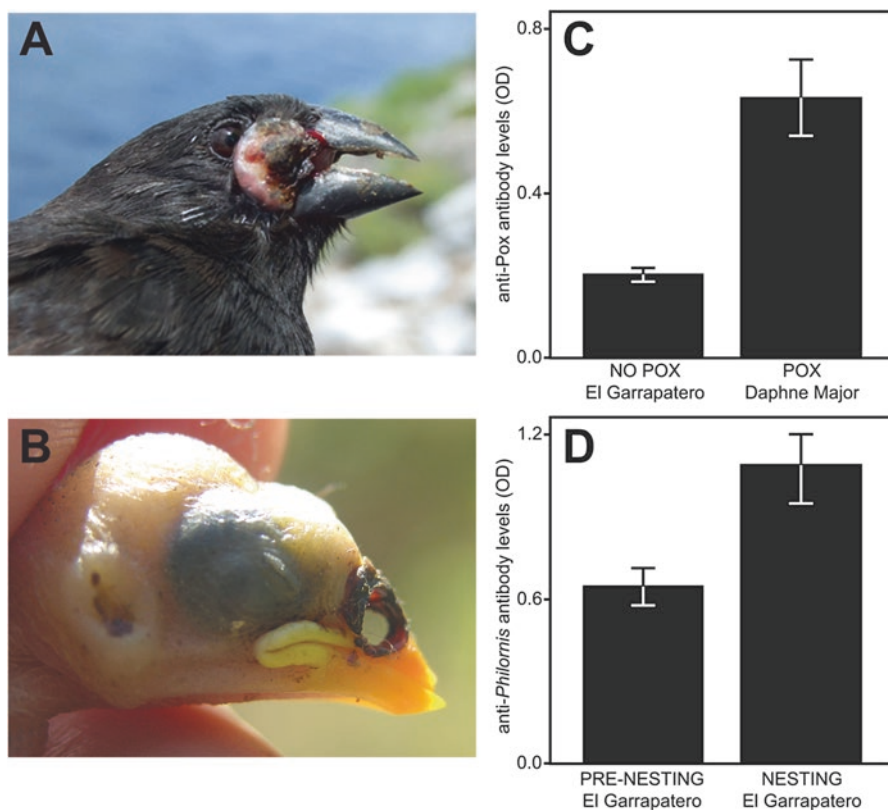


Fig. 5.6 Antibody responses to avian pox and a nest parasite in the Medium Ground Finch (*Geospiza fortis*) in Galapagos (Figure 1 in Huber et al. 2010)

cloud the picture and resist generalization at present (Adamo 2004; Beadell et al. 2007).

Absence or reduced diversity of parasites on islands could allow a newly arrived species to increase its fitness and population growth and reduce the need to invest in costly immune defenses, potentially giving it a competitive advantage against indigenous species (Mack et al. 2000; Blackburn and Ewen 2016). Over time this absence of parasites could make species vulnerable when challenges from old or novel parasites finally arrive and require stronger immunologic responses (Stringer and Linklater 2014), resuming an evolutionary race between a species and its parasites or predators (Van Valen 1973; Dawkins and Krebs 1979). There may also be a tradeoff between the health or fitness of an individual and that of the population which may be especially of concern for the conservation of small island populations (Spencer and Zuk 2016). The end result for island endemics is likely to be a greater vulnerability to the arrival of new competitors or parasites or to environmental change or to some combination of these than for their mainland counterparts (e.g., Blackburn et al. 2004; Fessl et al. 2001).

5.5 Discussion

As in most of ecology, theories on the arrival and establishment of species on islands and the role of genetics and parasites represent a tension between the desire for broad theories and generalizations and the limitations that arise when trying to apply these to particular species, environments and islands (e.g., Simberloff 1976; Case and Cody 1987). While we can make generalizations about island species and their parasites, the reality is that each situation is different, a product of the taxa involved, their colonization, subsequent history, and environment (Hutchinson 1965).

In addition, the study of islands faces the limitations of history (Steadman 1995). Biologists too often arrive after the event so they have to infer behavior or distribution from museum specimens or guess the disease involved, such as those that devastated Native Hawaiians (Schmitt 1970; Bushnell 1993). In the absence of pollen or fossil records, we are often unclear about whether species are indigenous or even endemic, being survivors of a wider distribution in an archipelago. Ideally, as exceptions and complications arise from additional research, they can be incorporated into newer models by intussusception (cf. Deevey 1972).

Enduring areas of controversy concerning island species and becoming sedentary include the extent of speciation in situ, dynamics of species diversity and community assembly, the role of history, the existence and importance of the “island rule” about size changes, and the extent and effects of immunological changes.

5.5.1 Conservation

Most of our theories ignore the role of humans; however, there are now few if any islands that have not been heavily affected by human habitat conversion and destruction and the deliberate or accidental introduction of plant and animal species and diseases (Crosby 2004). Unfortunately, we appear to be in a race to understand island species before they disappear. Island biology runs the risk of becoming solely a discipline of history and paleontology rather than a study of contemporary conditions. As a result, the field has a vested interest in the conservation of islands which may in turn inform conservation efforts.

Biosecurity, identification of species likely to be successful and disruptive invaders, prioritizing habitats and providing the science to manage, restore or protect habitats and species: all require basic science. For example, ex situ conservation needs science to identify which species may benefit from it, the minimum populations needed, and the conditions under which species can be successfully released. Gaining these insights may prove challenging and the results may be counter-intuitive. Captive rearing and reintroductions may lead to inbreeding or to the removal of parasites that stimulate immune systems in rare and vulnerable island species (Stringer and Linklater 2014). Ensuring the health of individuals in captive rearing programs may be counterproductive at the population level in the wild unless there is planned and continuing exposure to parasites (Spencer and Zuk 2016).

Ultimately, with the accidental and deliberate arrival of species, continued human population growth, and anthropogenic climate change, we will live in a panmictic world with less and less room for sedentary/endemic species and habitat diversity. This will be particularly true of oceanic islands. Loss of species may pass largely unnoticed because few people live on or visit islands. Will this loss matter to a growing human population dealing with challenges such as increased drought, rising seas, and the spread of disease? Yes, as islands may be especially useful in studying the ecology and dynamics of epidemics and the emergence of new diseases.

Those who work on islands may be like the monks and scholars who safeguarded Roman and Greek manuscripts at island monasteries following the collapse of the Roman empire (Cahill 1995). They preserved for preservation's sake with no expectation of a future that would later repay their efforts with the flowering of Western science (Lindberg 1992).

Similarly, island biologists and conservationists can only persist while being acutely aware of the ecological losses they can delay but not prevent.

One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise. Aldo Leopold (1949).

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