Chapter 22
Current Knowledge and Conservation of the Wild Mammals of the Gulf of Guinea Oceanic Islands

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Abstract Oceanic islands are usually difficult for mammals to colonize; consequently, the native mammal fauna is typically species-poor, often consisting of just a few species of bats. The oceanic islands of the Gulf of Guinea are no exception to this pattern. Still, the known mammal richness is relatively high for the small size of the islands. Out of a total of 13 native species, including 11 bats and 2 shrews, at least 7 species and 3 subspecies are single-island endemics. In addition to native species, at least 6 other wild mammals have been introduced to the islands purposely or accidentally by humans. Some of these are among the world's most notorious invasive species and cause damage to native species, ecosystems, and humans. Predation by exotic species can threaten native island mammals, which are especially sensitive due to their small populations and limited ranges. These impacts are likely worsened by other threats, such as forest degradation and climate change, and a general lack of knowledge about the natural history of most species also hampers the implementation of conservation measures. Therefore, fostering further research on the endemic-rich mammal fauna of these islands is vital to ensure their persistence.

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Introduction

Large expanses of ocean are often extreme barriers to mammal dispersal, and even some bat species are known to be reluctant to fly over open bodies of water (Castella et al. 2000). Therefore, it is not surprising that oceanic islands typically host a small number of native mammals, usually only a few species of bats (Whittaker and Fernández-Palacios 2007). How non-flying mammals overcome this obstacle to naturally reach oceanic islands is a controversial topic. The most frequent explanation, natural rafting, makes assumptions that sometimes seem impossible to meet, particularly in the case of small animals with high metabolic rates and freshwater requirements (Ali and Vences 2019; Mazza et al. 2019). In addition, as humans colonized oceanic islands, they usually brought with them a large number of mammal species, which often came to exceed the number of native mammals (Tennyson 2010). As a result of this process, humans have caused the extinction of several mammals native to oceanic islands and also biotic homogenization (Longman et al. 2018).

The oceanic islands of the Gulf of Guinea are an excellent example of these processes of natural and human-mediated colonization. Considering the small size of the islands, they host a surprisingly large number of mammal species. Of the 19 known wild species (Appendix), 13 are native and, of these, at least 7 species and 3 subspecies are single-island endemics. Most endemic and native species are bats (Juste and Ibáñez 1994a; Rainho et al. 2010), but there are also two endemic shrews (Bocage 1887; Ceríaco et al. 2015). Their presence on oceanic islands at such a long distance from the mainland is still puzzling (Heim de Balsac and Hutterer 1982; Ceríaco et al. 2015). Even with the potential ability to use torpor in situations of food scarcity (McKechnie and Mzilikazi 2011), shrews would have had substantial limitations to obtain freshwater during the long dispersal trip to the islands. Furthermore, the number of reproducing individuals reaching the islands would be expected to be far too small to sustain a viable population.

The remaining six species of mammals were introduced by humans (Dutton 1994), either purposely or accidentally. Two of these, the house mouse *Mus musculus* Linnaeus 1758 and the ship rat *Rattus rattus* (Linnaeus, 1758), are among the 100 worst invasive species globally, due to the impacts they cause on ecosystems when they are introduced (Lowe et al. 2000). Thus, their abundance on the Gulf of Guinea islands is concerning for the native flora and fauna. Although there are also domestic and feral mammals on these islands, such as dogs, cats, pigs, goats, cows, horses, and others that might have arrived at the islands more recently, these species will not be addressed in detail in this chapter.

Knowledge is the basis of conservation, and this chapter aims to compile the information available to date on the species of wild mammals that occur on the

islands of Príncipe, São Tomé, and Annobón. Threats to endemic and native species and knowledge gaps will also be discussed.

A Brief History of Mammal Research

Records of the presence of mammals on the oceanic islands of the Gulf of Guinea date to the first manuscripts of the first Portuguese travelers to these islands. An example of this is the excerpt presented by Sousa (1888) of a manuscript entitled "*Da viagem de dom Francisco d'Almeyda primeiro visorey da Índia*" [The journey of Dom Francisco d'Almeyda, India's first viceroy] dated ca. 1505. In this text, it is mentioned that "*n'esta ilha ha gatos d'algalia que criam que fugiram aos armadores que trouxerom da terra firme*" [on this island there are breeding civets that fled from the shipowners who brought them from the mainland] confirming the presence of the African civet *Civettictis civetta* (Schreber, 1776) in São Tomé already at the beginning of the sixteenth century.

More systematic surveys of mammals began much later. During the nineteenth century, Richard Greeff visited São Tomé and Rolas Islet between 1879 and 1880. Although this expedition did not focus on mammals, it confirmed the presence of two bat species *Cynonycteris stramineus*—currently *Eidolon helvum* (Kerr, 1792)—and *Phyllorhina caffra*—currently *Hipposideros ruber* (Noack, 1893). Greeff also confirmed the presence of the least weasel *Mustela nivalis* Linnaeus 1766 in São Tomé, based on a specimen found in the digestive tract of a cobra-preta *Naja* (*Boulengerina*) *peroescobari* Ceríaco et al. 2017 (Greeff 1884; Bocage 1905). These observations were further confirmed by A. F. Nogueira who also listed monkeys, bats, civets, weasels, and many rats in São Tomé (Nogueira 1885). In 1885, a botanical survey of São Tomé led by Adolpho F. Möller was commissioned by the Botanical Gardens of the University of Coimbra. Although focusing on botanical matters, some animal specimens were also collected. A list published by L. Vieira (1886) included mona monkey *Cercopithecus mona* (Schreber, 1774), *Viverra civetta* (currently *C. civetta*), *Cynonycteris stramineus* (currently *E. helvum*), *Phyllorhina caffra* (currently *H. ruber*), *Mus ducomanus* (currently *Rattus norvegicus* (Berkenhout, 1769)), *Mus rattus* (currently *Rattus rattus*), and *Mus musculus*.

Between 1885 and 1895, Francisco Newton was hired by the National Museum of Lisbon to conduct a zoological survey in the Gulf of Guinea. This survey included all the Gulf of Guinea islands, being the first known zoological survey in Annobón (Peris 1961). The mammal specimens were studied by J. V. Barbosa du Bocage, at the time director and curator of Zoology at the National Museum of Lisbon, resulting in several papers describing new species for the islands (see Bocage 1905). Such was the case of the São Tomé shrew *Crocidura thomensis* (Bocage, 1887), Newton's long-fingered bat *Miniopterus newtoni* Bocage 1889, the São Tomé horseshoe bat *Phyllorhina (Commersoni) thomensis* (currently *Macronycteris thomensis* (Bocage,

1891)) and the São Tomé collared fruit bat *Cynonycteris brachycephala* (currently *Myonycteris brachycephala* (Bocage, 1889)).

In 1954, a scientific expedition to São Tomé was undertaken by researchers from the Centro de Zoologia da Junta de Investigação do Ultramar. A report lists the bat specimens collected during this expedition (Lopes and Crawford-Cabral 1992), deposited in the collection of the Portuguese Institute of Scientific and Tropical Research. In 1955, Father Aurelio Basilio remained in Annobón for 3 months, reporting the presence of *R. norvegicus* for the first time on this island (Peris 1961).

During the 1970s, the French zoologist Henri Heim de Balsac took advantage of the presence of Father René de Naurois on the islands and asked him to collect pellets of Barn owl *Tyto alba* (Scopoli, 1769) during his ornithological surveys. Heim de Balsac believed that this would be an easy way to identify the spectrum of micromammals present on the island. Despite the high number of pellets collected, the diet of the barn owl proved to be composed essentially of ship rats *R. rattus*, and other than those, only one bird and one house mouse were found. Further efforts were made, and finally, some shrews were captured in São Tomé by R. Naurois, and in Príncipe by R. Naurois and Daniel Nunez, confirming the presence of *Crocidura thomensis* in São Tomé and identifying the species present in Príncipe as *C. poensis* (Fraser, 1843) (Heim de Balsac and Hutterer 1982). This mammal family was further reviewed by John Dutton and Jan Haft, based on the results of three expeditions, two German and one British, that visited São Tomé between 1989 and 1991 (Atkinson et al. 1994; Dutton and Haft 1996).

During the early 1990s, bats were the focus of Spanish investigators who started working in this region. This team made a massive contribution to the knowledge of this group, publishing several papers focusing on bat taxonomy (Juste and Ibáñez 1992, 1993b; Juste et al. 2007), morphology, and genetics (Juste and Ibáñez 1993a; Juste et al. 1996, 2000) and even echolocation (Guillén et al. 2001). They also described one new species, the São Tomé free-tailed bat *Chaerephon tomensis* (Juste and Ibáñez, 1993) and discovered the presence of an undescribed pipistrelle of the genus *Pseudoromicia* Monadjem et al. 2020 in Príncipe (Juste and Ibáñez 1993c, 1994a).

During the first decade of the twentieth century, bats were again the focus of research on the islands. In 2002, a study of the abundance of *E. helvum* in Príncipe was carried out by a team of English researchers (Dallimer et al. 2006). In 2010, a team from the University of Lisbon studied the status and distribution of bats on São Tomé (Rainho et al. 2010), adding a new species for São Tomé, the tricolored mouse-eared bat *Myotis* cf. *tricolor* (Temminck, 1832). In 2012, Peel and colleagues published a study on the persistence of several viruses on the isolated population of *E. helvum* in Annobón (Peel et al. 2012).

Among the studies published recently, it is worth highlighting the reviews on the species of *Crocidura* in São Tomé (de Lima et al. 2016) and Príncipe (Ceríaco et al. 2015), the latter describing the shrew of Príncipe as *Crocidura fingui* Ceríaco et al. 2015, and demonstrating that it is endemic to the island. Ecological studies have also included information on the mammals of the oceanic islands of the Gulf of Guinea; for example, studies on the hunting of wild species in São Tomé (Carvalho et al.

2015a, b; Hayman and Peel 2016), and the study of seed dispersal networks on this island (Mendes 2017; Coelho 2018; Heleno et al. 2021). Studies of broader geographical scope also addressed some mammal species from the Gulf of Guinea islands. This is the case of the work by Peel and colleagues (e.g., Shi et al. 2014; Peel et al. 2016, 2017), who studied ecology, traits, genetics, and possible zoonosis associated with *E. helvum,* and hypothesized on colonization and movements of this species between the islands. Rodrigues and colleagues (2017) have investigated the origin and process of invasion of the least weasel on the Atlantic islands, including São Tomé. Finally, a recent expedition was carried out in 2019 by a team from the University of Lisbon on the bats of Príncipe Island (JMP and ST, pers. obs). Their main results are included in the following sections of this chapter.

Current State of Knowledge

Order Primates

Family Cercopithecidae

Only one species of non-human primate occurs on the islands. The mona monkey was introduced in São Tomé and Príncipe 150–500 years ago (Glenn and Bensen 2013). The reason for its introduction is not fully known, but it is possible that it was used as food by enslaved plantation workers or, more likely, sailors and slavers kept them as pets (Denham and Denham 1987). The mona monkey was also introduced on the Caribbean island of Grenada, with animals originating from São Tomé and Príncipe (Glenn and Bensen 2013). No reference was found to the historical or contemporary presence of monkeys in Annobón.

The mona monkey is a forest species native to West Africa. Once common across its native range, it has become rare and even extirpated in some areas due to habitat loss and over-hunting by humans (Goodwin et al. 2020). Where it is still common, its densities vary between 15 and 49 ind/km^2 (Glenn et al. 2014). It is common on the islands, with estimates of 19 ind/km^2 in São Tomé and 21 ind/km^2 in Príncipe (Glenn 1998; Glenn et al. 2014), even though it is also hunted for human consumption on both islands (Carvalho et al. 2015a). The mona monkey is considered a generalist because it uses various types of forest, has a very diverse diet, and has been successful in colonizing forests outside its native range (Glenn et al. 2014). In Príncipe, this species seems to be particularly abundant in the transition zones between the forest and the agricultural areas where food is plentiful (JMP pers. obs. and Filipa Soares pers. comm.). It mainly feeds on fruits and arthropods but also eats leaves, flowers, small lizards, and bird eggs and chicks (Glennet al. 2014). Mona monkeys are among the introduced species that may affect the seed dispersal networks on São Tomé because they favor plant species with large fruits and seeds (Heleno et al. 2021). They are often regarded as agricultural pests. Dutton (1994) mentioned that they can impact forest regeneration, and Carvalho et al. (2015a)

suggested that monkeys can potentially become significant predators of small vertebrates, particularly of endemic birds that have low resilience and small populations. Their predation of bird nests has recently been confirmed (Guedes et al. 2021), but further work is required to determine the impacts on bird populations.

Order Rodentia

Family Muridae

São Tomé and Príncipe support populations of all three introduced murid rodents in Africa: the ship rat, the brown rat, and the house mouse. Both the house mouse and the brown rat occur and are abundant also on Annobón (Bocage 1893; Peris 1961; Jones and Tye 2005; Fry 2008; Martim Melo pers. comm.).

These commensal species may have reached the islands as stowaways in boats arriving from Europe. The ship rat and the house mouse are likely to have been accidentally introduced with the arrival of Portuguese ships to the islands during the fifteenth century. According to Dutton (1994), the brown rat only reached the islands during the eighteenth century, when it became abundant in the ports of western Europe (Atkinson 1985).

Given their invasive character, even in mainland Africa (Denys et al. 2009; Dalecky et al. 2015), these three species are likely to occur across the three islands and to be most abundant in anthropogenically-modified environments. Atkinson (1994) confirmed the presence of all three rodents around villages in São Tomé and referred to the occurrence of rats at the margins of the primary forest and in the secondary forest along the Quija River. They also highlighted the capture of several young brown rats in Lagoa Amélia and Morro Esperança (Atkinson et al. 1994). A recent pilot study was performed in São Tomé, confirming the presence and high abundance of ship rats throughout the island, while recording only one brown rat in the capital city (Ward-Francis et al. 2017). Ship rats seem to be abundant in Príncipe (Fundação Príncipe 2019, Martim Melo pers. comm.), where the presence of brown rats has recently been confirmed in the south of the island (JMP and ST pers. obs.). These species can also be a problem to the human inhabitants of the islands. For instance, in 2004, the farmers of Annobón faced huge crop damages caused by an overabundance of rats on the island (Martim Melo pers. comm.).

Other Species

In 2019, a non-identified rodent was observed and photographed at Lagoa Amélia on São Tomé island (Fig. 22.1, 1; Leonel Viegas and Francisco Alamô pers. comm.). The overall external morphology of the observed individual (reddish fur, long snout, black dorsal stripe, long tail) suggests it may belong to the sub-Saharan genus

Fig. 22.1 Some of the poorly known mammal species of the islands of the Gulf of Guinea: (**1**) Small rodent probably belonging to the genus *Dendromus*; (**2**) *Hypsignathus monstrosus*; (**3**) *Myotis* cf. *tricolor*; (**4**) *Pseudoromicia* sp., a novel species occurring in Príncipe; (**5**) *Crocidura thomensis*; (**6**) *Myonycteris brachycephala*; (**7**) *Miniopterus newtoni*; (**8**) *Civettictis civetta*. Photo credits: (**1**) Leonel Viegas, (**3**, **7**) Ana Rainho, (**4**) Jorge Palmeirim and Sólveig Thorsteinsdóttir, (**5**) Ricardo de Lima, (**6**) Javier Juste, (**2**, **8**) unknown photographer

Dendromus Smith, 1829 (Family Nesomydae). This is a tentative identification, by no means conclusive, particularly taking into consideration the confusion that still prevails in the field of African rodent taxonomy and the frequent lack of external morphological characters separating taxa (Monadjem et al. 2015). Further research is necessary to clarify the identity, distribution, and natural history of this species.

Order Eulipotyphla

Family Soricidae

Two species of shrew are known to occur on the oceanic islands of the Gulf of Guinea: the São Tomé white-toothed shrew *Crocidura thomensis* (Fig. 22.1, 5) endemic to São Tomé, and the Príncipe White-Toothed Shrew *Crocidura fingui* endemic to Príncipe (Heim de Balsac and Hutterer 1982; Dutton and Haft 1996; Ceríaco et al. 2015; de Lima et al. 2016). No shrews have been found on Annobón (Heim de Balsac and Hutterer 1982).

Crocidura thomensis was described by Bocage (1887) based on a specimen captured by Francisco Newton in 1886 at Roça Minho. A few years later, it was also captured by Newton and António Lobo de Almada Negreiros at Santa Maria and another unknown location (Bocage 1905). By the end of the twentieth century, the species had been recorded from fewer than ten locations (Dutton and Haft 1996). Recent data suggest, however, that it may not be as rare as initially suspected. Without directed sampling effort, this species was recorded 23 times in 15 new locations in recent years (de Lima et al. 2016). It seems to be widely distributed, occurring from near sea level to high mountainous areas (Fig. 22.2), inhabiting humid areas across a variety of habitats ranging from mist forests to lowland plantations (Dutton and Haft 1996; de Lima et al. 2016). The use of humid habitats may result from the higher availability of arthropod prey (Dutton and Haft 1996; de Lima et al. 2016). *Crocidura thomensis* is listed as Endangered in the IUCN Red List of Threatened Species (Kennerley 2016). This status is due to its reduced extent of occurrence and the continuing decline in the extent and quality of the available habitat. Other possible threats are predation by introduced species, use of pesticides, and agricultural intensification (Dutton and Haft 1996; de Lima et al. 2016). If confirmed, the dependence on humid habitats may make this species vulnerable to climate change (de Lima et al. 2016).

The taxonomic status of the shrew species occurring in Príncipe has undergone several changes since its first records. It was first identified as *C. thomensis* by Bocage (1887) based on a specimen captured by F. Newton at Oquê Nazareth in 1894. A century later, Heim de Balsac and Hutterer (1982) identified the species as *C. poensis*, a species also occurring in West Africa, based on 12 new specimens (plus 4 young) captured on the island by R. de Naurois and Daniel Nunez. Four other individuals were captured in 2013 (Ceríaco et al. 2015). The morphological and molecular analysis of these latter specimens led Ceríaco et al. (2015) to conclude that

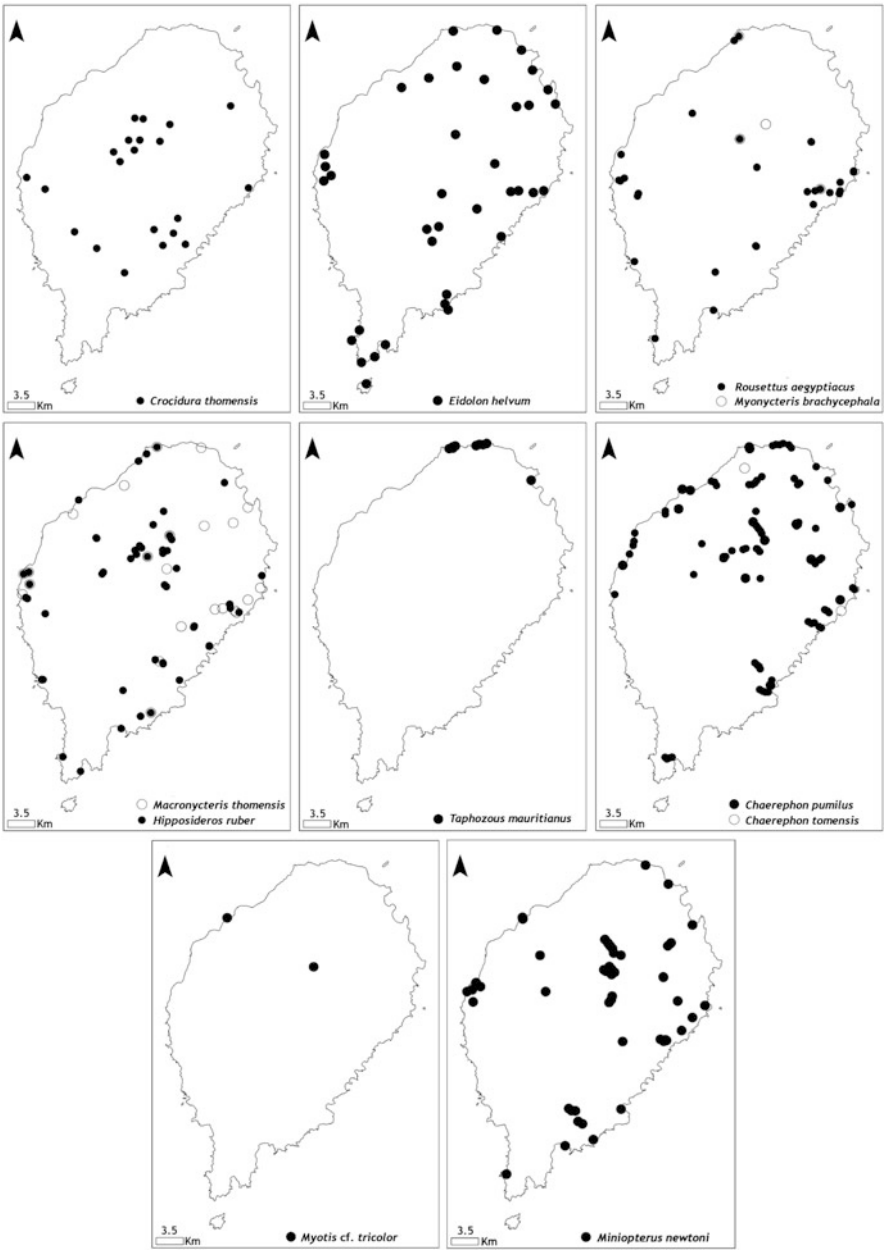

Fig. 22.2 Locations where different wild mammal species were recorded on the island of São Tomé. Sources: Lopes and Crawford-Cabral (1992), Juste and Ibáñez (1994a), Rainho et al. (2010), de Lima et al. (2016), Peel et al. (2017), and ACR (2020)

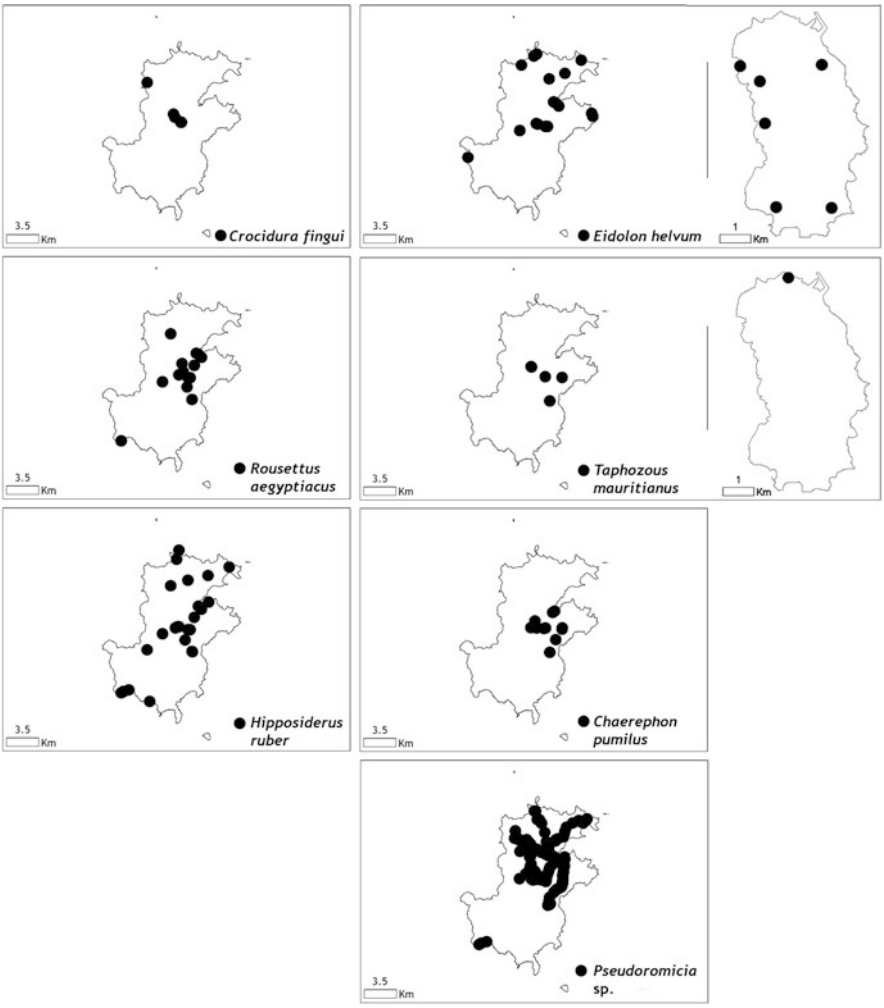

Fig. 22.3 Locations where different wild mammal species were recorded on the islands of Príncipe and Annobón. Sources: Lopes and Crawford-Cabral (1992), Juste and Ibáñez (1994a), Ceríaco et al. (2015), Peel et al. (2017), ACR (2020), Juste (2020), and JMP and ST (pers. obs.)

this is indeed a distinct species, endemic to Príncipe, that they named *C. fingui*. Based on molecular clock estimates, this island endemic diverged from the Central-East African lineage of *C. poensis* ~1.0–1.2 Ma (Nicolas et al. 2019). The distribution of *C. fingui* has not been studied, but so far, it has only been recorded in the northern part of the island (Fig. 22.3). It seems to be versatile in terms of habitat, occurring both near human settlements and in forest (Ceríaco et al. 2015). Due to the lack of knowledge about the distribution of this species, its ecological requirements,

and potential threats, it is listed as Data Deficient in the IUCN Red List of Threatened Species (Ceríaco et al. 2019).

Order Chiroptera

Family Pteropodidae

Three species of fruit bats occur in the oceanic islands of the Gulf of Guinea. In 2019, photos of a fourth species, a male hammer-headed bat *Hypsignathus monstrosus* H. Allen, 1862, allegedly captured in the town of São Tomé, appeared on social media (Fig. 22.1, 2). Since we have not been able to collect more information, we refrain from commenting on this observation.

The conspicuous and noisy African straw-colored fruit bat, *Eidolon helvum*, is the largest bat and probably one of the most abundant native mammals on the islands. Dallimer et al. (2006) estimated the density of this species on Príncipe at between 82 and 111 ind/km^2. Peel et al. (2017) produced a slightly higher estimate for Príncipe at between 156 and 159 ind/km^2 and estimated a density between 94 and 176 ind/km^2 for Annobón. All estimates show that this species reaches densities similar to those found in mainland Africa (Dallimer et al. 2006). *Eidolon helvum* is commonly seen flying with slow strokes high above the canopy in forests, plantations, and even city gardens and orchards, foraging on native and planted fruits (all authors, pers. obs.).

Eidolon helvum is migratory on the African mainland, where it is considered monotypic despite its broad distribution (O'Toole 2019). Conversely, all three island populations are considered non-migratory (Juste et al. 2000; Peel et al. 2016, 2017). The populations of *E. helvum* from São Tomé, Príncipe, and Annobón show genetic differentiation in a clear geographic pattern (Peel et al. 2013). Genetic and demographic analyses provide evidence that *E. helvum* of Príncipe and São Tomé are broadly part of the same genetic population cluster, though dispersal between the islands is rare (Juste et al. 2000; Peel et al. 2013). By contrast, the Annobón population is recognized as a taxonomically distinct entity (*E. helvum annobonense* Juste et al. 2000). It exhibits island dwarfism, with individuals being significantly smaller than those of the other two islands (Juste et al. 2000; Peel et al. 2016, 2017).

Despite its high density on the Gulf of Guinea islands, *E. helvum* was classified as Vulnerable on São Tomé because of its reduced range and habitat degradation (Rainho et al. 2010). Moreover, it is hunted in large numbers on São Tomé (Carvalho et al. 2015b; Hayman and Peel 2016; Peel et al. 2017) and on Príncipe (Hayman and Peel 2016, JMP and ST pers. obs.). Hayman and Peel (2016) quantified the effects of hunting on the demographic structure of the population on São Tomé but did not find detrimental impacts on Príncipe. Increased hunting pressure may result in the unsustainable exploitation of this species, a problem compounded by the frequent disturbance of its colonies (Rainho et al. 2010; Peel et al. 2017). Globally, *E. helvum* is Near Threatened on the IUCN Red List due to a significant decline of its

population and over-harvesting, making this species close to qualifying for Vulnerable status (Cooper-Bohannon et al. 2020).

The Egyptian rousette, *Rousettus aegyptiacus* (Geoffroy, 1810), is found on Príncipe and São Tomé islands (Figs. 22.2 and 22.3). The genus *Rousettus* Gray 1821 is unique among Old World fruit bats for its echolocation capacity (Holland et al. 2004; Table 22.1), allowing roosting in total darkness in caves and buildings. The populations on Príncipe and São Tomé are clearly differentiated morphologically and genetically from other African forms and recognized as endemic at subspecies rank (Juste and Ibáñez 1993b). These two subspecies represent classic examples of island dwarfism in the case of *R. aegyptiacus princeps* Juste and Ibáñez 1993 on Príncipe and gigantism by *R. aegyptiacus tomensis* Juste and Ibáñez 1993 on São Tomé (Juste and Ibáñez 1993b; Juste et al. 1996). Still, both forms share features (like their massive dentition) that point to a common evolutionary history (Juste and Ibáñez 1993b). *Rousettus aegyptiacus* is a cave-dwelling species that forages in multiple habitats on the islands, feeding on native and cultivated fruits (Rainho et al. 2010). On São Tomé, it was observed sharing a roost with *H. ruber* and *M. newtoni* in a large marine cave (Rainho et al. 2010). On Príncipe, a small colony was found roosting in a cliff in Pico Papagaio (Juste 1990). *Rousettus a. tomensis* is listed as Vulnerable because of its small range and projected habitat degradation (Rainho et al. 2010). Although harvested for human consumption, it remains relatively common on both Príncipe and São Tomé (Rainho et al. 2010; JMP and ST pers. obs). However, an increase in harvesting, aggravated by the disturbance of the colonies in their roosts, may become a threat (Rainho et al. 2010).

A third fruit bat species, the São Tomé collared fruit bat *Myonycteris brachycephala* (Fig. 22.1, 6) is only found on São Tomé (Fig. 22.2). This endemic species is unique in having lost a lower incisor, hence displaying the only asymmetrical dental formula known in any mammal (Juste and Ibáñez 1993a). It is very elusive, and despite netting efforts, it is only known from two localities beyond the type locality (Cascata, São Tomé), both in a rugged landscape, one (Morro Palmira) in montane forest and the other (Belavista) in lowland cocoa plantations (Juste and Ibáñez 1994a). It is considered Endangered (Juste 2016).

Family Hipposideridae

The family Hipposideridae comprises many insectivorous species spread throughout the Old World tropics, all featuring a highly complex leaf-nose. The oceanic islands of the Gulf of Guinea host two species: *Hipposideros ruber* and *Macronycteris thomensis*. The latter is endemic to São Tomé and was described by Bocage (1891) based on specimens from Ribeira Peixe and Roça Saudade. It is a large microbat (forearm (FA) ~85 mm, weight ~56 g) and is part of a group of leaf-nosed bat species that were recently moved from the genus *Hipposideros* to *Macronycteris* (Foley et al. 2017). Very little is known about the biology of this species; however, it is presumably somewhat similar to that of *M. gigas* (Wagner, 1845), a close relative present on Bioko (Juste and Ibáñez 1994a) and the adjacent mainland (Happold

Table 22.1 Characteristics of the echolocation calls of different bat species present in São Tomé

Species	F_{min} (kHz)	F_{max} (kHz)	F_{maxE} (kHz)	Duration (ms)	Interval (ms)	*N*
Rousettus aegyptiacus	9.3 ± 2.4	110.5 ± 48.0	–	0.33 ± 0.12	122.5 ± 28.7	8
	4.1–11.9	44.0–150.0		0.2–0.5	81.7–165.0	
Hipposideros ruber	139.7 ± 0.2	141.5 ± 0.4	140.9 ± 0.3	5.9 ± 0.2	14.1 ± 4.2	6
	139.3–139.8	140.8–141.9	140.4–141.1	5.7–6.1	10.4–22.1	
Macronycteris thomensis	66.0 ± 0.8	68.0 ± 1.0	67.2 ± 0.4	20.7 ± 4.0	66.8 ± 17.4	10
	64.3–66.8	66.8–70.2	66.4–68.0	15.6–28.6	43.2–106.4	
Myotis cf. tricolor	39.3 ± 2.0	117.3 ± 3.3	78.4 ± 2.1	1.84 ± 0.1	82.7 ± 16.2	5
	36.6–41.6	112.0–120.8	76.4–81.8	1.74–1.92	58.4–102.6	
Miniopterus newtoni	50.3 ± 1.3	101.7 ± 16.7	55.9 ± 2.7	4.8 ± 2.1	61.4 ± 23.6	14
	47.8–52.2	69.6–119.0	53.2–61.0	2.3–7.8	31.8–105.7	
Taphozous mauritianus	24.2 ± 0.7	31.9 ± 0.6	28.3 ± 0.2	14.8 ± 1.7	77.4 ± 6.4	5
	23.4–25.2	31.4–32.5	28.1–28.4	12.8–16.8	70.7–86.4	
Chaerephon pumilus	24.9 ± 2.7	36.0 ± 8.7	28.4 ± 2.3	13.6 ± 3.0	258.4 ± 156.5	32
	19.8–29.4	24.7–51.5	23.4–31.5	8.1–18.6	62.8–472.0	
Chaerephon sp.	21.0 ± 1.1	23.0 ± 1.1	22.1 ± 1.0	16.3 ± 1.7	350.7 ± 97.2	26
	19.0–22.4	20.4–25.5	19.9–24.1	12.7–19.9	137.0–558.5	

Values indicate mean, standard deviation and range of observed values. F_{min}, minimum pulse frequency; F_{max}, maximum pulse frequency; F_{maxE}, maximum energy frequency. Note that the values indicated for *Chaerephon* sp. may refer to *Chaerephon pumilus* or another species of the same genus (e.g., *Ch. tomensis*)
Adapted from Rainho et al. (2010)

2013a; Foley et al. 2017). *Macronycteris thomensis* looks like a dwarf form of *M. gigas*. A colony of several hundred individuals was found in an underground roost, and a single individual was observed roosting under the leaves of a palm tree. It is common throughout the island but much less so than *H. ruber* (Rainho et al. 2010).

Hipposideros ruber is a small leaf-nosed bat (FA ~50 mm, weight ~11 g) with two very distinct color forms: dull brown and orange. The species is part of a species complex present across much of Africa (Patterson et al. 2019) and is common throughout Príncipe and São Tomé. On both islands, the species is mostly associated with primary and secondary forests, but it is also present in other ecosystems. On São Tomé, it seems to be somewhat less common in the dryer northeast of the island than in the well-forested and humid center and south (Rainho et al. 2010). It uses a wide variety of roost types and has been found in caves and abandoned buildings on Príncipe (JMP and ST pers. obs.). On São Tomé, in addition to these types of roosts, it uses artificial tunnels (Rainho et al. 2010). On the mainland, it is known to also roost in tree hollows (Happold 2013b) and likely does so on the islands as well. *Hipposideros ruber* has very broad wings and highly maneuverable flight, capable of foraging by hawking and gleaning in cluttered forest habitats (Happold 2013b). Both foraging behaviors have been observed on the islands. Its diet has not been studied on São Tomé or Príncipe, but on the mainland, it feeds on a variety of insects, including beetles, moths, dipterans, and isopterans (Happold 2013b). An unusual feature of the population of *H. ruber* on São Tomé is its daytime flying habits. Although most of its activity takes place during the night, it is common to find this bat flying and foraging in the forest during the day (Russo et al. 2011). São Tomé and Príncipe populations produce constant frequency (CF) calls that are typical for the family and include two harmonics, where the second and higher-pitched one is the information carrier (Guillén et al. 2001). The resting frequency is the same as that reported for bats from the mainland and averaged 136.6 and 136.1 kHz for females and 139.7 and 136.7 kHz for males on São Tomé and Príncipe, respectively (Guillén et al. 2001). Although *H. ruber* is classified as Least Concern globally (Monadjem et al. 2017), it was considered Near Threatened in São Tomé due to the probable decline in the number of individuals and colonies resulting from the reduction of roost availability (Rainho et al. 2010).

Family Emballonuridae

The Mauritian Tomb bat *Taphozous mauritianus* (Geoffroy Saint-Hilarie, 1818) is the only emballonurid species known to be present on the Gulf of Guinea oceanic islands. This species, originally described from the island of Mauritius, is quite common across sub-Saharan Africa (Bonaccorso 2019). As an open-space forager, *T. mauritianus* is quite good at colonizing islands (Bonaccorso 2019). In mainland Africa, its diet consists of aerial insects such as Lepidoptera, Isoptera, and Coleoptera (Dengis 1996 and references therein). It typically roosts at the base of the crown of leaves in coconut trees. It was found at several sites along the northern

coast of São Tomé (Fig. 22.2) and is presumably common across other coastal areas of the island (Juste and Ibáñez 1994a). It has not been collected on Príncipe, but its presence there has recently been confirmed acoustically (JMP and ST pers. obs.; Fig. 22.3) Finally, *T. mauritianus* seems to be very rare on Annobón (Fig. 22.3), where a single specimen was found dead and is now housed at the Estación Biológica de Doñana (EBD-CSIC) collections in Seville (Juste 2020). In São Tomé, it was classified as Endangered, given its reduced area of occupancy, the number of known locations, and projected decline in habitat quality (Rainho et al. 2010).

Family Molossidae

Two species of molossids occur on the islands and both are insectivorous, the São Tomé free-tailed bat *Chaerephon tomensis* endemic to São Tomé (Juste and Ibáñez 1993c), and the little free-tailed bat *Chaerephon pumilus* (Cretzschmar, 1826), which is found on both São Tomé and Príncipe (JMP and ST pers. obs.). The latter is an abundant habitat generalist, widely distributed across Africa and the islands around the continent and is currently classified as Least Concern (Bouchard 1998; Mickleburgh et al. 2019). By contrast, *C. tomensis* is classified as Endangered, reflecting its small extent of occurrence and likely decreasing population trend as a result of habitat loss associated with coastal development and land conversion for agricultural use, and possibly competition with its much more abundant congener (Monadjem et al. 2019).

During recent island-wide surveys, Rainho et al. (2010) captured several dozen individuals of *C. pumilus* on São Tomé, in shade cocoa plantations, coconut groves and at roosts (Fig. 22.2). On Príncipe, JMP and ST (pers. obs.) captured it at a roost in the roof of a house near Porto Real and recorded its calls at several locations in the NE of the island (Fig. 22.3). By contrast, *C. tomensis* seems to be so rare that recent extensive trapping efforts have failed to document it. The only records to date are the type series of three specimens captured in two lowland localities, in a coastal lagoon at Praia das Conchas in the drier northern area of São Tomé and at the mouth of a river in cocoa plantations in Água Izé (Juste and Ibáñez 1993c). Acoustic sampling further confirmed the ubiquitous presence of *C. pumilus* on São Tomé (Table 22.1). In addition, these data revealed that *Chaerephon* emits vocalizations that fall into two distinct groups that differ in a number of call characteristics (Table 22.1). The first can unequivocally be assigned to *C. pumilus* (FmaxE $\approx$ 28 kHz), while the second group (FmaxE $\approx$ 22 kHz) could potentially correspond to *C. tomensis* (Rainho et al. 2010), thus offering a glimmer of hope that this species still occurs on the island.

Family Vespertilionidae

In São Tomé and Príncipe, this large family of insectivorous bats is represented by one species on each island. On São Tomé, recent surveys led to the detection of a species of mouse-eared bat, *Myotis* Kaup, 1829 (Rainho et al. 2010). While its general morphology suggests the species is a tricolored mouse-eared bat (Fig. 22.1, 3), *M.* cf. *tricolor*, genetic and morphological comparisons, as well as its echolocation calls (Table 22.1), indicate differentiation from mainland specimens (authors' unpublished data). An integrative taxonomic assessment is underway to establish its phylogenetic placement with respect to other Afrotropical *Myotis*. Rainho et al. (2010) captured several individuals in a single roost in a coastal cave at Ponta Figo, south of Neves, comprised of several dozen individuals of *M.* cf. *tricolor* and several thousand *M. newtoni* (described below). No other roosts of the species were found, the species has not been captured elsewhere on the island, and has merely been recorded acoustically at one other location (Bom Sucesso, Fig. 22.2) attesting to its overall rarity (Rainho et al. 2010).

The island of Príncipe is home to a very small pipistrelle bat that is considered an endemic form for the island (Fig. 22.1, 4). Although first reported over 30 years ago (Juste 1990; Juste and Ibáñez 1994b), its formal description is still pending, and its phylogenetic placement in one of the most entangled African bat groups requires clarification. Its general dark brown morphology, baculum characteristics, and genetic comparisons indicate that the pipistrelle belongs to the *Neoromicia* group (JJ pers. obs.) and possibly to the recently described genus *Pseudoromicia* (Monadjem et al. 2020). The species is abundant and ecologically eclectic, having been captured or recorded in urban, agricultural, and forest areas (JMP and ST pers. obs.). As is the case for other bat species, the distribution map suggests that the species is more common in the northern part of Príncipe (Fig. 22.3), but this is mostly a result of biased sampling due to difficulty accessing the southern part of the island.

Family Miniopteridae

Only one species of this family occurs on the Gulf of Guinea oceanic islands, *Miniopterus newtoni*. It has only been recorded on São Tomé (Fig. 22.2), and was first reported for the island and described as a new species by Bocage (1889, 1903). The original material used by Bocage was lost in a fire in Lisbon, and Juste and Ibáñez (1992) provided a neotype from Santa Catarina. These authors distinguished the species morphologically from the mainland western (*occidentalis*) and eastern (*minor*) little *Miniopterus* forms, all considered subspecies of *M. minor* Peters, 1867. A subsequent genetic assessment confirmed the specific rank of this endemic (Juste et al. 2007). The species seems relatively common across São Tomé (Juste and Ibáñez 1994a; Rainho et al. 2010) and was found in modified habitats (e.g., foraging around streetlamps in urban areas) as well as in primary lowland forests, from sea

level up to 1300 m in Morro Palmira (Juste 1990). It appears to roost strictly in caves, water mines, and tunnels. It can form colonies of thousands of individuals, often with other species. *Miniopterus newtoni* emits low duty cycle frequency-modulated echolocation calls with maximum energy of around 56 kHz (Table 22.1). It was locally considered Near Threatened due to a probable decline in the number of individuals and locations because of the destruction and/or disturbance of underground roosts (Rainho et al. 2010). However, it is listed as Data Deficient in the IUCN Red List (Juste 2019).

Order Carnivora

Family Mustelidae

One of the wild carnivores present on São Tomé is the least weasel (Bocage 1895; Dutton 1994). To the best of our knowledge, this species was not reported for Príncipe or Annobón. Although the Portuguese were most likely responsible for the introduction of the least weasel on São Tomé, genetic analyses by Rodrigues et al. (2017) revealed that the animals that occur on this island do not appear to be closely related to mainland Portugal populations. Instead, they are identical to those from the Azores (a Portuguese volcanic archipelago in the mid-Atlantic), which, in turn, are thought to have been introduced from the Balearic Islands in the Mediterranean. Morphological similarity between individuals of São Tomé and the Azores had already been highlighted by Bocage (1895), and Barrett-Hamilton (1904) mentioned that the animals of São Tomé might have been imported from the Azores.

There is little information about the abundance and distribution of the least weasel on São Tomé and Príncipe. Atkinson et al. (1994) observed weasels both at Fernão Dias and Ribeira Peixe. The least weasel feeds mainly on rodents, both in its native and introduced range, but can also consume birds and their eggs, small reptiles, and invertebrates, particularly if the rodent population declines or if an easy predation opportunity arises (Sheffield and King 1994 and references therein; King et al. 2001). According to Dutton (1994), the abundance of rodents on the islands may reduce the impact of weasels on other animal groups. However, shrews are frequently part of the weasel's diet and the endemic shrews might thus be vulnerable to its presence (Sheffield and King 1994).

Family Viverridae

The African civet (Fig. 22.1, 8) is endemic to sub-Saharan Africa, occurring between latitudes 15° N and around 29° S (Ray 2013). It is naturally present on Zanzibar but absent from other offshore African islands (Ray 2013). It is likely that the Portuguese introduced the African civet to both São Tomé and Príncipe (Bocage 1905; Dutton 1994; Fundação Príncipe 2019), not only for the control of rodents but also for the

exploitation of its musk (Frade 1958). No reference was found to the presence of this species on Annobón.

The African civet is a solitary, silent species that is active only at night. Thus it is not easy to observe, and information on its distribution and abundance is scarce. Atkinson et al. (1994) observed a fresh civet hole in a secondary forest between Santo António and São Miguel, and JJ (pers. obs.) recorded this species near São Tomé and at Cantagalo, Monte Belo, Monte Café, and Praia das Conchas in the early 1990s. During the last decade, the species has been observed across São Tomé, from the savannas in Morro Peixe to Monte Café and Monte Carmo, and from the road to the native forest (Ricardo de Lima pers. comm.). In Príncipe, it was camera-trapped at Morro Leste (Fundação Príncipe 2019). In mainland Africa, this species does not usually dwell in primary forests, but will use this habitat if accessible by logging roads (Ray and Sunquist 2001). African civets are omnivorous and opportunistic, feeding mainly on fruit, arthropods, mammals, and, less frequently, on birds and reptiles (Ray 2013 and references therein). The African civet is not a good climber or digger (Ray 2013), so tree-dwelling species should be relatively safe from civet predation (Dutton 1994). The potential impact on native ground-dwelling fauna is not known.

Conservation

The long-term isolation of Príncipe, São Tomé, and Annobón allowed the differentiation of insular populations, resulting in a very high level of endemism and an exceptional mammal conservation value. The taxonomy of these mammals is still in flux but of the 13 native species currently recognized, 7–9 are endemic species, and 3–4 are endemic subspecies, with no endemism shared between islands (Appendix). Most of these native and endemic species are bats (Appendix), though Príncipe and São Tomé each have an endemic species of shrew, and São Tomé may have a yet undescribed rodent. All the remaining mammals were introduced by humans.

Little is known about the threats faced by these species, although they should all be considered somewhat fragile due to their very small ranges (Le Breton et al. 2019). In particular, further deforestation and forest degradation would likely result in a potentially threatening situation for several mammal species. All the endemics likely evolved in humid forest, and several species show some level of association to this habitat (e.g., *Ch. tomensis*, *E. helvum annobonense* and *H. ruber*). Although much of the forest on the three islands has, at some point in the past, been converted to plantation agriculture or profoundly altered, there are still areas of relatively undisturbed habitat in rugged parts of the islands (Jones and Tye 2005; de Lima et al. 2022). The remaining primary forest is mostly in protected areas and, along with complementary areas of secondary forest, is likely to provide suitable habitat to maintain populations of all native mammals. The area of native forest on Annobón is very small, but the only mammal that is endemic to this island, the subspecies *E. helvum annobonense*, also uses secondary habitats (JJ pers. obs.).

Hunting of *E. helvum* and *R. aegyptiacus* for food is common on São Tomé (Carvalho et al. 2015b; Peel et al. 2017) and on Príncipe (Peel et al. 2017; JMP and ST pers. obs.). Still, both species remain quite numerous, presumably because these frugivorous species take advantage of the increase in fruit resources due to agriculture. The endemic *M. brachycephala*, however, is quite rare and it may be caught in traps set up to capture the two more abundant species, so hunting is a potentially significant threat to this species.

Some carnivorous mammals, both wild and domestic, have been introduced in São Tomé, all of which are also widespread in Príncipe, except for the least weasel. Although the impact of these species on the native wildlife has not yet been studied, they are all known to consume small mammals, so they are potential predators of the native shrews. Rats prey on smaller mammals and may thus also prey on both shrew species and potentially bats (Racey and Entwistle 2003).

Because so little is known about the real impact of the various potential threats to native mammals on these islands, it is not possible to formulate very specific conservation recommendations. However, it is evident that the protection of forest is essential. The expansion of conservation management to areas of well-preserved secondary forest and increased surveillance and enforcement are necessary to ensure the continuity of the forests on the islands and all the biodiversity they sustain. Integrated management actions directed at the control of exotic predators are also urgently needed, within the forest but also in anthropogenic systems (Courchamp et al. 2003). Alien invasions are recognized as a significant cause of species endangerment and extinction, and the rodents present on the islands are among the most damaging invasive alien species (Lowe et al. 2000). Their devastating effects on natural systems, particularly on islands, and impacts on human activities and health have been thoroughly documented around the globe (Dutton 1994; Drake and Hunt 2009; Harris 2009; Russell et al. 2017).

In the case of bats, cave-dwelling species are always of particular concern, because the availability of suitable underground roosts is limited and the concentration of bats in these roosts exposes them to additional risks. Five cave-dwelling bat species are known to occur on São Tomé, two of which have populations also on Príncipe. It is thus essential to take measures to ensure that these roosts are adequately identified and protected. The importance of each roost should be evaluated, using criteria based on the number of individuals and number of species using the site and their conservation status. High-ranking roosts should be identified, regularly monitored, and human access physically limited if necessary (Rainho et al. 2010). Frugivorous bat species are considered pests by many farmers because they consume planted fruits. In extreme damage and food-loss situations, the use of wildlife-friendly exclusion nets to protect individual trees or fruits may be licensed and supported (Tollington et al. 2019). However, this conflict should be managed with care and in partnership with farmers.

Educational outreach about the value of biodiversity is needed to provide citizens with a better understanding of the importance of their local mammal species. In the case of bats, for instance, highlighting their importance in seed dispersal and in the control of insects that are agricultural pests as well as vectors of diseases. Finally, it

is important to highlight the need to carry out more research on which to base the conservation of the endemic-rich mammalian fauna of the islands.

Challenges and Future Research

Although recent efforts have advanced our understanding of the mammal fauna and in particular the bat fauna of São Tomé and Príncipe (Rainho et al. 2010), the preceding sections clearly highlight that our knowledge is fragmented, and important gaps remain to be addressed in future research. Detailed taxonomic assessments that integrate multiple lines of evidence based on craniometric, morphological, genetic, and (for bats) acoustic data are needed to resolve the identity and taxonomic relationships of several species, specifically *M.* cf. *tricolor* in São Tomé, *Pseudoromicia* sp. in Príncipe and of the putative *Dendromus* species recently discovered in São Tomé.

At least 7 of the 19 wild mammal species occur only on one of the Gulf of Guinea islands, including 3 Endangered and 2 Data Deficient species (Appendix). The long-term conservation of this large number of single-island endemics, such as the bats *Ch. tomensis* and *M. brachycephala* or the shrews *C. fingui* and *Cr. thomensis,* constitutes a fundamental challenge. In this regard, further detailed surveys of the islands are needed, to gather reliable data to assess the ecology, distribution, threats, and current status of populations. In particular, Annobón should be targeted since it has not been surveyed for decades. Ideally, such surveys should be conducted at regular intervals to be able to monitor population trends (Meyer et al. 2010) and to trigger appropriate management interventions if needed. Such detailed surveys are also urgently needed to fill important knowledge gaps concerning basic biology and ecological requirements—information that is scant or lacking for many species (e.g., *Ch. tomensis*, *M. thomensis*, *M. newtoni*). Finally, further field surveys are needed to assess the population status of the invasive species, particularly the murid rodents, and to quantify their impact on the Gulf of Guinea island ecosystems.

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Appendix

List of the wild terrestrial mammals of the Gulf of Guinea oceanic islands. Occurrence status per island: E, endemic; R, resident; I, introduced; ?, uncertain. IUCN Red List category: NE, not evaluated; DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Order Primates					
Family **Cercopithecidae**					
Cercopithecus Linnaeus, 1758	*Cercopithecus mona* (Schreber, 1775)	I	I		NT
Order Rodentia					
Family **Muridae**					
Mus Linnaeus, 1758	*Mus musculus* Linnaeus, 1758	I	I	I	LC
Rattus Fischer, 1803	*Rattus rattus* (Linnaeus, 1758)	I	I	?	LC
	Rattus norvegicus (Berkenhout, 1769)	I	I	I	LC
Order Eulipotyphla					
Family **Soricidae**					
Crocidura Wagler, 1832	*Crocidura fingui* Ceríaco et al 2015	E			DD
	Crocidura thomensis (Bocage, 1887)		E		EN
Order Chiroptera					
Family **Pteropodidae**					
Eidolon Rafinesque, 1815	*Eidolon helvum* (Kerr, 1792)	R	R		NT
	E. helvum annobonense Juste et al., 2000			E	
Rousettus Gray, 1821	*Rousettus aegyptiacus* (É. Geoffroy, 1810)				NT
	R. aegyptiacus tomensis Juste and Ibáñez, 1993		E		
	R. aegyptiacus princeps Juste and Ibáñez, 1993	E			
Myonycteris Matschie, 1899	*Myonycteris brachycephala* (Bocage, 1889)		E		EN
Family **Hipposideridae**					
Macronycteris Gray, 1866	*Macronycteris thomensis* (Bocage, 1891)		E		LC
Hipposideros Gray, 1831	*Hipposideros ruber* (Noack, 1893)	R	R		LC
Family **Emballonuridae**					
Taphozous É. Geoffroy, 1818	*Taphozous mauritianus* É. Geoffroy, 1818	R	R	R	LC

(continued)

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Family **Molossidae**					
Chaerephon Dobson, 1874	*Chaerephon pumilus* (Cretzschmar, 1826)	R	R		LC
	Chaerephon tomensis (Juste and Ibáñez, 1993)		E		EN
Family **Vespertilionidae**					
Myotis Kaup, 1829	*Myotis cf. tricolor* (Temminck, 1832)		R		
Pseudoromicia Monadjem et al., 2020	*Pseudoromicia sp.*	E			NE
Family **Miniopteridae**					
Miniopterus Bonaparte, 1837	*Miniopterus newtonii* Bocage, 1889		E		DD
Order Carnivora					
Family **Mustelidae**					
Mustela Linnaeus, 1758	*Mustela nivalis* Linnaeus, 1766		I		LC
Family **Viverridae**					
Civettictis Pocock, 1915	*Civettictis civetta* (Schreber, 1776)	I	I		LC

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