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Alfred Russel Wallace and the destruction of island life: the *Iguana* tragedy

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Abstract The Galápagos Islands (Ecuador) are usually associated with the explorations and theoretical deductions of Charles Robert Darwin (1809–1882), but Alfred Russel Wallace (1823–1913) also investigated these islands and published several reports on the living world of this unique archipelago. In contrast to Darwin, Wallace described the destruction of natural ecosystems by humans and foresaw the resulting extinction of species. Here, we outline two case studies pertinent to Wallace's prediction. First, we summarize the behavior of the predator-naive marine iguanas (*Amblyrhynchus cristatus*) on the Galápagos Islands, which are threatened by feral dogs and cats imported by humans. We also describe the unique life cycle of the spiny-tailed iguana (*Ctenosaura bakeri*) from the island of Utila (Honduras), a rare species whose populations are declining because of habitat destructions. In contrast to these threatened, endemic island species, the Green iguana (*Iguana iguana*) is still widely distributed, although, as a result of de-forestation, in some areas of South America local populations have disappeared. We conclude that Wallace was correct in his prediction that, because of human activities, numerous species of animals and plants will be driven to extinction, notably on islands.

Keywords Evolution · Extinction · Darwin · Iguanas · Island life · Wallace

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Introduction

The British naturalist Alfred Russel Wallace (1823–1913) was a proficient writer, and the author/editor of 22 books on scientific and social issues (Shermer 2002; Smith and Beccaloni 2008). After the publication of his bestseller *The Malay Archipelago* (1869), Wallace wrote several additional monographs on similar topics, which were related to each other. Accordingly, Wallace considered his 1880 book *Island Life* as a "popular supplement to and completion" of his earlier 2-volume-treatise entitled *The Geographical Distribution of Animals* (Wallace 1880, p. VII). The 57-year-old author dedicated his "Island book" to "Sir Joseph Dalton Hooker, who, more than any other writer, has advanced our knowledge of the geographical distribution of plants, and especially to insular faunas", and mentioned in his preface that "Sir Joseph D. Hooker has given me the invaluable benefit of his remarks on my two chapters dealing with the New Zealand flora" (Wallace 1880, p. VIII).

The British botanist Joseph D. Hooker (1817–1911) (Fig. 1) was a close friend of Charles Robert Darwin (1809–1882), and director of the Royal Botanical Garden at Kew. Hooker is regarded as the founder of geographical botany (Morton 1981), and was one of the most influential plant biologists of his time, with a focus on the systematics and distribution of angiosperms. Like Wallace, Hooker visited little explored tropical regions, where he collected plants, with a special interest in island life and biogeography.

Naturalists have long known that islands, i.e., unique, isolated habitats with strong restrictions for the movements of organisms, are dynamic places (Darwin 1839, 1859). After severe storms, beaches erode away, and volcanoes may erupt; it is obvious that these physical or geological processes have drastic effects on the animals and plants

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Fig. 1 Joseph Dalton Hooker (1817–1911) wrote about islands and their role in plant geography. The botanist is depicted during one of his excursions into the Himalaya region (adapted from a drawing of 1854)

that inhabit these ever changing terrestrial ecosystems (Whittaker 1998; Franks 2010).

In this article, we discuss the biology and conservation status (2013) of some lizards (iguanas) on islands, with reference to the corresponding work of Wallace (1855, 1869, 1876, 1880, 1898, 1910, 1913). We will focus on the marine reptiles of the Galápagos Islands that Darwin (1839) mentioned, and on the spiny-tailed iguanas from the island of Utila, Honduras. Our account is to a large extent based on direct observations of these vertebrates in their natural island habitats.

Wallace and the Galápagos archipelago

As a teenager, Alfred Wallace had read the *Journal of Researches* of Darwin (1839), wherein the older naturalist described his excursions and discoveries on the Galápagos Islands in 1835 (Kutschera 2009a, b; Mayr 1984, 2001; Haffer 2007) (Fig. 2). Accordingly, in his Sarawak-paper, Wallace (1855) referred to this group of islands in the following words: "… the Galápagos Islands … contain little groups of plants and animals peculiar to themselves, but most nearly allied to those of South America …. The Galápagos are a volcanic group of high antiquity, and have probably never been more closely connected with the continent than they are at present. They must have been first peopled, like other newly formed islands, by the action of wind and currents, and at a period sufficiently remote to

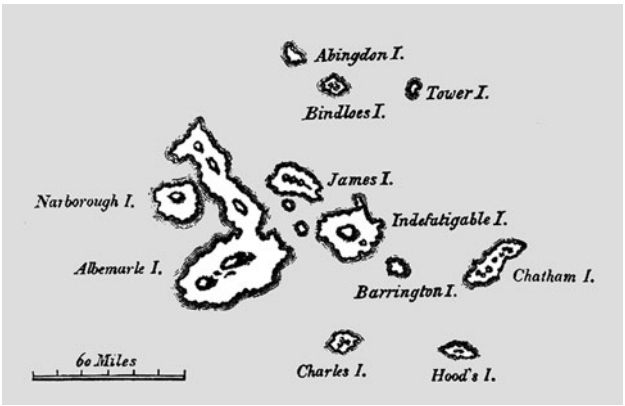

Fig. 2 The 13 main islands of the Galápagos archipelago, with their historic names and a scale bar (adapted from Darwin 1839)

have had the original species to die out, and the modified prototypes only remain" (Wallace 1855, p. 188).

Twenty-five years later, Wallace (1880) described the flora and fauna of the Galápagos archipelago in more detail. He noted that humans have introduced carnivores, such as dogs and cats, to the islands: "The Galapagos have also, during three centuries, been frequently visited by Europeans, … who found an ample supply of food in the large tortoises which abound there, and to these visits we may perhaps trace the introduction of some animals whose presence is otherwise difficult to account for. The vegetation is generally scanty, but still amply sufficient for the support of a considerable amount of animal life, as shown by the cattle, horses, asses, goats, pigs, dogs, and cats, which now run wild in some of the islands" (Wallace 1880, pp. 267–268). The author also pointed out that mammals are not part of the natural fauna of the Galápagos archipelago: "The islands are completely destitute of truly indigenous mammalia, and frogs and toads, are equally unknown" (Wallace 1880, p. 268).

Today, the imported mammals that Wallace (1880) mentioned are no longer present on all of the islands of the archipelago (Nicholls 2013). However, carnivores, such as cats and dogs, which are the descendants of those individuals that were introduced centuries ago, are still abundant on some islands. These mammals are opportunistic predators and prey on a variety of vertebrates, including reptiles, birds and small mammals (Nogales et al. 2004). Therefore, these carnivorous mammals pose a serious threat to the marine iguanas that Darwin (1839) described as "ugly reptiles." This topic is discussed in the next section.

The predator-naive Galápagos marine iguanas

The Galápagos marine iguanas that Darwin (1839) briefly mentioned represent one biospecies (*Amblyrhynchus*

cristatus) that can be separated into numerous sub-species or color variants (Alberts et al. 2004). Today, these large, polymorphic, endemic lizards inhabit all 13 larger islands in the Pacific archipelago. About 10 million years ago, when the South American ancestral marine iguana population arrived on the young Galápagos Islands, the landmasses consisted of bare volcanic rocks, with no or very few land plants (Levin 2003; Gradstein et al. 2004; Wikelski 2005). As a result, only those individuals were able to survive and reproduce that foraged in the intertidal marine areas, where food supply (algae etc.) was sufficient to support large, interbreeding populations of lizards. Since the endemic marine iguanas evolved in isolation from the mainland, they were not exposed, over millions of years, to predators, such as large terrestrial mammals. Accordingly, *A. cristatus* belongs to those endemic island species that show a weak escape response towards aggressive predators, compared with relatives that inhabit the mainland (Berger et al. 2007).

Since populations of *A. cristatus* evolved without the risk of being attacked by predators, it is obvious that domestic dogs and cats introduced by humans over the past centuries (Wallace 1880) exert a strong selection pressure on these island endemics (Endler 1986; Bell 1997; Hendry 2005; Kutschera 2008, 2009a, b, 2011). Today, the Galápagos Islands are inhabited by ca. 30,000 humans, and many tourists are admitted to visit the Charles Darwin Research Station every year (Fig. 3a).

Kruuk and Snell (1981) were among the first to analyze the behavior of feral dogs (*Canis familiaris*) during attacks on predator-naive marine iguanas on the Galápagos island Isabela (Ecuador). Their study revealed that anti-predator behavior of *A. cristatus*-individuals was without detectable beneficial effect for the attacked reptiles. The authors concluded that the marine iguana populations are seriously threatened by dog predation, since a mortality rate of up to 27 % was found in some populations of these endemic iguanas (Kruuk and Snell 1981; Laurie 1983). It was recently reported that on San Cristobal, near the town Puerto Baquerizo Moreno, feral dogs were responsible for the almost complete extinction of a local population of Galápagos iguanas (Rödl et al. 2007).

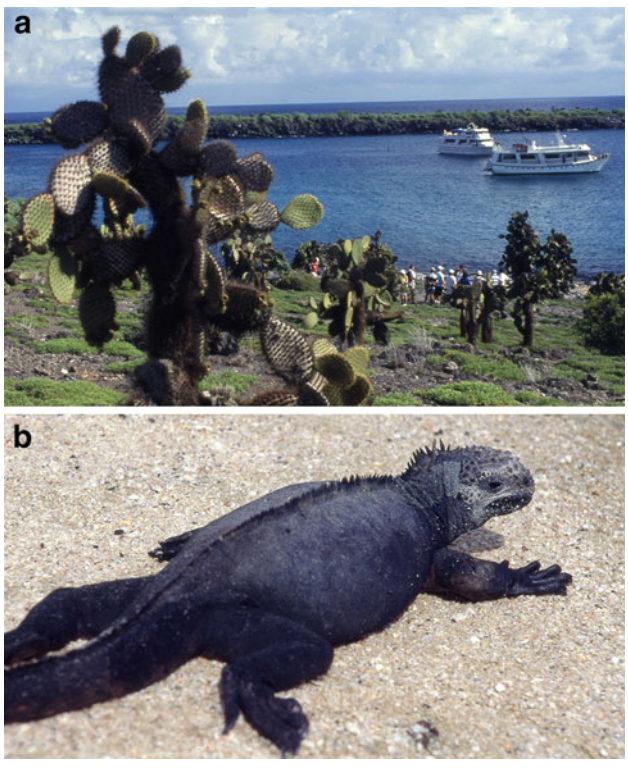

Fig. 3 The Galápagos island Espanola (Ecuador). Groups of humans (tourists) visit this place in high numbers, where Giant *Opuntia* sp.-plants dominate some areas (**a**). Adult individual of a marine iguana (*Amblyrhynchus cristatus*) (**b**). These large lizards (body length ca. 90 cm) forage in the sea, where they feed on marine algae (original photographs, 1996)

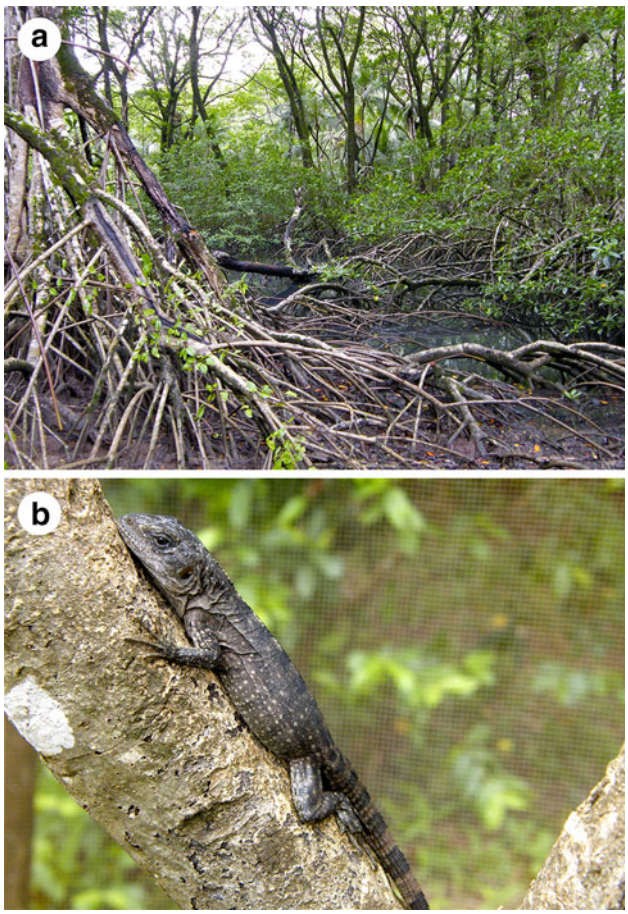

Fig. 4 Brackish mangrove forest in the eastern part of the island of Utila (Honduras) (**a**). The trunks of the trees in these dense forests are the habitat of the endemic Utila iguana (*Ctenosaura bakeri*) (**b**). These large lizards (body length ca. 30 cm) feed on plant material, and sometimes also eat small animals (original photographs, 2009)

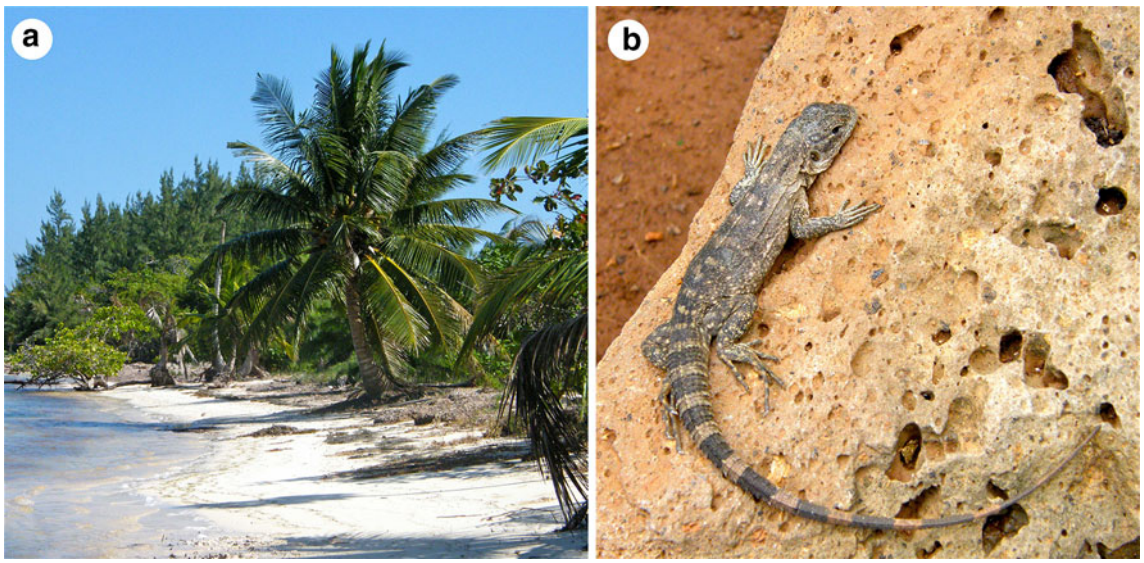

Fig. 5 Sandy beach in the northern part of the island of Utila, where female iguanas (*C. bakeri*) lay their eggs and bury their clutches (**a**). Thereafter, the females abandon their nest and return back to the mangrove forest. A representative juvenile (body length ca. 15 cm) sitting on a stone is shown in the second photograph (**b**). After a first terrestrial year, the juveniles return to the upper regions of the forests where their mothers came from (original photographs, 2009)

The physiological basis of the low wariness of the "predator-naive" marine iguanas (Fig. 3b) was studied in detail by Rödl et al. (2007). The authors have shown that, in response to experimental chasing of "naive" *A. cristatus*-individuals, a corticosterone stress response is not induced, but with experience, such a "natural" reaction is rapidly restored. Low wariness was also found to be increased with experience. However, this "anti-predator response" is not particularly strong and does not allow a rapid escape from introduced carnivores, such as feral dogs (Rödl et al. 2007). Since flight initiation distances of the reptiles are likewise insufficient to cope with new predators (Berger et al. 2007), these endemic iguanas, which are regularly affected by food shortages caused by recurrent global climate events (El Niño), may become extinct on some islands of the archipelago (Rödl et al. 2007; Berger et al. 2007; Romero and Wikelski 2010). However, dogs and cats have not yet reached all of the islands—there is a chance that *A. cristatus* can survive in some of these more remote island habitats (Wikelski and Nelson 2004).

Fig. 6 Adult specimen of the more widely distributed species *Ctenosaura similis*, which is currently not threatened. These black spiny-tailed iguanas are aggressive predators (body length ca. 110 cm), which feed on smaller vertebrates. *C. similis* are largely terrestrial lizards that may have pushed the smaller *C. bakeri* into its specific arboreal habitat (original photograph, 2009)

The Utila spiny-tailed iguana and its relatives

Another critically endangered endemic island species is the herbivorous Utila iguana (*Ctenosaura bakeri* Stejneger 1901), a lizard that is also known under the common names "swamper" or "Baker's spinytail iguana" (Alberts et al. 2004; Köhler 1995; Köhler et al. 2000). On the island of Utila, one of the Islas de la Bahia (Honduras), these large arboreal members of the order Squamata inhabit brackish mangrove swamps (Fig. 4a), where they spend their entire life (Fig. 4b). Gravid females (which occasionally feed on small animals) briefly leave the mangrove trees to deposit their eggs in sandy beaches (Fig. 5a). However, the hatched, terrestrial juveniles (Fig. 5b) soon return to the forests to live like the adults in the mangroves (Fig. 4a) (Köhler 1995; Gutsche and Köhler 2008; Gutsche and Streich 2009).

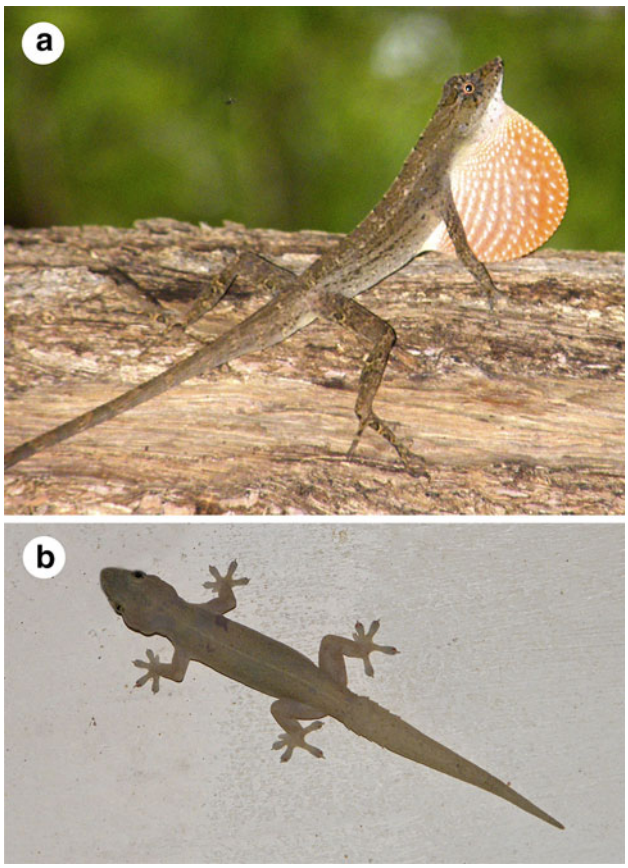

Fig. 7 Smaller reptiles, such as the Utila anole (*Norops bicaorum*) (**a**) and the Asian gecko (*Hemidactylus frenatus*) (**b**) are prey organisms of the much larger iguana species of the genus *Ctenosaura* (original photographs, 2009)

Circumstantial evidence suggests that the species *C. bakeri* (Figs. 4b, 5b) was forced to inhabit the mangrove forests as a result of fierce competition from a related species, the black spiny-tailed iguana (*Ctenosaura similis*) (Alberts et al. 2004). These larger and considerably more aggressive lizards (Fig. 6) live in drier habitats of the island of Utila, where they feed on small vertebrates, such as anolis (*Norops bicaorum*) and geckos (*Hemidactylus frenatus*) (Fig. 7a, b).

The specific habitat of *C. bakeri*, tree trunks in the brackish mangrove forests, led to a number of unique adaptations in the behavior and diet of this endemic species. Like the widely distributed, common Green iguana (*Iguana iguana* L. 1758) (Fig. 8), *C. bakeri* is primarily herbivorous, and eats leaves, stems, flowers and fruits of a number of plant species. Only rarely, in the mangroves, small vertebrates, arthropods or eggs, are consumed. However, one report documents that adult *C. bakeri* also eat geckos, such as *H. frenatus* (Fig. 7b) and juvenile Green iguanas (Fig. 8) (Dirkson and Gutsche 2006). Like the Galápagos marine iguanas (Fig. 3b), the Utila spiny-tailed iguana is an endemic, threatened island species.

Fig. 8 Adult specimen of the Green iguana (*Iguana iguana*) in its natural habitat. Sub-populations of this large, arboreal, herbivorous species from Middle- and South America (body length up to 190 cm) also inhabit the island of Utila. Juveniles of *I. iguana* are sometimes eaten by adult individuals of *Ctenosaura bakeri* and *C. similis* (original photograph, 2009)

Because of harvesting of eggs that are sold by local dealers on the island of Utila and on the mainland, the small population had almost gone extinct by the early 1990s. In 1994, the Honduran government enacted a ban on hunting, and in 1997, the Utila Iguana Research and Breeding Station was established (Alberts et al. 2004) to protect the last populations of this rare animal species. Nevertheless, this unique arboreal iguana, which is only known from three localities in a small area on the island of Utila (Honduras), is still seriously threatened. Fragmentation and loss of its habitat, tourism, and the introduction of foreign plants, as well as rats, cats and dogs, all contribute to the steady decline of this rare iguana species (Gutsche and Köhler 2008; Gutsche and Streich 2009).

In a recent study, Gutsche et al. (2012) analyzed the infection rate by ectoparasites in populations of *C. bakeri* in their natural habitat. They observed that infestation intensity was positively correlated with body size of male iguanas. However, because of a lack of parasitoses, the authors concluded that ectoparasites are not responsible for the current decline in natural populations of this endangered species.

Conclusions

In his book *Island Life*, Wallace (1880) mentioned that, because of human activities, endemic species that inhabit islands may become rare or driven to extinction. He further elaborated on this idea in *The Wonderful Century*, wherein Wallace described human destructiveness and summarized the negative effects of the "clearing of forests" and the

"devastation" of the landscapes by careless humans (Wallace 1898, p. 373). In his last monograph, *Social Environment and Moral Progress*, Wallace (1913) described man's "power over Nature" with respect to the deterioration of natural resources in the nineteenth century, and the spread of factory systems. Hence, the "man in the shadow of Darwin" was one of the first scientists who issued a warning stating that humans may be responsible for the destruction of the environment and the extinction of rare species (Kutschera 2013).

In this article, we have shown that Wallace's predictions were largely correct. His concern that the domestic mammals (dogs, cats, rats etc.) released by humans on the Galápagos archipelago will lead to a decline of the endemic fauna on these islands (Wallace 1880) has been confirmed by recent studies (Dowler et al. 2000; Berger et al. 2007; Rödl et al. 2007), and on other islands similar "iguana tragedies" occurred (Iverson 1978; Gibbons 1984; Whittaker 1998; Gutsche and Köhler 2008; Gutsche and Streich 2009). There is some room for optimism; however, the widely distributed Green iguana (*I. iguana*) (Fig. 8) was once regarded as a threatened species in some areas of South America, so that the Iguana Management Project/Panama was established in 1983 (Alberts et al. 2004). Today, this species, which has been hunted by humans for the consumption of its muscle tissue (meat) over the past centuries, appears to be so well established throughout Middle- and South America that this "Pro-Iguana-Agenda" was given up. Currently, *I. iguana* is not regarded as a threatened animal species, although local populations have disappeared, because of over-hunting and forest destruction (Böhm et al. 2013).

In summary, our analysis documents that Wallace (1880, 1898, 1910, 1913) was correct when he predicted that habitat fragmentation and destruction, accompanied by the establishment of facilities for humans (building of new houses, factories etc.) will lead to a decline in the populations of wild animals and plants. The IUCN Red List of Threatened Species documents this ongoing process.

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References

Alberts AC, Carter RL, Hayes WK, Martins EP (eds) (2004) Iguanas: biology and conservation. University of California Press, Berkeley

Bell G (1997) Selection: the mechanism of evolution. Chapman and Hall, New York

Berger S, Wikelski M, Romero LM, Kalko EKV, Rödl T (2007) Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana. Horm Behav 52:653–663

Böhm M, Collen B, Baillie JEM, Bowles P, Chanson J, Cox V et al (2013) The conservation status of the world's reptiles. Biol Conserv 157:372–385

Darwin C (1839) Journal of the researches into the geology and natural history of the various countries visited by H. M. S. Beagle. Henry Colburn, London

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Dirkson L, Gutsche A (2006) Beobachtungen zur Saurophagie bei *Ctenosaura bakeri* (Squamata: Iguanidae). Elaphe 14:51–52

Dowler RC, Carroll DS, Edwards CW (2000) Rediscovery of rodents (genus *Nesoryzomys*) considered extinct in the Galápagos Islands. Oryx 34:109–117

Endler JA (1986) Natural selection in the wild. Princeton University Press, Princeton

Franks SJ (2010) Genetics, evolution, and conservation of island plants. J Plant Biol 53:1–9

Gibbons J (1984) Iguanas of the South Pacific. Oryx 18:82–91

Gradstein FM, Ogg JG, Smith AG (eds) (2004) A geologic time scale 2004. Cambridge University Press, Cambridge

Gutsche A, Köhler F (2008) Phylogeography and hybridization in *Ctenosaura* species (Sauria, Iguanidae) from Caribbean Honduras: insights from mitochondrial and nuclear DNA. Zoosyst Evol 84:245–253

Gutsche A, Streich WJ (2009) Demography and endangerment of the Utila Island spiny-tailed iguana, *Ctenosaura bakeri*. J Herpetol 43:105–113

Gutsche A, Mutschmann F, Streich WJ, Kampen H (2012) Ectoparasites in the endangered Utila spina-tailed iguana (*Ctenosaura bakeri*). Herpetol J 22:157–161

Haffer J (2007) Ornithology, evolution, and philosophy. The life and science of Ernst Mayr 1904–2005. Springer, Berlin

Hendry AP (2005) The power of natural selection. Nature 433:694–695

Iverson JB (1978) The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. Biol Conserv 14:63–73

Köhler G (1995) Freilanduntersuchungen zur Morphologie und Ökologie von *Ctenosaura bakeri* und *C. oedirhina* auf den Islas de la Bahia, Honduras, mit Bemerkungen zur Schutzproblematik. Salamandra 31:93–106

Köhler G, Schroth W, Streit B (2000) Systematics of the *Ctenosaura* group of lizards (Reptilia: Sauria: Iguanidae). Amphibia-Reptilia 21:177–191

Kruuk H, Snell H (1981) Prey selection by feral dogs from a population of marine iguanas (*Amblyrhynchus cristatus*). J Appl Ecol 18:197–204

Kutschera U (2008) Darwin–Wallace principle of natural selection. Nature 453:27

Kutschera U (2009a) Symbiogenesis, natural selection, and the dynamic Earth. Theory Biosci 128:191–203

Kutschera U (2009b) Charles Darwin's *Origin of Species*, directional selection, and the evolutionary sciences today. Naturwissenschaften 96:1247–1263

Kutschera U (2011) From the scala naturae to the symbiogenetic and dynamic tree of life. Biol Direct 6(33):1–20

Kutschera U (2013) The age of man: a father figure. Science 340:1287

Laurie A (1983) Marine iguanas in Galápagos. Oryx 17:18–25

Levin HL (2003) The Earth through time, 7th edn. Wiley, Hoboken

Mayr E (1984) The growth of biological thought. Diversity, evolution and inheritance. Harvard University Press, Cambridge

Mayr E (2001) What evolution is. Basic Books, New York

Morton AG (1981) History of botanical science. Academic Press, London

Nicholls H (2013) News feature: the 18-km^2 rat trap. Nature 497:306–308

Nogales M, Martin A, Tershy BR, Donlan CJ, Veitch D, Puerta N, Wood B, Alonso J (2004) A review of feral cat eradication on islands. Conserv Biol 18:310–319

Rödl T, Berger S, Romero LM, Wikelski M (2007) Tameness and stress physiology in a predator-naïve island species confronted with novel predation threat. Proc R Soc B 274:577–582

Romero LM, Wikelski M (2010) Stress physiology as a predictor of survival in Galápagos marine iguanas. Proc R Soc B 277: 3157–3162

Shermer M (2002) In Darwin's shadow: the life and science of Alfred Russel Wallace. Oxford University Press, Oxford

Smith C, Beccaloni G (eds) (2008) Natural selection and beyond: the intellectual legacy of Alfred Russel Wallace. Oxford University Press, Oxford

Stejneger L (1901) On a new species of spiny-tailed iguana from Utila island, Honduras. Proc US Nat Mus 23:467–468

Wallace AR (1855) On the law which has regulated the introduction of new species. Ann Mag Nat Hist (N S) 16:184–196

Wallace AR (1869) The Malay Archipelago; the land of the orang-utan and the bird of paradise; a narrative of travel with studies of man and nature, vol 1 and 2. Macmillan & Co., London

Wallace AR (1876) The geographical distribution of animals; with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface, vol 1 and 2. Macmillan & Co., London

Wallace AR (1880) Island life: or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. Macmillan & Co., London

Wallace AR (1898) The wonderful century; its successes and its failures. Swan Sonnenschein & Co., London

Wallace AR (1910) The world of life; a manifestation of creative power, directive mind and ultimate purpose. Chapman & Hall, London

Wallace AR (1913) Social environment and moral progress. Cassell & Co., London

Whittaker RJ (1998) Island biogeography: ecology, evolution and conservation. Oxford University Press, Oxford

Wikelski M (2005) Evolution of body size in Galapágos marine iguanas. Proc R Soc B 272:1985–1993

Wikelski M, Nelson KN (2004) Conservation of Galápagos marine iguanas. Iguana 11:190–197