Amphibians and reptiles of the French West Indies: Inventory, threats and conservation

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Abstract. At least five marine turtles and 49 terrestrial or freshwater amphibians and reptiles have been listed from the French West Indies since the beginning of human settlement. Among terrestrial or freshwater species, two groups may be distinguished. The first group comprises 35 native species, of which seven are currently extinct or vanished. These species are often endemic to a bank and make up the initial herpetofauna of the French West Indies. Disregarding two species impossible to rule on due to lack of data, the second group includes twelve species that were introduced. Except for marine turtles and some terrestrial species for which the decline was due to human predation, the extinctions primarily involved ground living reptiles of average size and round section body shape. Habitat degradation and mammalian predator introductions have probably contributed to the extinction of these species, in addition to a possible direct impact of man. To better understand the threats to species, we suggest studying the interactions between native herpetofauna and introduced competitors or predators, taking into account the habitat structure. This would help to give the necessary information for successful management measures for conservation or restoration. As an example, the conservation of the Petite Terre (Guadeloupe) *Iguana delicatissima* population requires identifying both the mechanisms that regulate its population and their relationships to catastrophic climatic events.

Key words: Amphibians; biological invasions; conservation; French West Indies; Guadeloupe; *Iguana delicatissima*; Petite Terre; Reptiles; threats.

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Introduction

The extensive work devoted to the amphibians and reptiles of the French West Indies during the last 100 years provides a good understanding of the distribution of the majority of the species. It allows estimation of the changes since the first human settlement, despite knowledge gaps for the Amerindian and Colonial Periods. It also allows highlighting the risks of new extinctions related to human activities.

One of the major causes of changes to the French West Indies herpetofauna is probably the introduction of alien competitor or predator species. These introductions are globally considered as the second cause of biodiversity losses, preceded only by habitat destruction and fragmentation (Diamond, 1989; Vitousek et al., 1997; Alonso et al., 2001). Insular species are particularly sensitive to introductions (Moors and Atkinson, 1984; Diamond, 1989; Lever, 1994). The commensal *Rattus*, at the world scale (Atkinson, 1985), and the mongoose *Herpestes auropunctatus*, in some areas like the French West Indies, belong to the vertebrate species that have had the strongest impact on the native fauna when introduced on islands (Lowe et al., 2000). This is why identifying mechanisms and quantifying interactions between native and introduced species are major stakes for insular ecosystem management and restoration policies.

The scope of this paper is to make an inventory of the extinct, vanished (that is, lost from the French West Indies but present elsewhere) or currently present (both native and introduced) species of the French West Indies herpetofauna. It also points out current threats to native species, and proposes steps to identify and quantify mechanisms that endanger native populations, in order to work out relevant conservation or restoration strategies.

Geographical area

The Lesser Antillean islands belong to banks, as defined by the 160 m isobath limit and by their mutual isolation since emergence. The French West Indies islands belong to five banks: Martinique, Les Saintes, Marie-Galante, Guadeloupe, and Anguilla. We split the Guadeloupe Bank into four subsets: Basse-Terre, Grande-Terre, La Désirade, and Îles de la Petite Terre (or simply Petite Terre). All these banks are wholly under French jurisdiction, except for the Anguilla Bank, of which we only consider the French part, i.e. Saint-Barthélemy and the northern part of Saint-Martin. Powell (2006) considers the other part of the latter island. Nine insular entities are thus included in this paper.

The French West Indies are administratively divided into two sets: Martinique alone; and Guadeloupe, which is a discontinuous archipelago including Les Saintes, Marie-Galante, Désirade and Guadeloupe Banks and further north some islands of the Anguilla Bank, i.e. French Saint-Martin and Saint-Barthélemy. Unless specified, in this paper the word Guadeloupe indicates the geographical and not the larger administrative entity. Information concerning biodiversity threats and protection measures were extracted from various monographs, from the synthesis prepared by the French Committee for IUCN (Gargominy, 2003), and is here updated. The legislation on protection of the species has been consulted. In addition, the status established by IUCN, according to the extinction threats under the Red List categories, is specified (IUCN, 2006), and conservation measures already carried out are described.

Herpetofauna Inventory: Methods and Definitions

Several species that are sometimes quoted from the French West Indies were not retained, either because their presence is improbable (*Gonatodes albogularis* and *Sphaerodactylus microlepis* in Martinique), or because of the lack of conclusive information. Nevertheless, the current or past presence of some species in the second category may be confirmed in future, so we give a summary of available information on some of these species.

Mainly on the basis of photographs, Breuil (2002) hypothesised the current presence in Guadeloupe of the piping frog *Eleutherodactylus* cf. *planirostris*, and the tortoise *Chelonoidis denticulata*. In the same publication, he pointed out the capture in Saint-Barthélemy of one just-introduced specimen of the colubrid snake *Elaphe guttata*. However, there is a lack of evidence concerning the naturalisation of these species in these islands. Breuil (2002) also hypothesized the presence in the past of an extinct Diploglossine lizard in Guadeloupe, on the basis of textual evidence (see also Lorvelec et al., 2000), and of an extinct or vanished colubrid of the genus *Clelia* on the basis of textual and archaeological evidence. However, the precise archaeological information for the *Clelia* sp. is absent from the text quoted (Grouard, 2001a). Breuil (2002) also indicated the past presence of an extinct *Eleutherodactylus* sp. from Saint-Barthélemy and Saint-Martin on the basis of textual evidence.

The case of the African tortoises *Kinixys homeana* and *Kinixys erosa* is of historical interest. In 1835 Duméril and Bibron included these species in the American fauna because two specimens of the first species were sent to the Paris Museum from Guadeloupe by two French naturalists, L'Herminier father and son. Analysing letters and all specimens from the L'Herminiers stored in the Paris Museum, Breuil (2002, 2003) reached the conclusion that these specimens belong to the two species and came from Africa through Guadeloupe. Presently, these species are absent from Guadeloupe and there is no evidence that feral populations lived in Guadeloupe in the past. In addition, following Fretey and Lescure (1999), we have excluded the marine turtle *Lepidochelys kempii* as absent from the sea around the Lesser Antilles. Moreover, *Anolis bimaculatus*, introduced into the Netherlands part of Saint-Martin (Powell et al., 1992) but never recorded from the French part, was also excluded.

Other species were retained although their local reproduction has not yet been confirmed. These species are the slider *Trachemys scripta*, which is presently widely distributed at least in Guadeloupe, two marine turtles, *Caretta caretta* and *Lepidochelys olivacea*, which are present in the sea around the French West Indies (Fretey, 1997; Chevalier and Lartiges, 2001), and the parthenogenetic snake, *Ramphotyphlops braminus*, which was recently introduced in Saint-Barthélemy and Saint-Martin and which is a good candidate for a prompt naturalization (Breuil, 2002; Henderson, 2004).

According to Breuil (2002), the extinct *Ameiva major* would have come from Petite Terre and not from Martinique as previously thought (Baskin and Williams, 1966). However, there is recent information of an undated museum specimen quoted from Martinique (Ineich et al., 2005). The history of this specimen deserves further investigation. Study of the numerous archaeological remains from Petite Terre and Martinique could also provide a definitive validation of Breuil's hypothesis.

Since Schwartz and Henderson (1991), several recent revisions re-established or put at species rank some taxa. We followed Powell and Henderson (2001) putting *Anolis pogus* Lazell, 1972, and *Sphaerodactylus parvus* King, 1962, at species rank. We followed Breuil (2002) re-establishing *Anolis terraealtae* Barbour, 1915, and *Alsophis sanctonum* Barbour, 1915, at species rank, each one with two subspecies. We followed Breuil (2002) and Henderson (2004) re-establishing *Typhlops guadeloupensis* Richmond, 1966, at species rank. Lastly, we followed Breuil (2002) and Miralles (2005), for the taxonomic position of the Lesser Antillean *Mabuya*. In conclusion, we have to keep in mind that the French West Indies species number may increase in the near future, by description of new *Eleutherodactylus* for Basse-Terre (e.g. Breuil, 2002; Kaiser et al., 2003) and revisions of the genera *Gymnophthalmus* and *Anolis*. Thus for *Anolis*, Roughgarden (1995: 83) elevated to species rank the taxa *chrysops*, *desiradei*, *kahouannensis*, and *caryae* described by Lazell in 1964 and generally considered as subspecies.

Inventories of terrestrial and marine species were then performed for each of the nine insular entities using mainly data from Barbour (1914), King (1962), Lazell (1964, 1972, 1973), Baskin and Williams (1966), Schwartz and Thomas (1975), MacLean et al. (1977), Schwartz et al. (1978), Schwartz and Henderson (1985, 1988, 1991), Powell et al. (1996), Censky and Kaiser (1999), Malhotra and Thorpe (1999) and the recent syntheses of Breuil (2002, 2003, 2004). The endemic species from the Lesser Antilles and from the French West Indies were quoted and the number of subspecies recorded for the French West Indies was recorded for each species (table 1).

For the purposes of this study, as for a previous one (Pascal et al., 2005), we defined a biological invasion as an event in which a species increased its distributional area during a specific period of time, whether or not because of human activities, and founded at least one self-perpetuating population in the newly invaded area. In the case of the French West Indies herpetofauna, biological invasions have concerned primarily species introduced, intentionally or not, by man. We chose island as the unit of study, and the period that began with the first Amerindian settlements, about 4000 BP (Pregill et al., 1994), and ended with present as the specific period of time. We considered as native to an island a species that was present on it before the beginning of this period, and as introduced a species that was absent before this period but now present.

Six groups of species were distinguished in order to appreciate the French West Indies herpetofauna turnover during the four last millennia (table 1). The first group comprises the marine turtles, the five other groups include terrestrial or freshwater species. The second group includes the native species extinct (vanished from all its distribution area) after the Amerindian settlement or not recorded for several decades (Honegger, 1981). The third group comprises the native species that have vanished from the French West Indies, but are not extinct. The fourth group is native present species, the fifth group is species with dubious status, and the sixth group is introduced species. Such categorization was used in a recently published book devoted to the French vertebrate fauna turnover during the Holocene (Pascal et al., 2006).

Table 1. Inventory and status of the French West Indies amphibians and reptiles.

Species	LA	FWI	ssp	MA	SA	MG	BT	GT	DE	PT	SB	FSM	IUCN	FL
Marine turtles (5)														
• Chelonians														
Cheloniidae														
Caretta caretta			–				?	?			?		EN	p
Chelonia mydas			–	(+)	+	+	+	+	(+)	+	(+)	(+)	EN	p
Eretmochelys imbricata			–	+	+	+	+	+	+	+	(+)	(+)	CR	p
Lepidochelys olivacea			–							?			EN	p
Dermochelyidae														
Dermochelys coriacea			–	+	?	(+)	+	+	?	(+)	(+)	(+)	CR	p
Other species (49)														
Native and extinct (5)														
• Lizards														
Teiidae														
Ameiva cineracea	e	e	–		+	+	+	+	?	?			EX	
Ameiva major	e	e	–	?						?			EX	
Tropiduridae														
Leiocephalus cf. *cuneus*	e		–				?	+					–	
Leiocephalus herminieri	e	e	–	+									EX	
• Snakes														
Colubridae														
Liophis cursor	e	e	–	+									CR	p
Native and vanished (2)														
• Anurans														
Leptodactylidae														
Leptodactylus fallax	e		–	+		?	?	?					CR	
• Snakes														
Boidae														
Boa constrictor			?	+		?	?	?					NE	

Table 1. Continued.

Species	LA	FWI	ssp	MA	SA	MG	BT	GT	DE	PT	SB	FSM	IUCN	FL
Native and currently present (28)														
• Anurans														
Aromobatidae														
Allobates chalcopis	e	e	–	+									VU	
Brachycephalidae														
Eleutherodactylus barlagnei	e	e	–				+						EN	p
Eleutherodactylus martinicensis	e	?	–	+	+	+	+	+	+		+	+	NT	p
Eleutherodactylus pinchoni	e	e	–				+						EN	p
• Lizards														
Gekkonidae														
Sphaerodactylus fantasticus	e		7		+	+	+	+	+	+			NE	p
Sphaerodactylus parvus	e	Ae	–								+	+	NE	p
Sphaerodactylus sputator	e		–								+	+	NE	p
Sphaerodactylus vincenti	e		6	+									NE	p
Thecadactylus rapicauda			–	+	+	?	+	+	+	+	+	+	NE	p
Gymnophtalmidae														
Gymnophthalmus pleii	e		1	+	?	?	?	?	?				NE	p
Iguanidae														
Iguana delicatissima	e		–	+	+	d	+	+	+	+	+	+	VU	p
Polychrotidae														
Anolis ferreus	e	e	–			+							NE	p
Anolis gingivinus	e	Ae	–								+	+	NE	p
Anolis marmoratus	e	e	9				+	+	+	+			NE	p
Anolis pogus	e	Ae	–								?	+	NE	p
Anolis roquet	e	e	6	+									NE	p
Anolis terraealtae	e	e	2		+								NE	p
Scincidae														
Mabuya mabouya	e		–	d?	?	d?	d?	+	+	+	d?	d?	NE	pG
Mabuya sloanii			1								+	d?	NE	p
Teiidae														
Ameiva plei	e	Ae	2								+	+	NE	p
• Snakes														
Colubridae														
Alsophis antillensis	e		1			?	+	+	?				NE	p
Alsophis rijgersmaei	e	Ae	–								+	d?	EN	p
Alsophis sanctonum	e	e	2		+								NE	p
Liophis juliae	e		2		?	d?	+	+	?				NE	p
Leptotyphlopidae														
Leptotyphlops bilineatus	e		–	+			?	?					NE	p
Typhlopidae														
Typhlops annae	e	e	–								+	?	NE	
Typhlops guadeloupensis	e	e	–		?	?	+	+	?				NE	p
Viperidae														
Bothrops lanceolatus	e	e	–	+									NE	

Table 1. Continued.

Species	LA	FWI	ssp	MA	SA	MG	BT	GT	DE	PT	SB	FSM	IUCN	FL
Dubious status (2)														
• Lizards														
Gekkonidae														
Hemidactylus mabouia			–	+	+	+	+	+	+	+	+	+	NE	
Gymnophtalmidae														
Gymnophthalmus underwoodi			–	+	?	+	+	+	+				NE	
Introduced (12)														
• Anurans														
Brachycephalidae														
Eleutherodactylus johnstonei	e		–	+	+	+	+	+	+	?	+	+	NE	p
Bufonidae														
Chaunus marinus			–	+			+	+					NE	
Hylidae														
Osteopilus septentrionalis			–								+	+	NE	
Scinax cf. *ruber*			–	+									NE	
Scinax cf. *x-signatus*			–				+	+					NE	
• Chelonians														
Emydidae														
Trachemys scripta			1	(+)		(+)	(+)	(+)					LR/nt	
Trachemys stejnegeri			1		+	+	(+)	(+)					LR/nt	p
Pelomedusidae														
Pelusios castaneus			–		?		+	+					NE	p
Testudinidae														
Chelonoidis carbonaria			–	(+)	(+)	(+)	(+)	(+)	(+)	?	+	+	NE	
• Lizards														
Gekkonidae														
Gekko gecko			1	+									NE	
Iguanidae														
Iguana iguana			–	+	+	+	+	+				+	NE	pG
• Snakes														
Typhlopidae														
Ramphotyphlops braminus			–								(+)	(+)	NE	

LA. e: Lesser Antilles endemic species.

FWI. e: French West Indies endemic species; Ae: Anguilla Bank endemic species; ?: see text.

ssp. #: Number of French West Indies sub-species; –: monotypic species or species with dubious sub-species or perhaps species complex.

Insular entities. MA: Martinique; SA: Les Saintes; MG: Marie-Galante; BT: Basse-Terre; GT: Grande-Terre; DE: La Désirade; PT: Petite Terre; SB: Saint-Barthélemy; FSM: French Saint-Martin.

IUCN. EX: Extinct; CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LR/nt: Lower Risk, Near Threatened in origin area; NE: Not Evaluated; -: sub-fossil.

FL. French legislation. p: Protected species; pG: protected species in the Guadeloupe administrative entity but not in Martinique.

Currently nesting (marine turtles). +: regular but sometimes rare; (+): casual or possibly disappeared; ?: potential or not confirmed.

Past or current presence (terrestrial or freshwater species). +: known; (+): known but reproduction not confirmed; ?: potential or not confirmed; d: locally disappeared; d?: possibly locally disappeared.

Herpetofauna Inventory and Turnover

Table 1 summarizes information on the presence of the French West Indies amphibian and reptile species since the beginnings of human settlement. This information will change with improvement of knowledge thanks to new data, particularly for extinct or vanished species. Our inventory contains five marine turtles, all having a transoceanic distribution area, and 49 terrestrial or freshwater species of which 42 are still present. Among terrestrial or freshwater amphibians and reptiles of the French West Indies, most are native species that are often endemic to one bank, and represent the initial herpetofauna. Other species were, with a high probability level, introduced by man; the status of two species, *H. mabouia* and *G. underwoodi*, is dubious.

Native herpetofauna

Thirty-five species (71.5% of the 49 terrestrial or freshwater species) are probably native of the French West Indies. All these native species are endemic of an island or sets of islands of the Lesser Antilles, except: *Boa constrictor*, which is distributed in South America, Central America and the Lesser Antilles and includes Lesser Antillean subspecies; *Thecadactylus rapicauda*, which is distributed in Northern South America, Central America and the Lesser Antilles; and *Mabuya sloanii* which is endemic to the Greater Antilles and the extreme north of the Lesser Antilles.

Seven species (20% of the 35 native species) present in the past have now disappeared from the French West Indies. Among these, five are extinct and two are vanished. *Leiocephalus* cf. *cuneus*, known from Grande-Terre fossil remains (Pregill et al., 1994), apparently still lived on small islets off Guadeloupe at the beginning of European Colonization (du Tertre, 1667-1671), and became extinct at an unspecified time. The same situation occurs for *Leiocephalus herminieri* which lived in Martinique (Breuil, 2002, 2003). The species description by Duméril and Bibron, under the name *Holotropis Herminieri*, goes back to 1837. According to Honegger (1981), *Ameiva cineracea* became extinct when Grand Îlet off Basse-Terre, its last refuge in Guadeloupe, was destroyed by the 1928 hurricane. *Ameiva major* had been extinct from Martinique (Baskin and Williams, 1966) at an unspecified time or, according to Breuil (2002), from Petite Terre during the 19th or at the beginning of the 20th century. Lastly, *Liophis cursor*, never recorded since 1962 from Rocher du Diamant (Lazell, 1967), its last refuge in Martinique, was considered as extinct by Honegger (1981). Two other species, *Leptodactylus fallax* and *Boa constrictor*, which lived in Martinique (Anonyme de Carpentras, 1618-1620), from where they vanished after 1796 (Lescure, 1979) and at an unspecified time (Breuil, 2002) respectively, persist outside the French West Indies.

Twenty-eight species (80% of the 35 native species) are still present in the French West Indies. Among them, *Eleutherodactylus martinicensis* has a controversial status. Looking at the present distribution and filling the “endemism gaps”, Censky and Kaiser (1999) considered that *Eleutherodactylus johnstonei* and *E. martinicensis* are native from Saint Lucia and Martinique respectively, and introduced everywhere else. However, Lescure (2000) proposed the Antigua and Barbuda Bank as the native place for *E. johnstonei* (see also Kaiser, 1997) and Saint Lucia, Martinique and Dominica for *E. martinicensis*. In addition, Kaiser (1992) emphasized that the differences in distribution of these species in the Lesser Antilles reflected the respective English and French influences during the Colonial Period. Whatever the theory selected, the statuses of these two species do not change for the French West Indies where only *E. martinicensis* is native. The arrival time of this species in Les Saintes, Guadeloupe and Marie-Galante Banks is unknown and its native status for these banks is dubious, but its introduction in Saint-Barthélemy (Magras, 1992) and Saint-Martin (Breuil, 2002) took place, according to these authors, at the latest during the beginning of the 1980's. Kaiser et al. (1994) described *Colostethus chalcopis*, discovered only in 1990 and recently renamed *Allobates chalcopis* (see Grant et al., 2006), as endemic of Martinique, rejecting the assumption of an introduction. Nevertheless, these authors emphasized that the occurrence of this species in Martinique constitutes a biogeographic enigma because no member of the superfamily Dendrobatoidea is native to an oceanic island. According to Hedges (1996), the Lesser Antillean populations of the gecko *Thecadactylus rapicauda* are morphologically close to the continental ones, and would have colonized the Lesser Antilles relatively recently during the Quaternary. However, genetic analysis shows that samples from the Lesser Antilles belong to a monophyletic group (Kronauer et al., 2005). This result suggests that the hypothesis of its introduction by man has to be taken cautiously, and increases the likelihood of native status for *T. rapicauda* in the Lesser Antilles.

Species of dubious status

Two species (4% of the 49 terrestrial or freshwater species) have a dubious status. Several authors considered that the synantropic gecko *Hemidactylus mabouia* was introduced in the American Continent from West Africa during the Triangular Trade (Lescure, 1983). However, Kluge (1969), suggested the hypothesis of a natural dispersal during former time based on *Hemidactylus* distribution and differentiation in the New World. According to Hedges (1996), *Gymnophthalmus underwoodi*, a parthenogenetic lizard from Northern South America and Lesser Antilles, would have colonized the Lesser Antilles relatively recently during the Quaternary. According to Kizirian and Cole (1999), this species came from a single hybridization event and the presence of *G. underwoodi* in the Lesser Antilles seems likely to be a result of dispersal of individuals from the mainland. Was it dispersed by rafts, taking advantage of parthenogenetic reproduction, or was it accidentally introduced in the French West Indies where it was recorded recently for the first time (Schwartz and Thomas, 1975)? These questions remain open.

Introduced species

Twelve species (24.5% of the 49 terrestrial or freshwater species) that are known today from the French West Indies, were introduced in our view. The introduction history of eight of these species is documented. *Eleutherodactylus johnstonei*, which can be distinguished from *Eleutherodactylus martinicensis* only by specialists, is the only one initially endemic of the Lesser Antilles (see above). Its introduction into all the French West Indies is probably recent considering that the 19th century rare descriptions of amphibians for Saint-Barthélemy and Saint-Martin have to be related to an endemic and extinct species of the Anguilla Bank (Breuil, 2002). Barbour (1914) recorded the species for the first time in Saint-Martin as *martinicensis* before Schwartz (1967) recorded it under its true name. Thereafter, it was recorded in Martinique by Lescure (1968), in Basse-Terre in 1970 by Kaiser (1997) and in Grande-Terre in 1991 by Henderson et al. (1992). It was recorded by Breuil (2002) for the first time in 1989 in Marie-Galante, 1999 in Les Saintes, and 2001 in La Désirade, and its introduction in Saint-Barthélemy goes back to 1995 or 1996 according to this author. The initial distribution area of the seven other introduced species is outside of the Lesser Antilles. *Chaunus marinus*, until recently named *Bufo marinus* (see Frost et al., 2006), was intentionally introduced in Martinique before 1844 (Waite, 1901), then in Basse-Terre and Grande-Terre. *Osteopilus septentrionalis* was recorded for the first time in the Netherlands part of Saint-Martin in 1987 (Powell et al., 1992) and in the French part of Saint-Martin and in Saint-Barthélemy in 1996 (Breuil, 2002). *Scinax* cf. *ruber* and *Scinax* cf. *x-signatus* were recorded respectively for the first time in 1997 in Martinique and 2003 in Basse-Terre and Grande-Terre (Breuil, 2004). The introduction is also documented for a slider, *Trachemys scripta*, recorded for the first time in Basse-Terre and Grande-Terre by Schwartz and Thomas (1975), and also released in Marie-Galante and Martinique according to Breuil (2002). Finally, *Gekko gecko* was introduced intentionally at the beginning of the 1970's in Martinique from Indo-China (Henderson et al., 1993) and *Ramphotyphlops braminus* was introduced unintentionally during the 1990's in Saint-Barthélemy and Saint-Martin (Breuil, 2002).

In our view, the four following species have to be considered as introduced, even if the modalities of these introductions are not yet clearly documented. According to Lescure (1983), an introduction from West Africa during the Triangular Trade is the most probable hypothesis to explain the presence of the terrapin *Pelusios castaneus* (see also Bour, 1983). According to Breuil (2002), an introduction from Puerto Rico (by Amerindians or more recently), is the most probable assumption to explain the presence of the slider *Trachemys stejnegeri* (see also Seidel, 1988). However Breuil (2004) favoured a later introduction of these two turtles by L'Herminier father and son during the first half of the 19th century. In the same way, according to Lescure (1983), the tortoise *Chelonoidis carbonaria* was probably introduced at various times. Thereafter, Censky (1988) and Censky and Kaiser (1999) considered four modalities to explain its presence in the Lesser Antilles: natural dispersion, introduction by Amerindians, introduction by the European colonists, and recent introduction. In the French West Indies, this species is often kept in captivity but seems to currently constitute feral populations only in Saint-Barthélemy (where it was introduced at the end of the Second World War; Breuil, 2004) and in Île Tintamarre off Saint-Martin. If Lazell (1973) recorded *Iguana iguana* as native in all the Lesser Antilles, Lescure (1983) assumed a combination of spontaneous dispersal and introduction by Amerindians as food resource. Breuil (2002) emphasized the numerous local introductions of this species during the 20th century (e.g. in the 1960's in Martinique and in the 1990's in Marie-Galante and Saint-Martin) as well as hybridization and competition between *I. iguana* and *Iguana delicatissima*, to refute the assumption of Lazell.

Processes of Extinction and Threats

In addition to the disappearance or extinction of at least seven native species, many are becoming rare or are at the fringe of extinction (table 1). According to the IUCN assessments (IUCN, 2006), the five marine turtles are Critically Endangered or Endangered. Among the terrestrial or freshwater species, only the two endemic piping frogs of Basse-Terre (*Eleutherodactylus barlagnei* and *Eleutherodactylus pinchoni*), and *Alsophis rijgersmaei*, the endemic racer of Anguilla Bank, are Endangered (Hedges et al., 2004a,b; Day, 1996). If the last species is currently very rare in Saint-Martin (maybe vanished), it seems present on the whole island of Saint-Barthélemy even if rare (Breuil, 2002). In addition, *Allobates chalcopis*, endemic of Martinique, and *Iguana delicatissima*, are Vulnerable (Hedges et al., 2004c; Breuil and Day, 1996). This last species, endemic of the northern part of the Lesser Antilles (islands located between Martinique and Anguilla), vanished from several islands including Marie-Galante. Except for populations from Dominica, La Désirade and Petite Terre, this species is currently very rare because of habitat destruction and fragmentation, hunting, human persecution, competition with introduced ungulates, predation by alien carnivores, hybridization and competition with *I. iguana* (e.g. Breuil and Sastre, 1993; Breuil and Thiébot, 1993; Day and Thorpe, 1996; Day et al., 1999; Breuil, 2002; Pasachnik et al., 2006).

According to Breuil (2002), the status of other species needs to be evaluated. *Anolis pogus*, endemic to Anguilla Bank, still present in Saint-Martin, may have disappeared from Saint-Barthélemy. The skink *Mabuya mabouya* was observed only twice recently, in Petite Terre (Lorvelec et al., 2000) and in La Désirade (Breuil, 2002). *Mabuya sloanii,* probably still abundant in Saint-Barthélemy, may have disappeared from Saint-Martin. *Typhlops annae*, endemic to Saint-Barthélemy, was recently described by Breuil (1999a), and is still not well known. Racers such as *Alsophis antillensis* and *Liophis juliae* are now very rare in Basse-Terre and Grande-Terre, and may not be present any more in Marie-Galante. *Alsophis sanctonum*, endemic of Les Saintes, is still common in Terre-de-Bas but rare in Terre-de-Haut.

Lastly *Bothrops lanceolatus*, endemic to Martinique, is endangered according to Breuil (2004).

Threats

What are the threats causing extinction or decline of the French West Indies species? Marine turtles were hunted by Amerindians, but their drastic decline has to be related to the over-fishing by Europeans that began during the 16th century (Breton, 1665; du Tertre, 1667-1671). Nowadays, in spite of their protection since the 1990s, threats mainly come from accidental mortality by fishing nets (including the bottom trammel), poaching on beaches (of eggs and females), destruction of feeding and egg-laying habitats, and hunting in some Antillean islands where these species are poorly protected (Chevalier, 2003, and personal observations). Moreover, substantial nest predation by mongooses (Lorvelec et al., 2004a) or dogs is reported from several beaches.

Terrestrial or freshwater species are subjected to natural or human threats. Natural threats such as hurricanes or fires increase the extinction probability of species that survive as relict populations in small islands. During the Amerindian Period, man hunted *Ameiva* sp., *Iguana* sp. and *Anolis* sp. (Pregill et al., 1994; Grouard, 2001a,b, 2004), and, maybe, *Leptodactylus fallax*, *Boa constrictor* and other species. The predation continued in the following centuries for species such as snakes or iguanas, but *Iguana iguana* poaching in Saint-Martin (Breuil, 2002) is currently the only significant human direct impact. Indirect human threats are the most important at present. They are the consequences of the socio-economic development and alien species introductions. Martinique and Guadeloupe islands have a dense human population (348 and 260 inhabitants per km^2 respectively in 2004), some parts of the territory being more urbanised than others. The increasing urbanisation, of roads (e.g cars running over gravid *Iguana delicatissima* in La Désirade), and of agricultural and tourist activities, induces destruction, fragmentation and pollution of natural habitats.

Two situations begin to be documented concerning the impact of introduced amphibians and reptiles as competitors of the native ones in the French West Indies. The first deals with the substitution of native *Eleutherodactylus* species by introduced ones. In Martinique, *E. johnstonei* has replaced *E. martinicensis* in terrestrial habitats, but not in arboreal ones (Breuil, 1997a). In Basse-Terre, Kaiser (1997) suspected *E. johnstonei* to be a competitor of the two endemic piping frogs of this island and, according to Breuil (2002), at least *E. pinchoni* would be restricted to the most humid forest habitat of this island. Besides, hybridization and competition between *I. iguana* and *I. delicatissima* would be responsible for the near disappearance of *I. delicatissima* from Les Saintes during the second part of the 20th century (e.g. Breuil and Sastre, 1993).

Mammal species have the most evident impact when introduced in islands. The native mammal fauna of the Lesser Antilles, restricted (apart from bats and marine species) to Sigmodontine rodents that are now extinct, has probably been completely replaced since human settlement (Morgan and Woods, 1986; Pregill et al., 1994; Lorvelec et al., 2001; Breuil, 2003), as in large Mediterranean islands (Vigne, 1999). In these two cases, the turnover of mammal species has been more important than that of amphibians and reptiles. Amerindians introduced dogs and some neotropical species. Among the latter, an agouti *Dasyprocta leporina*, a much appreciated game animal, was present at the beginning of the 17th century in the French West Indies (du Tertre, 1667-1671), and an opossum *Didelphis marsupialis* was introduced in Martinique at an undetermined period. In addition to feral populations of domestic species such as cat, pig, goat, sheep and rabbit (du Tertre, 1667-1671; Pinchon, 1967), six other mammal species were introduced by Europeans (Lorvelec et al., 2001). Three of them are commensal Murine rodents: the ship rat, *Rattus rattus*, and the house mouse, *Mus musculus*, introduced a long time ago (du Tertre, 1667-1671), and the Norway rat, *Rattus norvegicus*, which would have been introduced at the end of the 18th century (Pinchon, 1967). The fourth species is the small Indian mongoose, *Herpestes auropunctatus*, introduced in 1870 in Trinidad (Husson, 1960), in 1872 in Jamaica (Espeut, 1882), then in 1888 in Guadeloupe (Grande-Terre and Basse-Terre), and between 1890 and 1891 in Martinique (Pinchon, 1967). Introduced very early in Saint-Martin, it is not present in Les Saintes, Petite Terre, Saint-Barthélemy and La Désirade. The fifth species was previously considered as endemic to Guadeloupe, but is now identified as the raccoon, *Procyon lotor* (e.g. Pons et al., 1999). Its absence from the archaeological Amerindian sites (Pregill et al., 1994; Grouard, 2001a,b) supports the hypothesis of an introduction that took place after the arrival of Europeans, but at an unknown date. In addition to Basse-Terre, Grande-Terre and Marie-Galante, the raccoon was present in Martinique since the middle of the 20th century (Bon Saint Côme and Tanasi, 1994), and has been recently introduced in La Désirade and Saint-Martin (Lorvelec et al., 2001). The sixth species is a squirrel belonging to the Indian subcontinent genus *Funambulus*, of which one pair, bought in a pet shop in Orlando, Florida, was introduced in 1968 in Guadeloupe (Lorvelec et al., unpublished data).

In the French West Indies, if man is the first and major agent of vegetation destruction, goats and sometimes sheep prevented regeneration (Questel, 1941) on different islands including Les Saintes (Terre-de-Haut). In Anegada, in the Greater Antilles, Mitchell (1999a,b) observed the senescence of the iguana *Cyclura pinguis* population (currently, this species has nearly disappeared everywhere but on this island), due to the degradation of the habitats by ungulates. This senescence was characterised by shift in diet, population density and body weight decrease, and unbalanced sex ratio.

The impact of introduced mammal predators in the Antilles is poorly documented. Mongoose, cat and rat impacts have usually been reported without quantitative data. Mongooses were introduced to control rats in sugar cane plantations and venomous snakes such as *Bothrops lanceolatus* in Martinique (Pinchon, 1967). It was quickly shown that this alien species has a great impact on other animal groups in Jamaica: terrestrial crabs, insects, amphibians, snakes, lizards, ground-nesting birds, mammals and domestic animals (Espeut, 1882; Allen, 1911). According to Barbour (1930), the mongoose *H. auropunctatus* may have been responsible for major changes in the fauna distribution in the Antilles, leading to extinction of ground-nesting birds and reptiles. According to this author, *Bothrops caribbaeus* would have become rare in Saint Lucia and *B. lanceolatus* very rare in Martinique. Among other studies, Seaman (1952) and Seaman and Randall (1962) reported its impact on reptile (*Iguana*, *Ameiva*, *Alsophis*, marine turtle eggs) and bird populations in the US Virgin Islands, Westermann (1953) reported its impact on *L. fallax* in the Lesser Antilles, and Pimentel (1955) draw similar conclusions on arthropods, amphibians, reptiles and mammals in Puerto Rico. The extinction of *Alsophis ater* in Jamaica (Powell and Henderson, 1996), of *Alsophis sanctaecrucis* in Saint Croix, of *Liophis cursor* in Martinique (Lazell, 1967) and of *Liophis ornatus* in Saint Lucia were supposed to be due mostly to mongoose predation by Honegger (1981). In 1966, Baskin and Williams described *Ameiva vanzoi*, today *Cnemidophorus vanzoi*, a species whose distribution is restricted to the Maria Islands off Saint Lucia, and made the hypothesis that its absence on the main island might be due to mongoose introduction. Besides, these authors underlined that the relation between *Ameiva* disappearance (*C. vanzoi* included), and the presence of the mongoose is unclear, because cohabitation occurred in some islands such as Saint-Martin, Saint Christopher and Grenada. Thus *Ameiva plei* could survive in Saint-Martin disturbed habitats, because these would be less used by mongooses. According to Henderson (1992), most of the extinction or disappearance in amphibians and reptiles in the Lesser Antilles would be a consequence of mongoose, dog and cat introductions, *Ameiva*, *Alsophis* and *Liophis* being the most susceptible genera. Breuil (1997b) reported cat faeces containing remains of juvenile *I. delicatissima* and *Anolis roquet*, in Îlet Chancel off Martinique. Concerning threats on iguanas in general, cats are identified as the main cause of *Brachylophus* population declines in Fiji (Gibbons, 1984), and cats and dogs drove to near disappearance the 5,500 *Cyclura carinata carinata* population of Pine Cay Island (390 ha) in the Caicos Islands in only three years (Iverson, 1978). According to Henderson (1992, 2004), the mongoose impact would be increased by high human population density, small island area and low physiographic complexity. Besides, the same author indicates that habitat destructions are more likely to have a negative effect on amphibian and reptile populations in the Greater Antilles than in the Lesser Antilles. This would be due to the ability of some generalist species to adapt to disturbed habitats in the Lesser Antilles (see also Henderson and Powell, 2001).

In the French West Indies, except for marine turtles (and, maybe, some terrestrial species such as *L. fallax*, *B. constrictor* and *B. lanceolatus*) for which the decline can be mainly related to human predation, extinctions or extinction threats primarily involved *I. delicatissima* (for several reasons) and ground living reptiles of average size and round section body shape (*Leiocephalus*, *Ameiva*, *Mabuya*, *Alsophis*, *Liophis*). In the case of these latest species, without forgetting the possible direct impact of man, our hypothesis is that these morphological characteristics indicate that these species have been more sensitive than others to the introduction of mammal predators.

Protection Status and Conservation Management

Since the beginning of the 1990s, all the marine turtle species are protected under the French legislation, and some terrestrial or fresh water species of the herpetofauna are protected since 1989 (table 1), although this does not take recent taxonomic revisions into account. Among native species, *Allobates chalcopis* and *Typhlops annae*, discovered after the publication of the 1989 texts, and *Bothrops lanceolatus*, have no protection status. *Mabuya mabouya* is protected in Guadeloupe but not in Martinique where it is regarded as vanished. The species with dubious status, *Hemidactylus mabouia* and *Gymnophthalmus underwoodi*, are not protected. *Eleutherodactylus martinicensis* is also protected although its native status outside of Martinique is dubious. Lastly, some probably introduced species are protected: *Eleutherodactylus johnstonei*, *Pelusios castaneus*, *Trachemys stejnegeri* and *Iguana iguana* (in Guadeloupe but not in Martinique where it was introduced recently). Legislation should be revised soon and this should lead to a status change for some species. For the species introduced, or supposed introduced, some cases will be complex. Indeed, if an absence of protected status seems logical for recently introduced species, the loss of protected status for some past introduced species, if it is decided, will have to be accompanied by precautions. It requires, as a preliminary, being able to evaluate the impact that this measure could have on similar native species distinguishable only by specialists (*Eleutherodactylus*, *Iguana*). It also requires being able to evaluate the functional role taken by the past introduced species into the current ecosystems which are very different from the originals; about half of the 3200 species inventoried in the Guadeloupe and Martinique Flora have been introduced during the last four centuries (Fournet, 2002).

Marine turtle species are on the CITES Annex I. France ratified this convention, so their international trade is forbidden in the French West Indies. *Iguana* sp. and *Chelonoidis carbonaria* are on the CITES Annex II, thus their trade is authorised under certain conditions.

What about protected areas that allow biodiversity conservation? The central area of the Guadeloupe National Park represents 20% of Basse-Terre. Nature Reserves (NR), that have been created between 1976 and 1998, include two in Martinique (Îlets de Sainte-Anne NR and Presqu'île de la Caravelle NR), both terrestrial reserves, and four in Guadeloupe, three being both marine and terrestrial (Grand cul-de-sac marin NR, Îlets de la Petite Terre NR and Saint-Martin NR) and one marine reserve (Saint-Barthélemy NR). Other areas have a weaker protection status, the largest being the peripheral area of the National Park in Guadeloupe, and the Regional Natural Park in Martinique. In Guadeloupe, a Man and Biosphere Reserve was created in 1992, its area including the National Park and the Grand cul-de-Sac Marin NR. Besides, egg-laying areas of *Iguana delicatissima* in Îlet Chancel off Martinique are specially protected, with an increase of their size, following the recommendations of Breuil (1997b).

Management and habitat restoration

In addition to these legal protections, threatened species require urgent and targetted management, and their habitats need to be restored. In 1998, a strategy on marine turtle conservation and a network of voluntary helpers were initiated in Guadeloupe administrative entity (Pavis et al., 2004). A similar network was reactivated in Martinique in 2003. The results obtained on habitats and threats led to the build up of a restoration programme of the French West Indies marine turtle populations (Chevalier, 2003).

Two programs on predator eradication showed a posteriori the negative impact of predators on native species. This was observed following the successful eradication of introduced mammal species in nature reserves of the French West Indies. The first one was carried out in 2001 on *Herpestes auropunctatus* in the 115 ha Îlet Fajou off Guadeloupe (Lorvelec et al., 2004a). The second one occurred in 2002 and concerned *Rattus rattus* in the 5.7 ha Îlets de Sainte-Anne off Martinique (Pascal et al., 2004). After the eradications, terrestrial crab and bird populations increased, and in the case of Îlet Fajou, the systematic destruction of the marine turtle *Eretmochelys imbricata* eggs was stopped.

Other eradication attempts were carried out in the Antilles. In the 8.3 ha Great Bird Island off Antigua, *R. rattus* eradication led in three years to a 100% increase of the *Alsophis antiguae* population (Varnham et al., 1998). This species had previously disappeared from Antigua (Henderson et al., 1996). In the 14.9 ha White Cay Island in the Bahamas, the eradication of *Procyon lotor* in 1997, and of *R. rattus* in 1998, were carried out in order to preserve the *Cyclura rileyi cristata* population (Day et al., 1998), a sub-species endemic to this island (Hayes, 1999). In the 5.7 ha Sandy Cay Island in the British Virgin Islands, the eradication of *R. rattus* was successfully performed in 2002 (K. Varnham, pers. comm., October 2003). In the 111 ha Long Cay Island in Caicos Banc, the eradication of cats was carried out in 1999 in the context of *Cyclura carinata* translocation (Mitchell et al., 2002). Lastly, in the 15 ha Monito Island between Hispanolia and Puerto Rico, the eradication of *R. rattus* was conducted in 1998 (García et al., 2002) to preserve the gecko *Sphaerodactylus micropithecus*, endemic of this island (Schwartz and Henderson, 1991).

Far from the Antilles, Towns et al. (2001) showed that seven geckos and ten skinks from New Zealand increased their population levels, following the eradication of rats. These authors predicted that these operations may have benefits on 26 rare and micro insular species. Pacific Rats (*Rattus exulans*) in 1986, then rabbits in 1987, were eradicated from Korapuki in the Mercury Islands, with the view to reintroduce skinks (Towns and Ferreira, 2001). According to Towns et al. (2001), the latter operation led also to a large increase of the skink *Oligosoma smithi* population, with variations according to habitats, size and sex, indicating selection effects of rats. The quality of refuges may be informative on the rat impact, large rocks (>25 cm length) allowing the skink survival. This hypothesis was confirmed in Mercury and Marotene Islands for another skink species, *Oligosoma suteri*, which may not coexist with rats if bouldery beaches are not available as refuges (Towns et al., 2003).

Introduced amphibian and reptile species may also have a great impact on native species. Henderson and Powell (1999) underlined that *Eleutherodactylus johnstonei* or *Anolis* introductions led to changes in other species' distributions. However, the processes involved seem complex. For instance, according to Cole et al. (2005), when the gecko *Hemidactylus frenatus* was introduced in islets off Mauritius (Mascarene Islands), the endemic gecko populations decreased drastically (*Nactus coindemirensis*, *Nactus durrelli* and *Nactus serpensinsula*), due to a competition for refuges. One can also wonder which was the role of *H. frenatus* in the extinction of *Nactus* sp. populations of Mascarene main islands (Arnold, 2000). In the Bahamas, Schoener et al. (2001) showed that after the 1999 hurricane Floyd, the predatory *Leiocephalus carinatus* was introduced in the 200 m^2 Great Abaco Islets, increasing the probability for *Anolis sagrei* to become extinct. This was due to a reduction in the amounts of prey, but also to a modification of its life history traits.

As a conclusion, we suggest modelling the interactions between native amphibians or reptiles, and introduced competitors or predators, taking into account the habitat structure (absence of refuges for some life history stages for sensitive species), following the approach used in New Zealand. Such studies on mechanisms would provide better understanding of the nature and importance of the threats allowing the best management measures for conservation or restoration.

Case Study: The Petite Terre *Iguana delicatissima* Population

Ecology, history and herpetofauna of Petite Terre

The Petite Terre Islands (148.6 ha) are located at 16°11′N and 61°07′W, 12 km south off La Désirade and 7.5 km south-east of Grande-Terre. They comprise two islands; Terre de Bas (117.1 ha, 8 ha of which is salt lagoons, 2.5 × 0.6 km, height < 8 m); and Terre de Haut windward (31.5 ha, 1.1 × 0.3 km, height < 8 m). A shallow channel, approximately 150 m broad at its narrow part, separates them (fig. 1). In the past these islands were subject to significant human impacts: deforestation, fishing and hunting, fields surrounded by dry-stone walls, construction of several sheds, and livestock production. Uninhabited since 1972, at present the channel and its surrounded beaches are subject to tourist activity. Since September 1998, Petite Terre is a terrestrial and marine nature reserve, in particular to protect its Lesser Antillean iguana, *Iguana delicatissima* (fig. 2a), population.

Petite Terre has great ecological interest due to the presence of a large population of *I. delicatissima*, and other significant species. The Gaïac, *Guaiacum officinale*, very rare in the French West Indies except in Saint-Barthélemy (Fournet, 2002), is

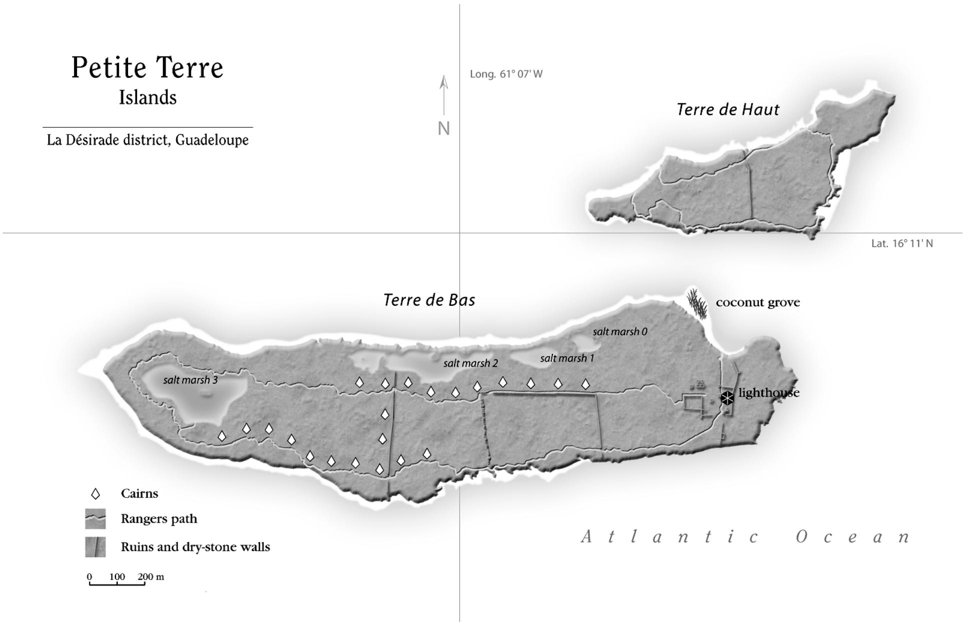

Figure 1. Petite Terre, Guadeloupe. The cairns delimit the line transects used for the adult *Iguana delicatissima* censuses in the Terre de Bas arborescent bush between 1995 and 2004.

one of the Terre de Bas dry forest tree species. Among invertebrates, the terrestrial crab *Gecarcinus ruricola*, very rare elsewhere in Guadeloupe, has to be mentioned. Birds such as *Sterna antillarum* and *Mimus gilvus* breed, and the four Petite Terre salt lagoons act as one of the two best resting areas in Guadeloupe for about twenty shorebird migratory species (Barré et al., 1997). Petite Terre is also a regular nesting site for few females of the marine turtles *Chelonia mydas* and *Eretmochelys imbricata* (Lorvelec et al., 2000), and a former resident reported nesting of two other marine turtles: *Dermochelys coriacea* very rarely, and possibly *Lepidochelys olivacea* (Lorvelec et al., 2004c). *D. coriacea* was then reported to lay eggs in 2004 (Saint-Auret and Dulormne, 2005), but the nesting of *L. olivacea* is not yet confirmed (this species is not known to breed in the Lesser Antilles). Six terrestrial reptile species have been reported (table 1). In addition to *I. delicatissima*, three of them are rare or with a restricted distribution: *Anolis marmoratus chrysops* (fig. 2b), a sub-species endemic to Petite Terre; *Sphaerodactylus fantasticus karukera*, a sub-species reported only in Terre de Bas and in part of Grande-Terre; and *Mabuya mabouya* which was recently observed only once in Terre de Bas (Lorvelec et al., 2000).

Although Lazell (1973) reported the absence of *I. delicatissima* in Petite Terre, Lorvelec et al. (2004b) collected credible accounts from former residents, arguing for its presence for a long time. The accounts lead to the conclusion that only the smallest island Terre de Haut had a visible iguana population from the 1920s (or before) to between 1945 and 1960. During this period, iguanas were absent or very

(a)

(b)

Figure 2. Two reptiles from Petite Terre, Guadeloupe which are rare or have restricted distribution: (a) *Iguana delicatissima*; (b) *Anolis marmoratus chrysops*, a subspecies endemic to Petite Terre. (Colour originals – see www.ahailey.f9.co.uk/appliedherpetology/cariherp.htm)

rare from Terre de Bas, from where they have been eliminated by man, because of their negative impact on agriculture. About 50 years ago, the present Terre de Bas iguana population built up, starting from some individuals coming from one or the other of the two islands, a corollary of the decline of agriculture. Besides, the strong 1928 hurricane impact on the Petite Terre herpetofauna is unknown, the sea elevation during this hurricane having caused the disappearance of some islets off Basse-Terre. The status of the Petite Terre iguana population before the 20th century is unknown. It was not mentioned by Breton (1665) and du Tertre (1667-1671) in the 17th century, but this absence of records cannot be conclusive. The Petite Terre resources were exploited over a long time, first by Amerindians, then by European colonists. The relations between these human populations and iguanas are unknown, but the study of the Petite Terre archaeological sites may bring answers.

Iguana survey methods

We review data from several studies on the dynamics of this iguana population that began in 1995 (Barré et al., 1997; Cabanis, 1998; Lorvelec et al., 2000, 2004b,c), and add unpublished results from 2003 and 2004. The iguana density in the Terre de Bas arborescent bush (27.2 ha) that bears the highest density, was estimated yearly between 1995 and 2004, except 1997, following the assumption that density variations would be more easily estimated in this habitat. Sixteen censuses of live and dead adults and sub-adults were carried out along a 2100 m line transect marked out every 100 m with cairns (fig. 1), following a standard protocol (Barré et al., 1997). The distance between each sighted iguana and the line transect was estimated and each sighting was assigned to one of four virtual bands distributed on both sides of the line transect (0-2 m, 2-5 m, 5-10 m, >10 m).

An abundance index was computed; the number of contacts inside the inner band (0-2 m), converted to 1 ha. The method used for density calculation, initially devised to estimate bird densities (Bibby et al., 1992), and later recommended for lizard populations (Hayes and Carter, 1999; Harlow and Biciloa, 2001), was adapted to the Petite Terre iguana population (Barré et al., 1997). This method is based on the determination of the model that describes the detection probability decline when the sighting distance increases. For all the Petite Terre habitats, this model was a negative exponential one. Therefore, the density follows the relation:

$$D = \frac{-5N \log_e(\frac{N-N_1}{N})}{LW},$$

where N = total iguanas; N_1 = number within W; W = centre to inner band (m); L = transect length (km); D = density iguanas per ha.

In 1995 and 1996, in addition to the Terre de Bas arborescent bush, all the phytoecological habitats (Rousteau, 1995) of the two islands were sampled. The ratios of density and iguana number between Petite Terre and the Terre de Bas arborescent bush were computed. The annual density and the size of the total population were estimated on the basis of these ratios.

The Petite Terre iguana population

Figure 3 represents the changes in the abundance index in the Terre de Bas arborescent bush between 1995 and 2004. The annual mean densities and numbers of adult iguanas are compiled in table 2, for the Terre de Bas arborescent bush and for both islands respectively. In 1995, the total population was estimated as about 12,300 individuals, of which most (more than 10,500) were in Terre de Bas and more than 1,500 in Terre de Haut (Barré et al., 1997). We use the 1995 population as a reference, because no major climatic event had occurred since the 1989 hurricane

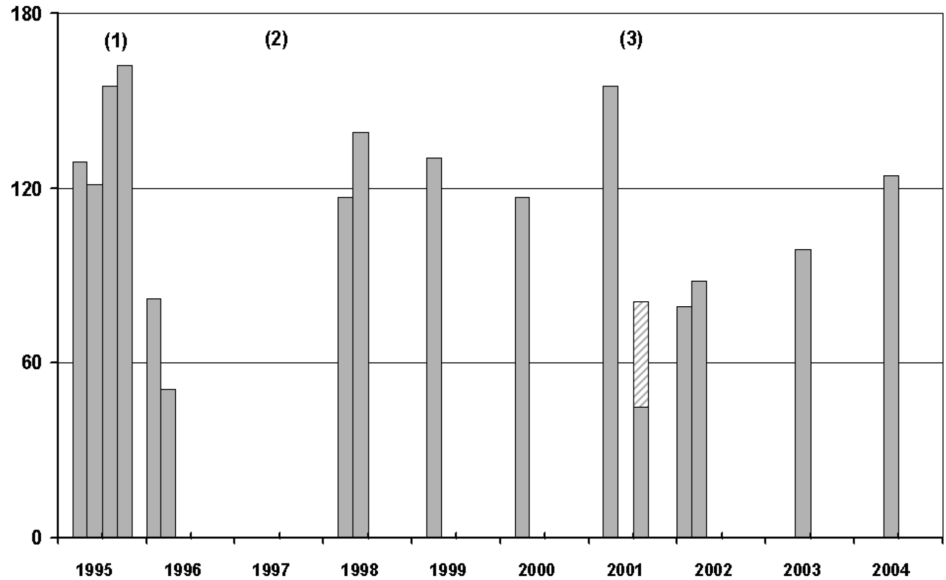

Figure 3. Adult *Iguana delicatissima* dynamics in the Terre de Bas arborescent bush between 1995 and 2004 (Petite Terre, Guadeloupe). Data are the number of contacts inside the census inner band (0-2 m), converted to 1 ha. Grey: alive; hatched: dead. 1995: April 16, May 13, June 24, September 23; 1996: January 13, March 23; 1998: May 17; May 24; 1999: April 24; 2000: April 15; 2001: April 10, August 27; 2002: February 10, March 24; 2003: May 21; 2004: June 5; (1): September 1995 hurricanes; (2): 1997 lack of data; (3): 2001 drought.

Table 2. Annual estimates of the *Iguana delicatissima* adult density and population size between 1995 and 2004 (Petite Terre, Guadeloupe).

Year	D TBAB	N TBAB	D PT	N PT
1995	184	5,014	88	12,283
1996	70	1,920	34	4,769
1997	–	–	–	–
1998	143	3,891	68	9,532
1999	152	4,135	73	10,130
2000	142	3,859	68	9,454
2001 April	174	4,745	83	11,624
2001 August, alive	49	1,335	23	3,270
2001 August, dead	55	1,496	26	3,665
2002	91	2,489	44	6,097
2003	101	2,755	48	6,749
2004	148	4,038	71	9,892

D: Density (ha^{-1}); N: population size; TBAB: Terre de Bas arborescent bush; PT: Petite Terre.

Hugo, five and a half years before. We observed a decline of 60% in the population in 1996. The two September 1995 hurricanes played a major role in this decline, though direct impact was not observed just after these climatic events, during the census carried out in September 1995 (Barré et al., 1997). As early as 1998, the population level increased and nearly reached the reference level after three years (Lorvelec et al., 2000). A drastic decline was again observed in August 2001, with high mortality occurring between April and August. As the cadavers were quickly eliminated by the terrestrial hermit crab *Coenobita clipeatus*, the 3,500 dead iguanas counted in August 2001 underestimate the total mortality, which probably reached 8,000 adults corresponding to 70% of the population (Lorvelec et al., 2004b). This estimate is double that of Breuil (2001, 2002). The mortality was linked to the extreme drought which occurred in 2001, which probably led to a water and food deficit for the iguanas.

The Petite Terre *Iguana delicatissima* population is one of the most important in the world, with those of La Désirade and Dominica. In 1993, three and a half years after hurricane Hugo, the number of adults was estimated as ranging from 4,000 to 6,000 (Breuil and Thiébot, 1993; Breuil, 1994). The counting methods used in these studies were not reported precisely, and do not allow comparison with our results. At this period, the population was considered to represent a quarter or a third of the world stock (Breuil, 1994). Our results suggest that the Petite Terre share is even more important, and represents the *I. delicatissima* population with the highest density in the world.

Conclusions and recommendations

The Petite Terre vertebrate biomass is dominated by a large vegetarian reptile, a currently rare situation. Similar situations are found only on: Aldabra island (Seychelles) dominated by the tortoise *Dipsochelys dussumieri*; Galapagos (Ecuador) dominated by the tortoise *Chelonoidis nigra* and two terrestrial iguanas (*Conolophus pallidus* and *Conolophus subcristatus*); the 70 ha uninhabited Yadua Taba island (Fiji) with the last abundant *Brachylophus vitiensis* population of 6,000 adults (Harlow and Biciloa, 2001); and some Antillean islands with *Cyclura* species, such as certain Turks and Caicos islands where the *C. carinata carinata* density can exceed 30 ha^{-1} (Iverson, 1979).

The large size of the healthy Petite Terre *Iguana delicatissima* population distributed on two islands preserved this species from the main threats. The strong protection status of nature reserve gives to these islands a major role for the conservation and the study of this threatened and protected species. Nevertheless, despite its very high density, this population is perhaps more vulnerable than those of Dominica and La Désirade because of drastic demographic fluctuations related to major hurricanes, intense droughts or possible fires. Nevertheless, in spite of the relatively recent establishment of the species in Terre de Bas and the major impact of climatic events detected in the past, the prompt recovery of the population after crashes suggests that *I. delicatissima* is a species adapted to strong climatic variations. Genetic studies would be welcome to determine the possible gene-flux and its direction between the two islands and, if extended to other populations, to document the colonization history.

Will the demography of this population reach equilibrium in the absence of major climatic disturbances? Answering this question implies exploring the qualitative and quantitative relationships between this species and others hosted by the insular ecosystem to estimate the role played by reproduction, food resources, predation, and invasive species. Such researches will be a major contribution to build up a well-founded management strategy (Lorvelec et al., 2004b,c).

The number of nesting areas increased in Terre de Bas with the opening of a management path. This event may induce a decrease of the female density in areas that were utilised in the past. We ignore the impact of this event on the total reproductive success. The female density reduction on nesting areas will decrease the risk of egg loss by excavation, but will also decrease the number of collapsed burrows. The latter effect will tend to increase hermit crab predation because open burrows are easier to enter than collapsed ones (Lorvelec et al., 2000). Lastly, does tourist activity have an unfavourable impact on the use of the nesting areas located behind the channel beaches?

Are the local food resources sufficient to allow long term survival of a high iguana density? Rousteau (1995) described the extreme slowness of the Petite Terre vegetation dynamics and Barré et al. (1997) showed the qualitative impact of the iguana on various flora species. As *Guaiacum officinale* leaves, flowers and fruits are eaten by iguanas, studies must be undertaken to evaluate the impact on this significant tree species (Barré et al., 1997; Monthieux, 2002). Lorvelec et al. (2004c) and Rousteau and Monthieux (2005) synthesized knowledge on the subject. *G. officinale* is missing in Terre de Haut and only about thirty trees are present in Terre de Bas, the youngest being 50 years old. The in situ seed germination capacity seems sufficient at the beginning of the reproductive season, but there is no local regeneration. The test of various hypotheses to explain this lack of regeneration is in progress: seedling destruction (by rats, iguanas, or hermit crabs), herbivore or pathogen attack, disseminator absence, inbreeding depression, edaphic or climatic restraints (Rousteau and Monthieux, 2005).

Although iguana eggs are subject to unquantified hermit crab predation, juveniles and adults are free of native predators, and *Rattus rattus* impact on eggs and young juveniles is unknown. Rats have been regularly recorded on the two islands since 1998. However, according to Terre de Bas former residents, rats and mice were present in the past (Lorvelec et al, 2004c) and the lack of rat sighting over several years in Terre de Bas has to be related to occasional chemical control (Lorvelec et al, 2000). A 2001 necropsy of a feral cat, present in Terre de Bas since at least 1995, revealed fresh remains of an *I. delicatissima* adult female or large juvenile (Lorvelec et al., 2004b). A major management measure is to prevent introduction of any alien predator and to consider regulation or eradication of the species already introduced.

Another threat is *I. iguana*, which has a large neotropical distribution. Absent from Petite Terre, it is present in other islands of the Lesser Antilles and competition and hybridization are known in sympatric areas (review in Breuil, 2002). Consequently, preventing the arrival of *I. iguana*, as recorded in Anguilla, Antigua and Barbuda after the 1995 hurricanes (Censky et al., 1998; Breuil, 1999b), constitutes a management goal for the continuity of the Petite Terre *I. delicatissima* population.

Identifying the mechanisms regulating the Petite Terre *I. delicatissima* population and their possible relationships with catastrophic climatic events, requires a thorough knowledge of the biology of this population. This will help managers to develop a strategy of conservation in the long-term, which must aim at ensuring the continuity of the population in good balance with the ecosystem and not by an artificial increase of its size.

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