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Kevin C. Burns
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1 Introduction

Emblematic Island Animals

This chapter provides an introduction to some general concepts in biogeography and evolution that are needed in order to digest the rest of the book. However, unlike subsequent chapters, it will focus on animals rather than plants. Three island animals in particular, when considered together, illustrate a variety of evolutionary trends that appear to comprise an 'island syndrome'. The first emblematic island animal is a large flightless rail from New Zealand known as takahe (*Porphyrio hochstetteri*: Rallidae), which is perhaps the best living example of insular naivety and flightlessness. When compared with other flightless island birds, takahe also illustrate the subtle, yet important, differences between parallel, convergent, and repeated pathways of evolution. Giant tortoises (Testudines: Testudinidae) come next. They illustrate how gender and outcrossing might vary during the process of island colonisation, and how species interactions can shape the course of island evolution. Giant tortoises also illustrate the difference between anagenesis and cladogenesis, and, perhaps most importantly, they are a poignant reminder of how scientific progress hinges on an objective and rigorous research philosophy. Lastly, from our own evolutionary lineage, is the controversial 'hobbit' from Flores Island in Indonesia (*Homo floresiensis*: Hominidae), whose diminutive stature has been a source of intense scientific scrutiny and debate. When viewed jointly, these three emblematic island animals illustrate many of the trends in plant life history that are explored in subsequent chapters. They also hint at the possibility that plants and animals might travel down the same evolutionary pathways on isolated islands.

TAKAHE

Takahe are far from ordinary birds. They look like feathered circus clowns, with purple, pear-shaped bodies, big red bills, and floppy feet that keep them firmly on the ground (Fig. 1.1). Takahe are also strikingly ambivalent to onlookers – as wild animals, they show little regard for their own safety when surrounded by people. However,

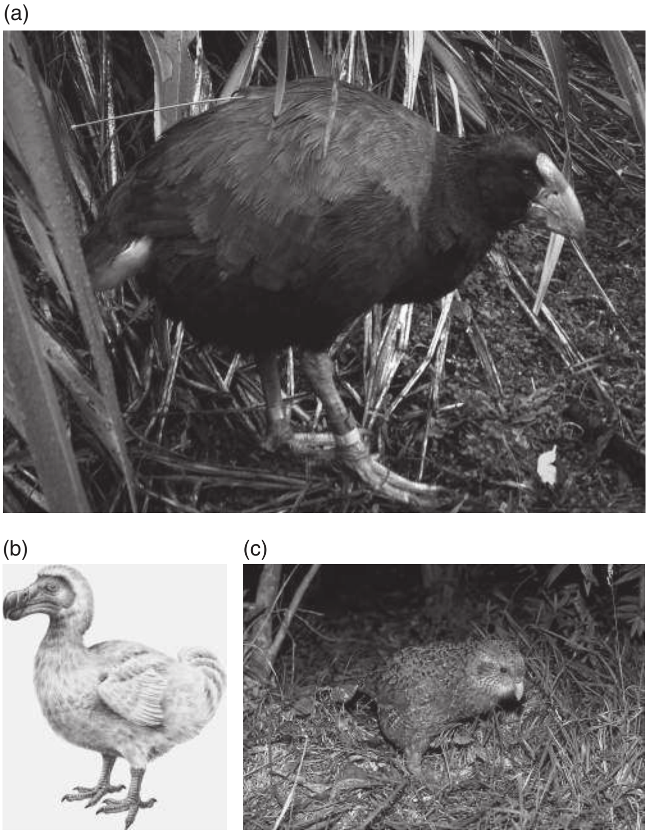

FIGURE 1.1 (a) Takahe (*Porphyrio hochstetteri*: Rallidae), (b) dodo (*Raphus cucullatus*: Columbidae; photo taken by Dorling Kindersley/Getty Images), and (c) kakapo (*Strigops habroptilus*: Strigopidae; photo taken by Robin Bush/Getty Images), which together provide a striking example of repeated evolution of predator naivety, flightlessness, and insular gigantism.

the takahe's position in the world of science is far from funny. Not only have they generated one of the 'greatest moments in ornithological history' (Fitzpatrick 2001), the evolutionary lineage to which they belong provides what is arguably the best example of repeated evolution in animals.

Differences in Defence

By the turn of the twentieth century, the takahe (*P. hochstetteri*) was thought to be extinct. In 1898, the 'last' bird was caught in a mountainous region of New Zealand's South Island by a hunter's dog. What was left of this unfortunate bird was then sold to a museum in Europe, as was common practice at the time (Balance 2001). Many New Zealand bird species were being driven rapidly to extinction at that time by changes brought by humans, and their rarity made them valuable to collectors.

Many other New Zealand bird species were in a similar predicament to the takahe. Since the arrival of people less than 800 years ago, approximately half of the archipelago's avifauna has gone extinct (Tennyson & Martinson 2006). Many factors have contributed to the demise of New Zealand's avifauna, but two factors stand out from the rest. Early accounts labelled many native birds, and the takahe in particular, as 'delicious' (Balance 2001). Many ended up on the dinner table. But perhaps even more damaging was the introduction of other mammalian predators. Rats, cats, and weasels (and many others) regularly accompany us on our travels to isolated islands and subsequently eat their way through the local checklist of island animals (Wilson 2004). A wave of extinction has coincided with the arrival of humans to virtually every archipelago on the planet, from Hawai'i to Mauritius, due in large part to the introduction of mainland predators (Steadman 2006; Duncan et al. 2013).

So why are island animals so susceptible to mainland predators? One factor seems obvious. Large stretches of open ocean present a formidable challenge to organisms colonising islands on their own, and only certain types of animals pass the test, dispersing to islands

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and becoming residents. While birds and reptiles are good at dispersing over the open ocean, mammals are not. With the exception of bats, terrestrial mammals are woefully equipped for traveling long distances over the open ocean, mainly because they cannot survive long periods without food, a prerequisite for long-distance dispersal on ocean currents. As a result, animals that are better at colonising islands walk an evolutionary pathway without the company of mammalian predators and they are wholly unprepared for the predatory onslaught when they arrive (Box 1.1).

In a way, the takahe was lucky. Half a century after the 'last' bird was sold to science, an amateur naturalist named Geoff Orbell began to comb the backcountry in New Zealand's Southern Alps in the hopes of finding one alive. In April 1948, his efforts paid off, much to the delight of bird lovers around the globe, some of whom labelled the discovery as the 'greatest moment' in the history of ornithology (Balance 2001; Grueber & Jamieson 2011).

Conservationists have learned a lot from the takahe's plight. The vulnerability of island biotas to mammalian predators is now widely recognised, and what's left of New Zealand's natural history is now painstakingly protected from mammalian predators. Intensively managed, mammal-free nature reserves are the only places that the takahe are now capable of calling home (Jamieson & Ryan 2001; Lee 2001).

Although the absence of adaptations to thwart mammalian predators characterises many island animals (Blumstein 2002), this does not mean that island animals are completely defenceless. Vertebrate predators do reach isolated islands, but they often have feathers instead of fur. Ironically, the biggest raptor known to science, Haast's eagle (*Harpagornis moorei*), evolved in New Zealand. Correspondingly, New Zealand birds often possess traits that help them avoid being eaten by bird predators rather than mammalian predators.

Birds hunt differently from mammals, relying more on sight than smell. Therefore, a good way to avoid avian predators is to evolve colouration that mirrors your surroundings, rather than concealing

BOX 1.1 Dispersal disharmony

Dispersal to isolated islands is governed primarily by chance. However, chance dispersal is more likely in some types of organisms than it is in others. The likelihood of dispersal to an isolated island is affected by two factors: over-water dispersibility and survivability during transit. Taxa with high dispersibility and/or high survivability are much more likely to populate isolated islands relative to taxa with low dispersibility and survivability, provided islands have suitable habitat for successful establishment (see Carvajal-Endara et al. 2017).

Dispersibility refers to an organism's rate of travel. Species that are capable of flight, most notably birds, have excellent dispersibility. Spiders which 'balloon' to new localities by spinning long dispersal threads that carry them passively on air currents also have high dispersibility. At the other end of the spectrum are reptiles and mammals, both of which cannot fly (aside from bats, which are functionally similar to birds in this regard). They have to either swim or float to islands – a much slower mode of transport.

Taxon-specific dispersibility can be described by a function $D(t)$, which characterises the distance travelled, D, through time, t (Fig. B1.1a). Assuming a constant rate of travel, $D(t)$ can be defined as a straight line with an intercept of zero and slope, ϕ, which varies among taxa according to their rate of travel, $D(t) = \phi t$. Birds have a higher value of ϕ than both non-volant mammals and reptiles, which are both

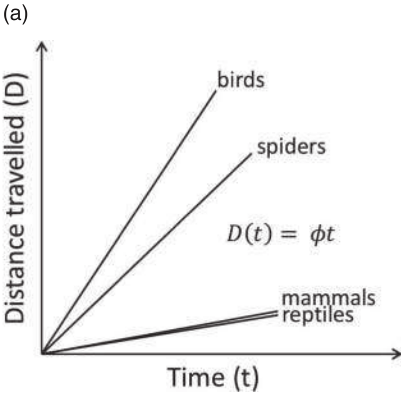

FIGURE B1.1A Relationships between the distance dispersing propagules travel per unit time in birds, spiders, mammals, and reptiles.

BOX I.I **(cont.)**

at the mercy of ocean currents and are therefore represented by *D(t)* curves with shallower slopes. Spiders have an intermediate value of ϕ, given that they can fly, albeit passively, so they are at the mercy of air currents.

Survivability refers to an organism's mortality rate during transect. It can be described by a second function. *S(t)*, which characterises the number of surviving propagules, *S*, per unit time, *t* (Fig. B1.1b). *S(t)* can be defined as a straight line with an intercept, *P*, which reflects the number of propagules present on the mainland that initiate the process of dispersal (i.e., *propagule pressure*), and a slope, α, which represents the mortality rate during dispersal, $S(t) = P - \alpha t$. Spiders should have a higher value of *P* than do reptiles, birds, and mammals, because they are present in higher densities across most continental landscapes. Reptiles should have relatively large (i.e., less negative) values of α, while birds and mammals should have relatively small (i.e., more negative) values of α because reptiles are ectothermic and can survive for longer periods without food or water relative to endothermic birds and mammals. Spiders might be expected to have intermediate values of α; although they are ectothermic, they have higher metabolic rates, shorter generation times and higher mortality rates, given they are smaller in size than reptiles.

Considering taxon-specific dispersibility and survivability jointly, the probability of chance dispersal is determined by three factors,

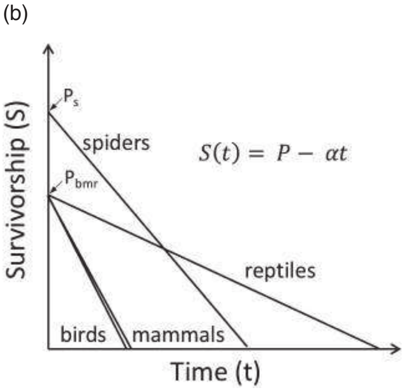

FIGURE B1.1B Relationships between the number of dispersing propagules surviving through time in birds, spiders, mammals, and reptiles.

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BOX 1.1 **(cont.)**

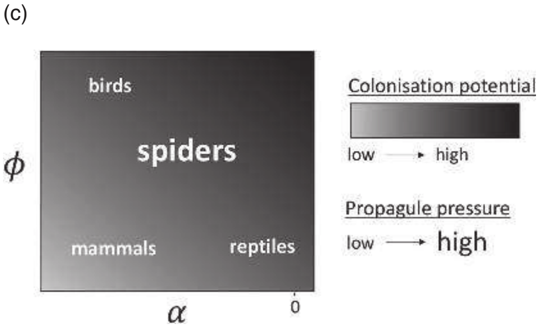

FIGURE B1.1C Differences in disperibility (ϕ) and survivability (α) in birds, spiders, mammals, and reptiles. Darker regions refer to greater colonisation potential and larger font size refers to higher propagule pressure (P).

ϕ, P, *and* α. It increases with ϕ and P, how fast a species can move across the landscape and how many individuals embark on the journey, respectively. It also increases with α, the taxon's probability of mortality during transit. These three parameters for birds, mammals, reptiles, and spiders can be potted together in a single figure representing the probability of chance island colonisation by each taxon (Fig. B1.1c).

olfactory cues. Although their bills are red and their flanks are purple, the top of the takahe's back is covered in feathers that are a greenish, mottled-brown colour, which may have rendered the takahe less conspicuous to predatory raptors trying to spot them against a background of greenish-brown vegetation from above. This is unusual in the evolutionary lineage to which the takahe belongs. Most of the takahe's continental cousins produce only blue and black feathers.

Mainland birds that evolved alongside mammalian predators often emit very little odour, giving predators that hunt by smell little to work with. On the other hand, freed from selection by predators

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that rely mostly on their sense of smell, many New Zealand birds ‘stink’ a bit, which has the unfortunate consequence of making them easier for introduced mammalian predators to detect (Azzani 2015).

As we shall see in Chapter 2, plants and takahe may not be so different when it comes to defending themselves against being eaten. Plant adaptations to thwart mammalian predators, such as thorns, are hard to find on many islands, perhaps echoing the takahe’s ambivalence to humans and other predatory mammals. On the other hand, island plants often display a suite of distinctive traits that are rare or absent on continents, which may have helped them avoid being eaten by unique island herbivores, most of which are now extinct. Given that many island herbivores are no longer with us, research into plant defences on isolated islands has a ‘whiff of mystery’ (Zotz et al. 2011) and has sparked decades of scientific debate and controversy.

Loss of Dispersibility

The takahe’s closest living relatives are found in open, marshy habitats throughout Australia, Southeast Asia, and parts of Europe and Africa. Unlike its comical island cousin, the purple swamphen or ‘pukeko’ (*Porphyrio porphyrio*) is always wary of onlookers and keeps its distance from would-be predators. The pukeko and takahe also differ morphologically. The pukeko’s bill is more modest than the takahe’s and is better suited to its omnivorous diet, which includes grasses, seeds, and small animals. The takahe’s bill is much larger and more heavily reinforced to suit a more specialised vegetarian diet (Mills & Mark 1977). In the summer, takahe forage above the tree line in alpine environments for their favourite food: the juicy tillers of tussock grasses. After pulling grass tillers out of the ground with their bill, they transfer them to their talons and gnaw on their nutrient-rich stalks, a bit like a parrot eating seeds from its feet. It takes quite a bit of effort to unearth the tillers of alpine tussocks (*Chionochloa* spp.). So a stoutly reinforced bill seems to have evolved to help it overcome its hard-to-break prey. A big, stout bill also helps the takahe forage efficiently in winter, when they travel downslope, below the treeline.

Here they dig up fern rhizomes, which they consume using the same, parrot-like technique.

Their feet are different too. The pukeko has long, spindly toes, which are ideal for walking along the top of soft, muddy surfaces in marshlands. The takahe's talons are short and stout, which better enable them to manoeuvre around tussocks and stunted shrubs on hard, rocky ground. Stout feet and legs are also required to support heavier bodies, and they are less susceptible to freezing temperatures.

Differences in bill and talon morphology between the takahe and pukeko are interpretable in light of differences in their preferred habitats, but these differences pale in comparison to differences in their body mass and wing length. The takahe are two to three times heavier than the pukeko, yet their wings are smaller. A bird's ability to fly is determined in large part by its 'wing-loading ratio', or the ratio of wing size to body mass (Van den Hout et al. 2010). So, as the size of a bird's body increases, the size of its wings must keep pace in order for it to fly. But, in the case of the takahe, disproportionate changes in body size and wing length have channelled it down an evolutionary trajectory where it can no longer take to the air.

At first glance, the presence of flightless animals on isolated islands seems strange. Flight is arguably the best way for organisms to disperse across inhospitable terrain. So how did the takahe come to call New Zealand home? Molecular analyses show that the takahe diverged from the pukeko long after New Zealand split from Australia geologically (Trewick 1997; Garcia-R & Trewick 2015). So, a common ancestor to both the pukeko and takahe probably flew to New Zealand from Australia and subsequently lost the ability to fly. But, given its obvious adaptive advantages, why would evolution then favour the loss of flight on islands, or anywhere else for that matter?

A likely explanation for insular flightlessness is that the selective advantages of functional wings are relaxed in island environments (Lahti et al. 2009). Ground-dwelling predators were often rare or absent on islands (Livezey 2003). So, once freed from selection by ground-dwelling predators, the surplus energy that was previously

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devoted to wing development can instead be 'invested' elsewhere morphologically (McNab & Ellis 2006).

Another possible explanation to the loss of flight in the takahe relates to the costs associated with being lost at sea. Islands are very windy places (Box 1.2). In the absence of terrestrial topography to slow wind speeds down, wind whips across the ocean surface at greater speeds than on continents. Consequently, flightedness could be directly disadvantageous on islands, given their close proximity to open ocean, if big wings make island animals more susceptible to being accidentally lost at sea (Darwin 1859; Cody & McC. Overton 1996). This hypothesis will be the focus of chapter 3, which reviews the evidence for the loss of dispersibility in plants.

Alternatively, insular flightlessness could also relate to the stability of island environments. Birds inhabiting continents often track changes in the landscape over large spatial scales (e.g., Burns 2002; 2004). For example, in fire-prone ecosystems, birds can fly over large distances not only to avoid the flames, but to also to recolonise sites as resource availability increases during post-fire succession (Loyn 1997; Watson et al. 2012). However, space is limited on islands and wildfires are less common. Therefore, increased dispersibility to avoid fire and track post-fire changes in resource availability are less advantageous on islands than on the mainland.

Sedentary organisms, and plants in particular, must cope with fire differently. Rather than avoiding fire, plants in fire-prone ecosystems display a variety of traits that help them either resist fire damage or be resilient to wildfires, given that they cannot flee from its harmful effects (Box 1.3). Whether plants repeatedly lose fire-adapted traits after colonising isolated islands will be explored in Chapter 6.

Parallel, Convergent, & Repeated Evolution

Subfossil bones of takahe-like birds have been found on both the North and South Islands of New Zealand. This led to initial speculation that, prior to the arrival of humans, a single species of takahe occurred throughout New Zealand. If so, it would suggest all takahe