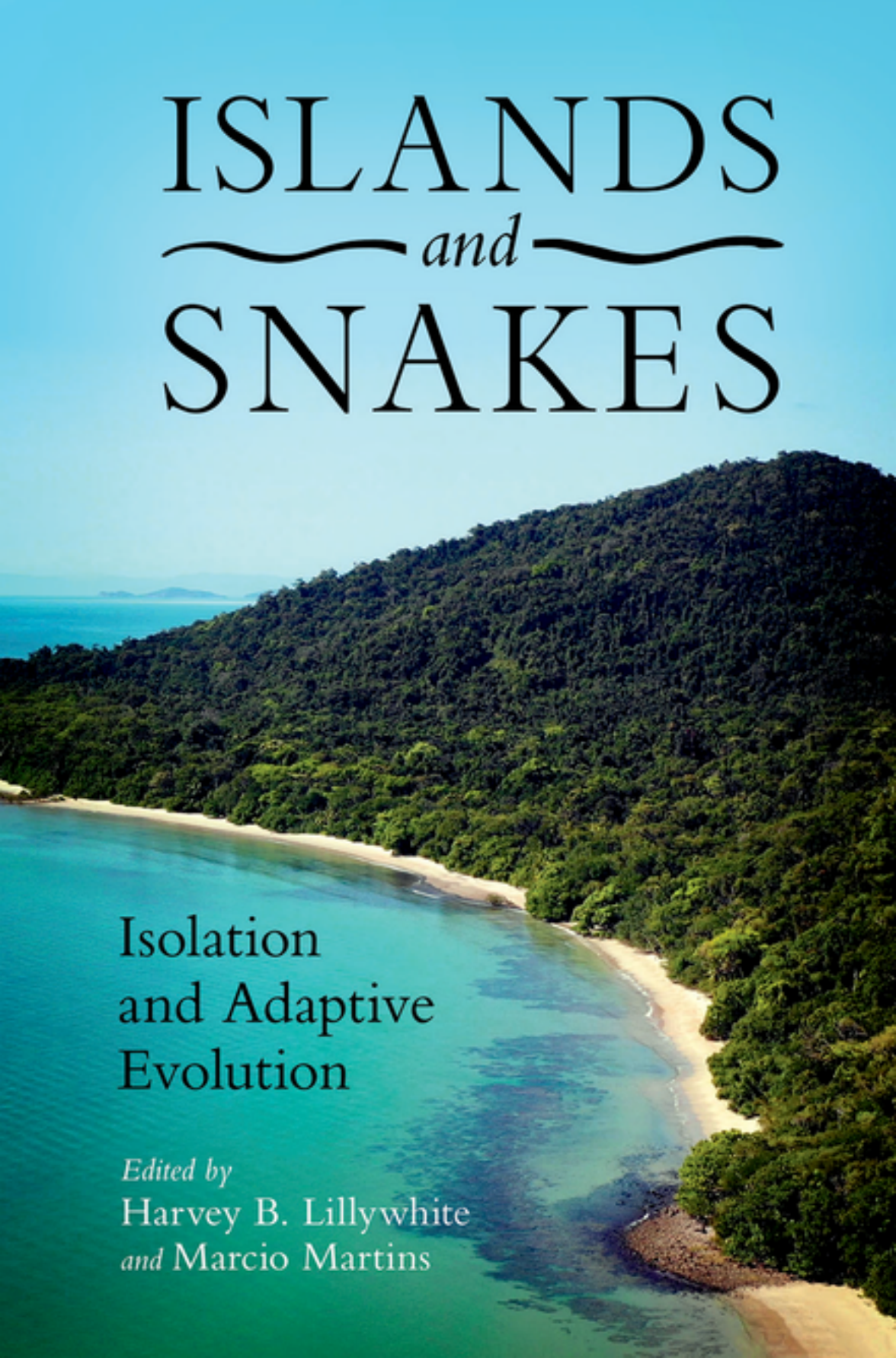


An aerial photograph of a tropical island coastline. The top half of the image shows a clear blue sky. Below the sky, a dense, dark green forest covers a steep hillside that slopes down to a narrow, crescent-shaped sandy beach. The water is a vibrant turquoise color, showing some darker patches of coral or rocks beneath the surface. In the far distance, other islands are visible on the horizon.

ISLANDS *and* SNAKES

Isolation
and Adaptive
Evolution

Edited by
Harvey B. Lillywhite
and Marcio Martins

ISLANDS AND SNAKES

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Isolation and Adaptive Evolution

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Marcio Martins

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I dedicate this book to my lovely wife Jamie, and I express my heartfelt appreciation for her love, encouragement and support for this work and throughout my career.

—Harvey B. Lillywhite

I dedicate this book to my lovely wife Eliana for having been a great source of inspiration and support throughout this work

—Marcio Martins

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FOREWORD

“Islands” and “snakes” are two words that evoke a powerful sense of discovery and adventure. Islands are realms of endemism and novelty, and their exploration has informed some of the most fundamental ideas in the history of biology. Snakes reflect the mystery and beauty in nature, and our hardwired fascination with them reminds us of our intimate connection with it. Editors Harvey Lillywhite and Marcio Martins reveal this world by drawing on their diverse collaborations and collective decades of scholarship and passion.

Nineteen accomplished snake biologists, alongside Lillywhite and Martins, have contributed chapters that together cover the ecology, behavior, evolution, and conservation of snakes on islands. Each chapter is illustrated with color photographs of spectacular snakes and their island habitats. These range from bird-eating tree boas in the Caribbean to amphibious sea kraits spanning Taiwan and New Caledonia and castaway Australian tiger snakes. The authors go far beyond the existing scientific literature by allowing the reader privileged insight into the passion and process behind their discoveries. The entertaining anecdotes shared in each chapter show that new questions and new knowledge are gained from lifelong curiosity and dedication, innovative thinking, and also some degree of risk-taking. Furthermore, by reflecting on their closest professional collaborations and enriching interactions with local communities, the authors reveal the human side of scholarship. Books such as this are vital for stimulating public enthusiasm for science and conservation.

Islands and Snakes: Isolation and Adaptive Evolution is timely. Island environments are under threat from development, rising sea levels, and an increasing incidence of invasive species. And biologists are racing against time to discover what species live on islands, the crucial roles they play there, and how they have adapted to island life. By relating ecological and evolutionary insights gained from field studies of snakes on islands, this book will no doubt inspire numerous new research and conservation initiatives. *Islands and Snakes: Isolation and Adaptive Evolution* is a must-have for students,

biologists, geographers, and anyone who values fragile island environments and their unique biodiversity.

Kate Sanders
Adelaide, Australia
August 2018

PREFACE

During the fall of 2013, we taught a seminar course together on island ecology at the University of Florida, and the genesis of ideas for this book was in large measure an outgrowth of this class. At the beginning, we had intended to write a review paper that covered both historical and contemporary aspects of the biology of snakes on islands. Then, we scrapped this idea and replaced it with a goal of producing an academic book that focused on aspects of island ecology and biogeography as viewed through the lens of the many studies in which snakes have been a biological focus of such investigation.

Islands have been appreciated as natural “laboratories” for investigations of ecology, biogeography, and evolutionary biology since the time of Wallace, who dedicated a large amount of his writings to islands, including his seminal work *Island Life*, and Darwin, who was profoundly affected by his observations in the Galapagos Islands. In the 1960s, MacArthur and Wilson produced an important and influential theoretic framework for subsequent investigations of biodiversity and dynamics of insular biogeography. Since MacArthur and Wilson’s pioneering efforts, a robust literature on insular ecology and biogeography has continued to grow, and understanding the successful existence and adaptations to conditions on islands has advanced. Various investigators have extended earlier theoretic studies to increase understanding of important phenomena such as adaptive radiation, energetics, paleogeography, plasticity of colonizing biota, trophic changes, morphological evolution, and climate change.

For reasons of practicality and personal interests, various specific elements of biota have been investigated as model organisms for clarifying insights regarding particular features of island ecology. Reptiles on various islands have replaced endotherms as primary herbivores and top carnivores. Because of ectothermy, reptiles have advantages over endotherms in exploiting scarce resources in circumstances that are challenging to the success of birds and mammals. Snakes are known to be very successful colonizers of islands, and

roughly 60% of literature on insular squamate reptiles deals with snakes. Indeed, studies of snakes have contributed much to our understanding of insular ecology, and these vertebrates are important subjects for investigating questions that might be difficult to approach in other systems. Details concerning the reasons why snakes have been successful in living on islands may be found in Chapter 1.

We have been fortunate to observe snake populations on many islands throughout the world, including key locations in South America, the Gulf of California, Taiwan, Australia, and the tropical Pacific. In many instances, snakes on islands occur in amazing numbers and are often a dominant aspect of the local fauna. To produce this book, we have recruited authors from among authorities throughout the world who have focused influential studies of snakes that occupy interesting and important systems on various islands or archipelagos. As a concluding chapter, we have included studies of the spectacular tepuis that comprise an exceptional example of “ecological islands” in South America. All of the various authors provide entertaining narratives of the system they studied, woven as a fabric with solid empirical information, scientific theory, and personal insights regarding ecological and evolutionary principles as revealed by spectacular snakes and their adaptations to living on islands.

Harvey B. Lillywhite
Marcio Martins

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We are grateful to the many persons who have made this book possible, especially our families, the various authors who have contributed thoughtful and stimulating chapters, numerous colleagues, reviewers, and others who have encouraged our adventures in science, including numerous visits to exciting islands. We also thank the editors and production staff at Oxford University Press for their professional guidance and assistance throughout this project. We hope that readers will find the enjoyment and satisfaction of reading this book that we have intended for them to discover.

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1 ECOLOGY OF SNAKES ON ISLANDS

Marcio Martins and Harvey B. Lillywhite

Introduction

Islands have been the subject of intense investigation—biologically and ecologically—since the time of Darwin and Wallace. Much research has focused on species assemblages and the dynamics of species richness on islands as well as other systems having geographic isolation and other characteristics similar to those of islands surrounded by water. An important theoretic model for insular biogeography was produced by MacArthur and Wilson (1963, 1967), and their work created a useful framework for subsequent investigations of biodiversity and its dynamics on islands (see reviews in Whittaker and Fernández-Palacios 2007; Warren *et al.* 2015; Santos *et al.* 2016; Patiño *et al.* 2017). Previously, insular faunas were regarded generally as either static or changing slowly and unpredictably due to environmental and climatic changes (Dexter 1978; Heaney 2000). However, the influence of more modern biogeographic theory enabled sometimes robust predictions of species richness in relation to the area of an island and its distance from a source of colonizing biota (MacArthur and Wilson 1967). Whether or not the biota of a given island or insular system is at “equilibrium” often remains debatable (Lomolino 2000; Warren *et al.* 2015).

Since the 1960s, a robust literature on insular biology and ecology has continued to grow, with numerous investigators focusing on a variety of insular systems with attention to increasing detail concerning the requirements and dynamics of ecological factors that favor adaptation and successful existence on islands. Numerous questions are being addressed that cannot be explained by the existing theoretic models of insular biogeography (Gillespie

and Roderick 2002). Examples include (but are not limited to) questions regarding adaptive radiation (Losos 1998; Gavrillets and Losos 2009), paleogeography (Iturralde-Vinent and MacPhee 1999), energetics and energy resources (McNab 1994a, 1994b; Polis and Hurd 1996; Bonnet *et al.* 2002), climatic change (Bellard *et al.* 2013a, 2013b; Wetzel *et al.* 2013), life history characteristics of insular biota (Foufopoulos and Ives 1999), and anthropogenic influence (Steadman *et al.* 2005).

For many practical reasons (often with advantages), various investigators of the ecology of islands focus on taxonomic elements of fauna or flora with which they have familiarity or interest or that represent “model” systems due to a prior database of information or suites of characteristics appropriate to particular questions. Such approaches have intrinsic value and also provide important data for more inclusive investigations of biodiversity (Myers *et al.* 2000). Reptiles have been the frequent subject of investigations of vertebrate faunas on islands, where they are often “replacements” of endotherms as primary herbivores and top carnivores. The favorable circumstances for ectotherms *versus* endotherms on islands include low rates of energy expenditure relative to resources that are often scarce or limited on islands, dispersal abilities, and superior colonizing abilities. Rates of energy expenditure in terms of field metabolic rates of endothermic mammals and birds are approximately 12 and 20 times higher, respectively, than those of equivalent size, ectothermic reptiles (Nagy 2005). Reptiles, therefore, have a crucial advantage in exploiting scarce resources and building populations in circumstances that preclude, or severely challenge, the success of birds and mammals.

Snakes are very successful inhabitants of islands, and there is a very rich literature concerning the insular ecology of this group of vertebrates (Figure 1.1). An accounting of scientific articles using Google Scholar indicates that roughly 60% of the literature on islands and squamate reptiles (including Tuatara) deals with snakes. Thus, studies of snakes have contributed much to our understanding of insular ecology and are important subjects for attention to questions that might be difficult to investigate in other systems (discussed later). We emphasize that there are numerous reasons why snakes are important elements of insular biotas and play critical roles on numerous islands that can offer further insights for understanding ecology of islands. Some of the more important attributes of snakes related to successful “island living” are (1) ectothermy and comparatively low energy requirements; (2) attributes favoring abilities for overwater dispersal; (3) life history features favoring comparatively rapid population growth; (4) range of body sizes favorable for inhabiting even very small islands; (5) breadth and plasticity of diet, including



FIGURE 1.1 Examples of snakes having high significance with respect to insular ecology and biogeography. (a) Blue-banded Sea Krait (*Laticauda laticaudata*) from Orchid Island, Taiwan. Sea kraits are amphibious and spend variable amounts of time secluded on numerous small islands of the Indo-Pacific oceans (see Chapter 2). (b) Southeast Asian Bockadam (*Cerberus schneideri*) is an amphibious snake associated with estuarine habitats in Southeast Asia, including many areas of the Philippines. (c) Brown Tree Snake (*Boiga irregularis*) is widespread in the Oriental and Oceanian regions, occurring naturally on more than 50 islands and accidentally introduced to Guam and other islands. See implications for conservation in Rodda and Savidge (2007). (d) The Oriental Blind Snake (*Indotyphlops braminus*) is native to almost 60 different islands and was accidentally introduced in dozens of other islands throughout the world (Wallach 2009). This specimen was found on Boca Chica Key, Florida. (e) The Solomon Island Ground Boa (*Candoia paulsoni*) is perhaps the most widespread snake on islands, occurring in more than 60 islands in the Oriental region. (f) Feick's Dwarf Boa (*Tropidophis feicki*) is representative of dwarf boas that occur throughout numerous islands of the Caribbean. This species occurs in Cuba, where the genus and family (Tropidophiidae) reach their highest diversity. There are 32 species of the genus *Tropidophis*, found in areas of South America and the West Indies, where this genus has more successfully speciated.

Sources: Photographs by Ming-Chung Tu (a), Mark O'Shea (b and e), Coleman Sheehy III (c), Jonathan Mays (d), and Javier Torres Lopez (f), all reproduced with permission.

scavenging; (6) effective means of prey acquisition; (7) infrequent feeding on relatively large prey and “slow” digestive physiology; (8) secretive behaviors and cryptic morphologies; (9) special scansorial capabilities in many species; and (10) thermal plasticity.

In this chapter, we review much of the key literature relating to islands inhabited by snakes and the insular ecology of snakes. Using a database on the occurrence of snakes on islands, we also provide broad patterns of snake diversity. Our goals are to illustrate how studies of snakes on islands can inform general principles related to biology of islands or fragmented habitat, evaluate what are considered to be novel features related to the ecology of snakes on islands that can serve to enhance understanding of complex situations, and stimulate future research as a result of forward-looking perspectives that emerge from the robust literature on snakes and islands.

Geography and Features of Islands Inhabited by Snakes

The main island types regarding their origin are oceanic islands (originated over oceanic plates), continental fragments (portions of continental rock originated by plate tectonic processes), and continental—or land-bridge— islands (located on continental shelves; Whittaker and Fernández-Palacios 2007). For practical reasons, here we combine continental fragments (*e.g.*, Madagascar and New Caledonia) and oceanic islands (*e.g.*, Hawaii and Canaries) into a single category, herein called oceanic islands (Pyron and Burbrink 2014; Figure 1.2). This review is concerned exclusively with islands in the sea—that is, we do not deal with lake, river, and estuary islands, including those separated from mainland by a narrow (<150 m wide) channel or similar feature. For instance, we consider Singapore as a sea island because it is separated from the remaining of the Malayan peninsula by the Strait of Johor, which is 615 m wide at its narrowest point. On the other hand, we do not consider the Cardoso Island, on the coast of southeastern Brazil, as a sea island because despite its name, the channel that separates it from mainland is only 88 m wide at its narrowest point. Finally, we do not deal with sea snakes because they generally are not confined to the islands where they occur. Additional details concerning how our database of insular snakes was built are provided in the Appendix.

The origin of snake populations in different island types differs, mainly because of variation in the origins of islands. Thus, understanding how these island types originated is crucial for understanding the diversity and biogeography of insular snakes. Land-bridge islands are originated by the variation in

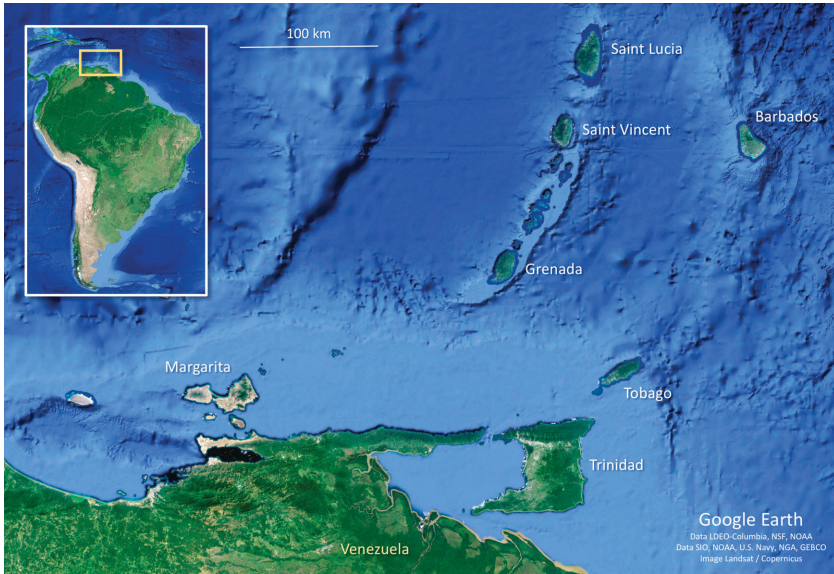


FIGURE 1.2 A satellite image of northern Venezuela and southern Lesser Antilles showing land-bridge (Margarita, Trinidad, and Tobago) and oceanic islands (Grenada, Saint Vincent, Saint Lucia, and Barbados). Note that land-bridge islands are located on the shallow (<100 m deep) continental shelf of coastal Venezuela, whereas oceanic islands are separated from the South American continent by deep sea (*e.g.*, the deep strait [>700 m] that separates Grenada from the Venezuelan continental shelf).

sea level during glaciation cycles. Most of them have been connected, disconnected, and reconnected to the mainland many times during the glaciations of the past 1.8 million years (Whittaker and Fernández-Palacios 2007). For example, many islands in continental shelves throughout the world were connected to their respective continents during the last glacial maximum approximately 29,000 to 21,000 YBP, when sea level reached approximately 130 m below the present level (Lambeck *et al.* 2014). Extensive portions of continental shelves were exposed by then. When sea level rose to the present level, mountains amid these coastal lowlands became the land-bridge islands that we see today.

Continental fragments are originated by plate tectonics processes in which a portion of a continent moves away from the main portion, becoming an island (Whittaker and Fernández-Palacios 2007). Madagascar, for instance, was part of the Gondwana supercontinent and became separated from Africa in the Late Jurassic–Early Cretaceous and from India during the Late Cretaceous (Ali and Atchison 2008). On the other hand, oceanic islands are originated mainly by volcanism in the areas of contact of tectonic plates,

and they were never in contact with continents, although they may be close to them in some instances. A detailed review of the origin of different island types is provided by Whittaker and Fernández-Palacios (2007).

Snakes are found on land-bridge and oceanic islands throughout the planet—on all five continents; in all oceans; and from 42 degrees south in Tasmania, Australia, to 63 degrees north at Hitra Island, Norway. Among land-bridge islands, snakes occur on islands varying in size from 1,000 m² (small Japanese islands in the South China Sea) to approximately 786,000 km² (New Guinea Island) and varying in elevation from less than 1 m above sea level (ASL) on Huevos Island (Trinidad and Tobago) to almost 5,000 m ASL on New Guinea Island. Among oceanic islands, those inhabited by snakes vary in area from less than 1 km² (*e.g.*, many islands in the Bahamas) to more than 580,000 km² (Madagascar) and vary in elevation from less than 5 m ASL on some small islands in the Cuban Archipelago to 3,700 m ASL on Lombok Island, Lesser Sunda Islands.

Most islands inhabited by snakes are located in the Eastern Hemisphere, where most tropical and subtropical islands are concentrated (Figure 1.3). This region harbors most groups of islands on which island snakes occur, including the Japanese and Malay archipelagoes as well as the Philippines. In the Western Hemisphere, most islands inhabited by snakes are located in the Caribbean and the Bahamas. The absolute middle latitude of islands explains just a small amount (10% or less) of the variation of snake richness on both land-bridge and oceanic islands ($r^2 = 0.104$, $p < 0.001$ and $r^2 = 0.058$, $p < 0.001$, respectively; both variables log transformed), with islands from lower latitudes tending to harbor more species. However, using their database with islands larger than 250 km², Pyron and Burbrink (2014) found a stronger effect ($r^2 = 0.25$) of middle latitude on insular richness of snakes. Finally, the vegetation cover of islands inhabited by snakes includes most of the terrestrial vegetation types found on continents, from the dry Sonoran Desert on islands in the Sea of Cortez, Gulf of California, to the luxuriant rainforests of lowland Borneo.

Patterns of Diversity and Endemism

Relatively few efforts have been made to describe global patterns of insular snake diversity and to understand the processes responsible for these patterns. The few recent exceptions include Pitta *et al.* (2013), who explored the compositional dissimilarity of reptiles and amphibians in oceanic and land-bridge islands, and Pyron and Burbrink (2014), who explored factors that could

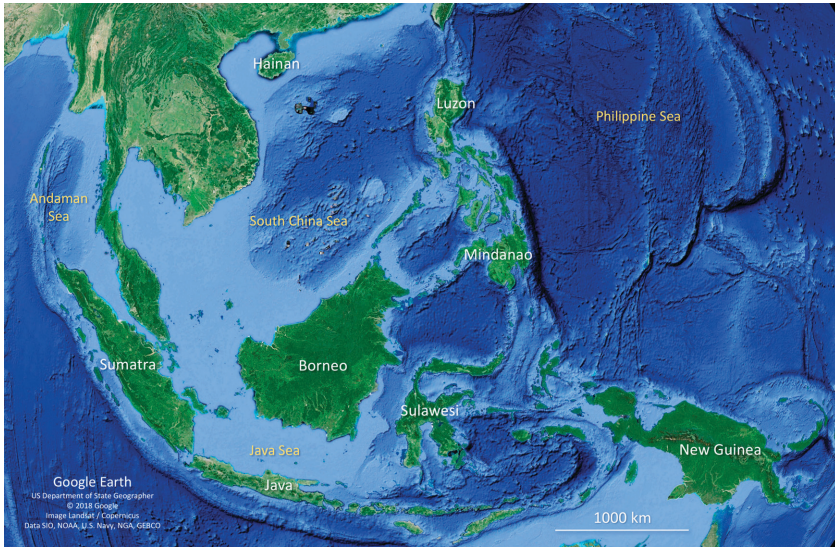


FIGURE 1.3 Satellite image showing a large portion of the Oriental zoogeographical region, where many of the largest and richest land-bridge islands are located, including Borneo (with 141 species of snakes), Sumatra (133 species), Java (96 species), and New Guinea (93 species). Large and rich oceanic islands are also found in this region, such as Sulawesi (with 63 species of snakes) and Luzon (51 species). Also in this region are some of the islands bearing a high number of endemic snake species, such as Sri Lanka (with 46 endemics, not shown), Borneo (31 endemics), New Guinea (26 endemics), Sumatra (19 endemics), and Sulawesi (16 endemics).

explain patterns of species richness and phylogenetic composition of snakes in oceanic islands. In this section, we provide a detailed description of the global patterns of diversity and phylogenetic composition of island snakes using a database of island snakes we built for this purpose, and we compare general patterns with those found by both Pitta *et al.* and Pyron and Burbrink.

Our database contains 1,223 snake species occurring on 987 islands—368 land-bridge islands on which 718 snake species occur and 618 oceanic islands on which 761 snake species occur. Snake richness on land-bridge islands varies from 1 to 141. Although 32.6% of the land-bridge islands have only a single species and 95.4% have 20 species or less, snake richness is very high in the five largest (61,411–743,330 km²) land-bridge islands, all of them located in the Oriental and Oceanian zoogeographical regions (Holt *et al.* 2013; see Figure 1.3): Borneo (141 species), Sumatra (133), Java (96), New Guinea (93), and Sri Lanka (89). Among oceanic islands, snake richness varies from 1 to 89 species. Similar to land-bridge islands, 31.7% of oceanic islands have only a single species of snake and 97.1% have 20 species or

less. On the other hand, only 3 oceanic islands (with areas from 104,688 to 587,041 km²) harbor more than 50 species of snakes: Madagascar (89 species), Sulawesi (63), and Luzon (51).

The mean number of snakes per island on land-bridge islands is higher than that on oceanic islands (respectively, 6.1 ± 14.2 snakes/island; range, 1–141; $N = 368$; and 4.7 ± 7.6 snakes/island; range, 1–89; $N = 618$). Island area explains slightly more than one-third of the variation in snake richness for both island types ($r^2 = 0.367$, $p < 0.001$ for land-bridge islands; $r^2 = 0.375$, $p < 0.001$ for oceanic islands; both variables log transformed). Fattorinni (2010) failed to find an effect of island size on lizard and snake richness on Italian land-bridge islands. On the other hand, using Bayesian models, Pyron and Burbrink (2014) found a significant effect of island size (as well as temperature, isolation, and elevation) on snake richness on oceanic islands.

The diversity of habitats on an island also may be a good predictor of species richness, probably because more niches are available on more heterogeneous islands (MacArthur and Wilson 1967; Ricklefs and Lovette 1999; Whittaker and Fernández-Palacios 2007). In general, larger islands typically show higher habitat heterogeneity compared to small islands (MacArthur and Wilson 1967; Whittaker and Fernández-Palacios 2007). Because habitat diversity tends to be strongly correlated with island maximum elevation (Ricklefs and Lovette 1999; Henderson 2004; Kalmar and Currie 2007), we used the maximum elevation of islands as a proxy of habitat heterogeneity (*cf.* Pyron and Burbrink 2014) to explore the effect of habitat diversity on snake richness using our database of island snakes. The maximum elevation of islands (both types) explains one-third of the variation in snake richness ($r^2 = 0.326$, $p < 0.001$), indicating that habitat heterogeneity explains at least part of the variation of snake richness on islands. When island types are considered separately, maximum elevation explains more variation of snake richness on land-bridge islands than on oceanic islands ($r^2 = 0.403$, $p < 0.001$ and $r^2 = 0.292$, $p < 0.001$, respectively). Henderson (2004) also provides evidence for an effect of habitat diversity on snake richness on the Lesser Antillean islands.

Compared to similar-sized regions of the mainland, islands tend to show higher levels of endemism (Kier *et al.* 2009). Approximately one-tenth (95) of the 987 islands in our database have at least one endemic snake (*i.e.*, a species that occurs on that island and nowhere else). Endemics are found on both land-bridge and oceanic islands, and the proportion of islands harboring endemics is higher on oceanic (11.6%) than on land-bridge islands (6.2%).

However, the mean number of endemic snakes on land-bridge islands (6.9 ± 12.0 ; range, 1–46; $N = 23$) is double that on oceanic islands (3.5 ± 9.1 ; range, 1–72; $N = 72$). Among land-bridge islands, the number of endemics is especially high in Sri Lanka (46 endemics), Borneo (31), New Guinea (26), and Sumatra (19). Among oceanic islands, the number of endemics is especially high in Madagascar (71 endemics), Cuba (28), Hispaniola (17), and Sulawesi (16). When endemism is considered in relation to island size, land-bridge islands have on average a much higher number of endemics per island area (0.68 ± 1.54 endemics/km²; range, <0.01 to 6.67 endemics/km²; $N = 23$) compared to oceanic islands (0.26 ± 1.36 endemics/km²; range, <0.01 to 11.11 endemics/km²; $N = 72$). Highest endemism per area of island is found on very small land-bridge islands (Franceses and Queimada Grande Islands off the coast of eastern Brazil, with 0.2 and 0.4 km², respectively) and oceanic islands (Great Bird Island in the Lesser Antilles and Round Island in the Mascarenes, with 2.15 and 0.09 km², respectively).

Among the 1,223 insular snakes in our database, 718 occur on land-bridge islands, 776 on oceanic islands, and 249 on both land-bridge and oceanic islands. Insular snakes occur on 1–48 land-bridge islands (3.1 ± 5.1 islands, $N = 718$) and on 1–59 oceanic islands (3.9 ± 6.4 islands, $N = 761$). Most snakes from land-bridge islands occur on few islands: Slightly more than half (55.7%) occur on a single island, 13.6% occur on two islands, and 87.3% occur on five or less islands. Similar proportions are found in snakes from oceanic islands: Approximately half (50.0%) occur on a single island, 15.0% occur on two islands, and 83.2% occur on five or less islands. At the other extreme, 50 species (4.1%) occur on more than 20 islands (both island types), of which there are 29 colubrids, 5 boids, 5 typhlopids, 4 viperids, 2 lamprophiids, 2 pythonids, and 1 species of each of the families Acrochordidae, Elapidae, and Homalopsidae. Most of these species are from the Oriental and/or Oceanian zoogeographical regions. Only 7 species occur on 50 or more islands (both types): *Telescopus fallax* (Colubridae, 50 islands), *Boiga irregularis* (Colubridae, 54 islands), *Malayopython reticulatus* (Pythonidae, 55 islands), *Natrix natrix* (Colubridae, 55 islands), *Indotyphlops braminus* (Typhlopidae, 57 islands), *Cerberus rynchops* (Homalopsidae, 60 islands), and *Candoia paulsoni* (Boidae, 61 islands) (see Figure 1.1).

The composition of insular faunas is highly variable and strongly dependent on the ability to disperse overseas (Whittaker and Fernández-Palacios 2007). For groups with high dispersal ability, faunal composition tends to be similar in nearby islands, whereas groups with lower ability to disperse overseas tend to show a higher dissimilarity of composition among islands. Pitta *et al.*

(2013) explored the patterns of compositional dissimilarity between islands with respect to dispersal ability of amphibians and reptiles, taking into account that lizards tend to show a higher dispersal ability compared to snakes and frogs. Indeed, lizards showed lower levels of compositional dissimilarity compared to snakes and frogs, but only on land-bridge islands. Furthermore, as expected, Pitta *et al.* also found that compositional dissimilarity between islands increases with distance between islands—that is, nearby islands tend to show a similar composition of snake faunas.

Based on our database, one-third (32.8%) of the insular snakes are endemics. The proportion of endemic species is higher among species that occur on oceanic islands (243 out of 761, or 31.9%) than those that occur on land-bridge islands (156 in 718, or 21.7%). Among the 156 endemic species that occur on land-bridge islands, almost half (46.1%) are colubrids, and four additional families comprise 10 or more endemics: Elapidae (10 endemics), Typhlopidae (14), Uropeltidae (15), and Viperidae (18). Among the 243 endemic species that occur on oceanic islands, 79.8% are concentrated in three families: Colubridae (76 species), Lamprophiidae (66), and Typhlopidae (52).

Regarding phylogenetic composition, snake faunas on islands are in most cases a random sample of faunas from mainland areas. However, there are some notable deviations from this general trend. Boids, ophiotrichine colubrids, calamariine colubrids, pythonids, and tropidophiids are more represented on islands than on mainland, whereas dipsadine colubrids and leptotyphlopids are less represented on islands than on mainland. Using ecological modeling and working only with oceanic islands larger than 250 km², Pyron and Burbrink (2014) suggested that the phylogenetic composition of island faunas is more dependent on colonization from regional mainland species pools than from *in situ* diversification, even for large islands. As a result, insular snake faunas are, in general, not phylogenetically distinct from mainland faunas. When the different general types of islands are compared using our database, a few differences are evident. The frequency of boids, lamprophiids, leptotyphlopids, tropidophiids, and typhlopids is higher on oceanic than on land-bridge islands. Remarkable differences are found in lamprophiids, which are approximately eight times more frequent on oceanic than on land-bridge islands, and tropidophiids, which occur (24 species) only on oceanic islands. On the other hand, elapids, gerrhopilids, pareids, uropeltids, and xenodermids are more frequent on land-bridge than on oceanic islands.

Biogeography: Origins of Island Populations, Immigration, Dispersal Abilities, Extinction, and Diversification

Inspired by analyses showing that species richness tends to be positively related to the area of the habitat—perhaps the oldest recognized ecological pattern—and that richness tends to decrease with increasing distance of an island to the mainland, MacArthur and Wilson (1963, 1967) consolidated the theory of island biogeography (see review in Warren *et al.* 2015). These authors proposed that island diversity is the result of a balance between immigration and extinction, assuming that immigration rate decreases and extinction increases as the richness of the island increases. Thus, species richness on islands would tend to an equilibrium (the equilibrium theory of insular zoogeography of MacArthur and Wilson [1963]). Since these milestone contributions by MacArthur and Wilson, the theory of island biogeography has contributed significantly to improve the understanding of community ecology taking evolution into account (see reviews in Warren *et al.* 2015; Santos *et al.* 2016; Patiño *et al.* 2017). In addition to its crucial contribution to the understanding of the consequences of habitat fragmentation (*i.e.*, the dynamics of man-made islands of habitat; reviewed in Laurance 2010), the theory of island biogeography was crucial also for understanding the processes involved in community assembly (Diamond 1975). In this section, we review several aspects of insular snakes that can increase our understanding of their biogeography, from the origin of insular snake faunas to the capacity of snakes to reach remote islands.

The processes involved in the assembly of snake faunas on islands tend to differ between land-bridge and oceanic islands (Gillespie and Baldwin 2010; Meiri 2017). The origin of snake populations on land-bridge islands is almost always a result of the isolation of a portion of a population that was previously widespread on coastal lowlands that were exposed during glaciations (Figure 1.4; (see the section titled Geography and Features of Islands Inhabited by Snakes and also Chapters 6 and 9 of this volume). Indeed, populations of a few to several species become trapped on these islands with sea level rise, but on most small islands very few of them persist. Thus, the history of snake communities on land-bridge islands is characterized by a series of extinctions after these populations become isolated (Fattorini 2010). Biogeographers refer to *faunal relaxation* as the transition from a state similar to that found on the mainland, with populations of different species co-occurring, to a

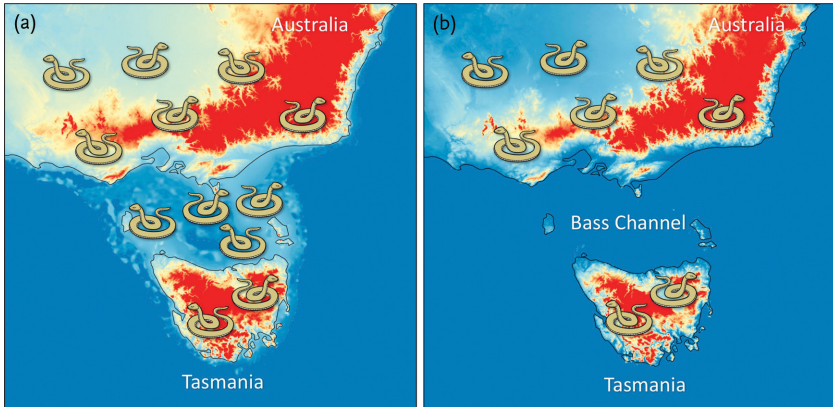


FIGURE 1.4 Relief maps of southern Australia and Tasmania depicting a putative scenario of how the snake fauna of land-bridge islands are originated. Map a shows the sea level in the peak of the last glaciation (approximately 19,000 years ago)—that is, approximately 120 m below the present sea level (Lewis *et al.* 2013). In this map, all areas with a blue tone lighter than that of the surrounding ocean were above sea level. Thus, the seafloor of the Bass Channel that today separates Tasmania from Australia (map b) was exposed and snake populations occurred in this exposed area. Map b shows the present situation, with Tasmania completely isolated by seawater from mainland Australia. Some of the snakes that were trapped in Tasmania gave origin to its present snake fauna.

state of equilibrium in which only a portion of the original fauna remains. Indeed, land-bridge systems are called extinction-driven systems, in contrast to colonization-driven systems on oceanic islands (Patterson and Atmar 1986). Reasons for these serial extinctions may include disappearance or extreme changes in ecological niches (*e.g.*, prey become too rare or absent; Marques *et al.* 2002), very small population size (that might easily go extinct through stochasticity; Melbourne and Hastings 2008), and genetic reasons (*e.g.* inbreeding and genetic drift; Frankham 2005).

Land-bridge islands of eastern Brazil are an example of the trend described previously (Figure 1.5). Islands inhabited by snakes in this region vary in size from tiny (0.2 km² on Franceses and Porcos islands) to enormous portions of Atlantic forest (347 and 676 km² on São Sebastião and Santa Catarina islands, respectively), with the smallest ones harboring a single species and the large ones harboring 21 species each. The snake communities found on these islands are a sample of the communities found on the mainland (Cicchi *et al.* 2007), although some populations are considered to have differentiated enough to be considered valid species (Marques *et al.* 2002; Barbo *et al.* 2016; see the section titled Conservation and also Chapter 5, this volume). Furthermore, island size explains more than half of the variation in snake



FIGURE 1.5 Satellite image of eastern Brazil showing the location of 17 land-bridge islands in which at least one species of snake occurs. The number of snake species in these islands is strongly affected by island size—that is, the larger the island, the larger the number of snake species found on it. This group of islands includes the tiny Queimada Grande Island (0.43 km²), where the Golden Lancehead occurs (see Chapter 5).

richness on the islands of eastern Brazil ($r^2 = 0.590$, $p = 0.001$, $N = 15$)—that is, the larger the island, the larger the fraction of the mainland communities that have persisted on these islands.

Variation of sea level during the Pleistocene probably underlay the origin of most snake populations of land-bridge islands that are currently located on continental shelves (Marques *et al.* 2002; Fattorini 2010). However, overseas dispersal is also a possibility, especially for islands that are very close to the coast. For example, Seahorse Key, located 2.9 km off the western coast of Florida, is a low barrier island close to the mouth of the Suwannee River. A dense population of the Florida Cottonmouth (*Agkistrodon conanti*) is found on this small island (0.67 km²) of sand dune origin, and sightings of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) on the island occur occasionally (Lillywhite and McCleary 2008). Both the resident population and the occasional rattlesnakes are suggested to have arrived on the island by overseas dispersal, perhaps during low tides or cyclonic storms (Wharton 1969; Lillywhite and McCleary 2008; see Chapter 9, this volume).

The origin of snake populations on oceanic islands, on the other hand, is primarily the result of ancient separation of land masses (the so-called continental fragments, such as Madagascar; see Figures 1.6a and 1.6b), colonization (mostly by overwater dispersal on floating islands; see Figures 1.6c and 1.6d), and *in situ* diversification (Hedges 1996, 2006; Nagy *et al.* 2003; Noonan and Chippindale 2006; Noonan and Sites 2010; Stelbrink *et al.* 2012; Reynolds *et al.* 2013). In some cases, ancient separation of land masses and overwater dispersal hypotheses have been suggested for different snake lineages occurring on the same island or archipelago (see reviews for the Caribbean islands in

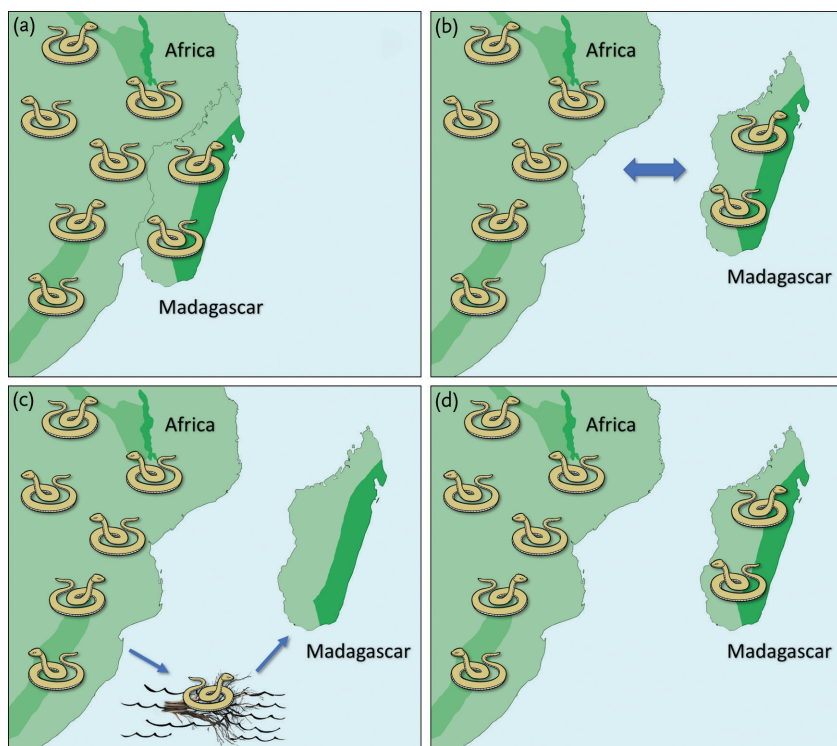


FIGURE 1.6 Maps of Madagascar and adjacent Africa depicting putative scenarios of how the snake fauna of oceanic islands are originated. Map a shows the land mass that today is called Madagascar while it was still connected with Africa (this is an oversimplification because Madagascar and Africa were part of the big Gondwanan continent, together with South America, Antarctica, and the Indian subcontinent, among other land masses). With the separation of Madagascar from Africa (map b), snakes that occurred in that region gave origin to the present snake fauna of Madagascar. In maps c and d, another possible origin is illustrated: Individuals of snake populations from Africa reached Madagascar by overseas dispersal (rafting). Indeed, the present snake fauna of Madagascar seems to have originated through both these processes.

Hedges [2006] and for Sulawesi in Stelbrink *et al.* [2012]). Exploring the evolutionary history of Malagasy Boas, Noonan and Chippindale provided strong evidence for a Gondwanan origin for these snakes—that is, the ancestor of Malagasy boas was a Gondwanan species that is believed to have been split by continental drift. On the other hand, using molecular data to elucidate phylogenetic relationships among colubrid snakes of Madagascar and the Socotra archipelago, Nagy *et al.* inferred that overwater dispersal was the most likely hypothesis for the origin of the Malagasy colubrid snake fauna. Similarly, Hedges (1996, 2006) reviewed the biogeography of amphibians and reptiles of the West Indies and suggested an origin through overwater dispersal for most West Indian snake lineages based on several lines of evidence, including phylogenetic relationships, fossils, and estimates of divergence time (see Chapter 7, this volume). Additional suggestions of island colonization by snakes through overwater dispersal are found in Boos (1984), Corke (1987), Karns *et al.* (2000), and Ota *et al.* (1993).

Mostly because of a lifestyle combining ectothermy and the consumption of bulky prey (see the introduction to this chapter), snakes tend to show a high capacity to survive fasting, with some species being capable of surviving 1–2 years of starvation (Wang *et al.* 2006; McCue *et al.* 2012). This ability makes snakes remarkably capable of long-distance, passive dispersal over water (Noonan and Sites 2010) and likely confers a capacity for colonization. As discussed previously, there are many suggestions in the literature that snakes are able to reach islands by overwater dispersal on floating islands (also called rafting). However, although this hypothesis is strongly supported by several lines of evidence, there are just a few examples of snakes actually being found on floating islands (King 1962; Schoener and Schoener 1984; Thiel and Gutow 2005). Guilding (1828) reported on a *Boa constrictor* that drifted to St. Vincent Island in the Caribbean, suggesting that it rafted for at least 400 km (the distance from the island to the mouth of the Orinoco River) on the trunk of a cedar tree. Clench (1925) reported on an observation made by a hotel owner in Sanibel Island, Florida, of a rattlesnake (probably *Crotalus adamanteus*) that was on one of several water hyacinth rafts that reached the island during the spring floods of the Caloosahatchee River in 1921. Based on the distribution of hyacinths in the low Caloosahatchee River, Clench concluded that the snake must have been on the raft for at least 43 km. Finally, Muir (1937) reported on a blind snake (Typhlopidae) found on drift material on the coast of South Africa. Indeed, the most widespread terrestrial snake, the Oriental Blind Snake *Indotylops braminus*, combines high dispersal ability with unisexual reproduction (Ota *et al.* 1991), which makes

it a very successful colonizer on islands (Wallach 2009). Not surprisingly, it is the most invasive species among snakes, having been introduced in many areas of the New World, including numerous islands (Wallach 2009).

Because a long overwater dispersal is successful only if it takes less time than the capacity of survival of the dispersing organism, an important question commonly raised when considering the possibility of overwater dispersal is the time needed for a floating island to travel long distances (Houle 1998). Houle, a primatologist aiming to understand the way primates spread throughout the world, estimated the number of days required for a floating island to cross Paleogene (66–23 Mya) water barriers: the Atlantic Ocean, the Caribbean Sea, and the Southeast Indian Ocean between Sundaland and the northern Australian Plate. Houle proposed that paleowinds, and not paleocurrents, were the main force affecting the velocity of floating islands. Surprisingly short periods of time were estimated: Depending on the point in time of his calculations, the Atlantic oceanic barrier (sailing paleodistance of 1,072–2,037 km) could have been crossed in only 7.7–14.0 days, the Caribbean Sea from South to North America (sailing paleodistance of 1,072–1,276 km) in 15.1–18.2 days, and the Southeast Indian Ocean from Australia to Sundaland (sailing paleodistance of 1,072–2,251 km) in 12.2–25.6 days. Therefore, assuming these estimates are accurate, the capacity of fasting by snakes would be much greater than that needed for long journeys of overwater dispersal.

Furthermore, no matter how snakes reach oceanic islands, an interesting question is whether a given island can be colonized multiple times by individuals of the same species; very few studies have been able to detect multiple colonization events. Perhaps the best way to assess this question is by building a phylogeographical hypothesis—that is, a molecular phylogeny of populations of a species or of closely related species. However, in the case of species that occur on islands, most studies use only a few samples from islands (Janzen *et al.* 2002; Rato *et al.* 2009). An elegant example of multiple colonization is provided by Kuriyama *et al.* (2011), who built a phylogeographical hypothesis for *Elaphe quadrivirgata*, which occurs throughout Japan, including Honshu Island (or Japan “mainland”) and different oceanic islands of the Izu Archipelago. The dated phylogeny indicates that the archipelago was colonized multiple times by *E. quadrivirgata* and by individuals from different populations of Honshu Island during the past 600,000 YBP. Moreover, one of the islands (Oshima, located approximately 23 km from coastal Honshu) was colonized at least three times during the past 150,000 YBP. This pioneer study indicates that the history of snake populations inhabiting islands may be much more complex than previously thought (see Chapter 2, this volume).

Because land-bridge islands in general have been isolated from the mainland relatively recently, *in situ* diversification (*i.e.*, speciation) is rare on these islands, except for the very large islands such as New Guinea, Sri Lanka, Borneo, and Sumatra (Figure 1.7; Allison 1996; Inger and Voris 2001; Pyron *et al.* 2013). However, population differentiation has occurred on many land-bridge islands (see Chapter 9, this volume), and this led some scientists to consider insular populations as separate species based on their morphology, despite the fact that they are genetically very similar to their mainland sister species or population (*e.g.*, *Bothrops alcatraz*, see Marques *et al.* [2002] and Suzuki and Furtado [2008]; *Crotalus tortugensis*, see Van Denburgh and Slevin [1921] and Castoe *et al.* [2007]; see discussion on this topic in the section titled Conservation). Although most oceanic islands are sufficiently old for *in situ* diversification of snakes, Pyron and Burbrink (2014) found evidence of this process in only 15 (7%) of the 217 oceanic islands included in their study, all of them in the Tropics. Of these, only Madagascar, Puerto Rico, Jamaica, Hispaniola, and Cuba have most of their snake fauna originated by *in situ* speciation. On the other hand, other large islands such as Borneo and New Guinea have only a small proportion of their snake fauna originated by *in situ* speciation (see also Allison 1996; Inger and Voris 2001). Furthermore, using ecological modeling, Pyron and Burbrink suggest that most of the variation

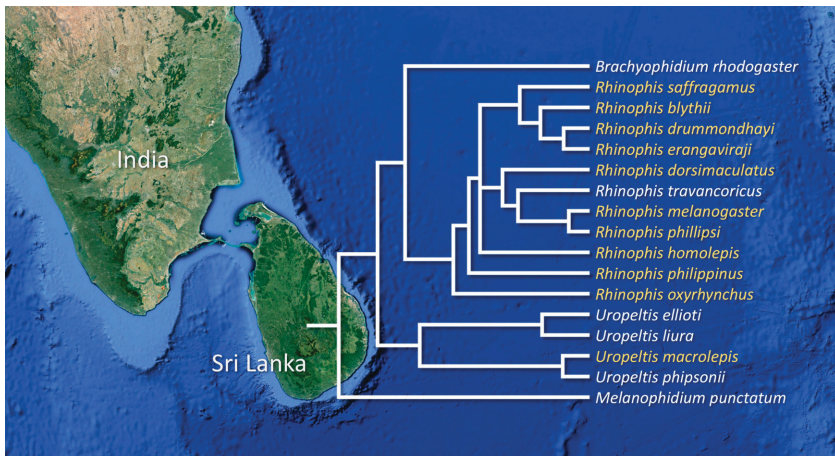


FIGURE 1.7 Satellite image of Sri Lanka (and southern India) as an example of *in situ* diversification of snakes on islands. The phylogeny of uropeltid snakes shown in the figure (from Tonini *et al.* 2016), in which Sri Lankan species are shown in orange, indicates that many species of this family originated through *in situ* diversification in Sri Lanka (see Pyron *et al.* 2013).

in snake species richness in oceanic islands is explained by colonization and that *in situ* diversification tends to be rare.

Although extinctions are much more difficult to detect than speciation (Rabosky 2010), fossils of snakes are found in some islands throughout the world. For instance, Bailon *et al.* (2010) described Early Pliocene (approximately 4,000–5,000 MYBP) fossil remains of a species of the genus *Vipera* from Mallorca, Spain. Pregill (1982) reported on fossils dated from the Wisconsin glaciation (approximately 85,000–11,000 YBP) of four different snakes (a typhlopoid, *Tropidophis canus*, *Chilabothrus strigilatus*, and *Cubophis vudii*) from New Providence Island, in the Bahamas; at least three of them still occur on the island. Hope *et al.* (1977) reported on Late Pleistocene (>16,000–10,000 YBP) elapid vertebrae (probably from *Notechis* or *Austrelaps*) from Kangaroo Island in Australia, and Worthy *et al.* (1999) reported on Holocenic vertebrae of the boid *Candoia bibroni* from the Fijian Viti Levu Island.

Energetics and the Evolution of Body Size on Islands

Animals undergo evolutionary changes in structure, function, and behavior in response to features of insular environments. A well-known behavioral change is that animals on islands often exhibit a reduction in escape or defensive behavior when they are subject to lower predation than on the mainland (“insular tameness”; Darwin 1839; Blumstein and Daniel 2005). Examples of studied insular tameness include that occurring in reptiles, but we know of no examples of it occurring in snakes (with the possible exception that is discussed in Chapter 9, this volume). One of the more noticeable and well-studied changes involving morphology is a change in body size, and many insular organisms become dwarfs or giants in comparison with their relatives living in mainland environments (see Chapter 6, this volume). Such size variation among mammals appears to be general, and Van Valen (1973) termed it the “island rule.” Previously, Foster (1964) described a set of tendencies among taxonomic categories of mammals, which formed part of the basis for this “rule.” He concluded that insular rodents tended toward gigantism, whereas insular artiodactyls, carnivores, and lagomorphs tended to decrease in size. Marsupials and insectivores showed no consistent trends. The essence of the island rule is that relative to mainland counterparts, species that are large tend to evolve smaller body size on islands, whereas species that are small tend to evolve larger body size on islands. Later analysis of body size for 71 species of non-volant mammals was consistent with the expected pattern

(Lomolino 1985). A spectacular example of such a shift in size of an insular mammal is the extinct dwarf elephant of the Mediterranean, which was no larger than a pony (Stock 1935). Data for 13 insular populations of insular woodrats (*Neotoma*) exhibit a significant tendency for insular forms to be larger than mainland forms (Smith 1992). There are many striking examples of insular “giants” among reptiles, including the giant tortoises of Galápagos and islands of the Indian Ocean, and the varanid lizards on several Indonesian islands. Among plants, many herbaceous mainland species have evolved to be perennial and tree-like on islands (Carlquist 1974).

The evolution of changes in body size on islands generally has been attributed to factors related to competition, predation, dispersal and colonization abilities, and availability of resources (Foster 1964; Case 1978; Lomolino 1985, 2005; Smith 1992; Meiri 2007; Pitta *et al.* 2013). The observed changes in body size are regarded as adaptive shifts, and the previously mentioned factors can be interpreted as components of mechanisms that drive the evolution of life history traits (Palkovacs 2003). The tendency for body size to vary with characteristics of islands is dependent on the nature of populations of particular species, and the observed variation in body size has been shown to be a distinct and scale-dependent phenomenon (Lomolino 2005). Some vertebrate taxa do not follow the island rule (*e.g.*, lizards; Meiri 2007).

There is a reasonably rich literature on changes of body size in insular species of snakes, which appear generally to follow the island rule. A relatively recent analysis of evolutionary changes in body size of insular snakes has been reported by Boback (2003), who determined that physiographic variables of area, latitude, age, and distance of islands from mainland were not important as causal agents among 30 species of snakes. The data also suggested that neither competition nor ability to colonize islands accounted for subsequent evolutionary changes in body size. On the other hand, changes in body size among insular snakes relative to mainland conspecifics were bimodal and consistent with a “diet alteration hypothesis” related to insular prey that are larger or smaller than what is encountered on the mainland (Figure 1.8). The body size of insular snakes appears to be influenced largely by encounters with prey that is either larger or smaller than the available prey on the mainland. In some cases, this could be happenstance, but the likely direction of change might also have some dependency on the size of the mainland species from which the colonizing population originates. Hence, analysis of largest body lengths from a distribution based on 618 species of snakes showed that mainland species smaller than 1 m became larger on islands, whereas species larger than 1 m became smaller on islands (Boback and Guyer 2003). It seems that

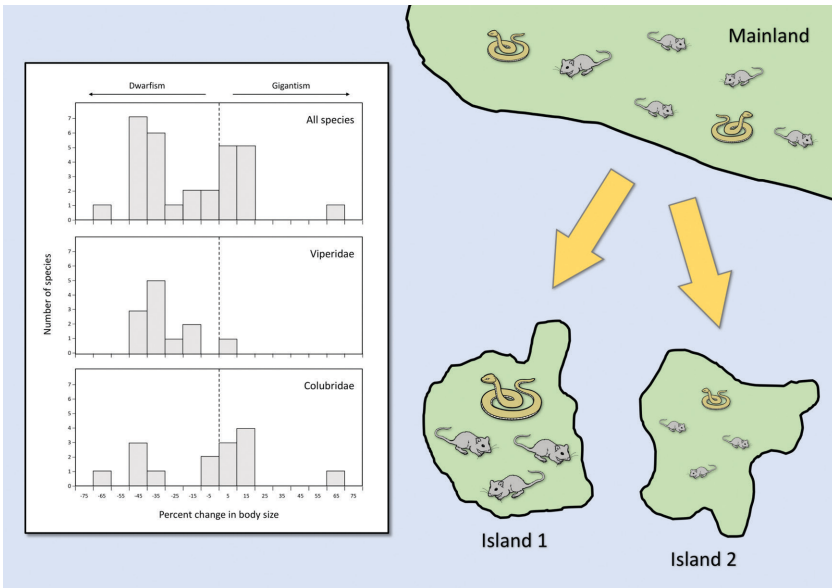


FIGURE 1.8 Schematic drawing of two islands in which snake populations were originated through the isolation of populations of a mainland species. In this figure, the rodent depicted is the main prey of the snake in both mainland and islands. When isolated on islands, snakes tend to change their size according to the size of the prey available on the island (for a review, see Boback 2003). On island 1, where the prey available is larger than the common prey of the mainland species, the snakes became larger. A change in the opposite direction occurred on island 2, where the prey available is smaller than the common prey of the mainland species. The inset shows a modification of data for changes in body size of 30 species of insular snakes (data from Boback 2003).

the driving influence and mechanism that changes body size in insular species of snakes involves the insular prey resources available, whereas the direction of change has some dependency on a “weighting factor” related to the body size of the source population.

Another factor that might account, in part, for trends to gigantism is the interaction between growth and resources. Most species of snakes grow asymptotically (“indeterminate growth”) during the course of their life, provided that food is available (Shine and Charnov 1992). As a result, insular populations of a snake species might tend toward an upward shift in the average adult body size simply as a result of abundant resources and extended longevity attributable to reduced predation if either or both of these factors characterize the island in question. Thus, both age and nutritional status might act alone or in concert with other selection forces to influence the size of insular snake populations. This is probably a key factor in the anecdotal