Overview of the Natural History of Madagascar’s Endemic Tortoises and Freshwater Turtles: Essential Components for Effective Conservation

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ABSTRACT. – Madagascar had seven endemic chelonian species, including six tortoises and one aquatic turtle. The now extinct tortoise species, Aldabrachelys grandidi and Aldabrachelys abrupta, as well as the extant species, Astrochelys yniphora, Astrochelys radiata, Pyxis planicauda, and Pyxis arachnoides, all occurred in the arid bush and in the mosaic of dry forests and wooded savannas from south to northwestern regions of the island. The aquatic Madagascar Big-headed Turtle, Erymnochelys madagascariensis, occurs in rivers and large lakes in western Madagascar. These species all have delayed maturity offset by a prolonged reproductive lifespan. They also have a moderate annual reproductive output that includes multiple small clutches of eggs within a season, thus their intrinsic population growth rates are low. The last two decades have brought an increased understanding of the demographic vulnerability of Madagascan chelonians to overexploitation. Particularly significant are the drivers of population dynamics relating to adult mortality and fecundity. The maximum level of harvest that their populations can sustain is low and is already greatly exceeded in most locations. This is the point at which the design of sound conservation strategies is crucial; increased integration of the natural history of Madagascan chelonians in conservation strategies could significantly improve their effectiveness.

KEY WORDS. – Reptilia, Testudines, Testudinidae, Podocnemididae, natural history, effective conservation, Madagascar

Madagascar’s very diverse habitats and climates have been important evolutionary determinants of the life-history patterns of its chelonians. The island supported seven contemporary endemic species, including six tortoises and one aquatic turtle. Recent field research on Madagascan chelonians has revealed much about the ecology of the different extant species (Smith 1999; Pedrono 2000, 2008; Leuteritz 2002; O’Brien 2002; Garcia 2006). Phylogenetic analyses undertaken during the same period have added to our understanding of these species’ histories (Caccone et al. 1999; Noonan 2000; Palkovacs et al. 2002; Austin et al. 2003; Le et al. 2006; Vargas-Ramirez et al. 2008). At present, we know more about Madagascan chelonians than we do about any other group of reptiles in Madagascar.

The Madagascar Big-headed Turtle (Erymnochelys madagascariensis), the island’s one endemic aquatic chelonian, is the only Old World representative of the family Podocnemididae and is most closely related to the South American genus Peltocephalus (Noonan 2000; Vargas-Ramirez et al. 2008). Molecular data support a monophyletic origin of the Madagascan testudinids (Caccone et al. 1999). The ancestral testudinid probably originated from mainland Africa and later diverged into three clades: the giant tortoises (genus Aldabrachelys), medium-sized tortoises (genus Astrochelys), and small tortoises (genus Pyxis). Extant Madagascan tortoises occupy a range of habitats in the arid south and western portion of the island, but are totally absent from the humid eastern slopes (Pedrono 2008). The two species of extinct Madagascan giant tortoises, Aldabrachelys grandidi and Aldabrachelys abrupta, occupied coastal areas and the colder highland region of the island and are thought to have filled an ecological role similar to that of large herbivorous mammals. Madagascar probably served as a source of dispersal for giant tortoises to most western Indian Ocean Islands (Bour 1994). Indeed, molecular analyses confirm the close relationship between extinct Madagascan Aldabrachelys spp. and the surviving lineage on the Aldabra Atoll, Aldabrachelys gigantea (Austin et al. 2003), which thus represents an unique restoration potential in parts of Madagascar (Pedrono et al. 2013). The giant chelonians did not fare well following human settlement of Madagascar, which occurred approximately 4000 years ago (Dewar et al. 2013). Giant tortoises vanished soon after human arrival, followed by the conversion of the mosaic of forests and wooded savannas to closed canopy forests and species-depauperate grasslands (Burney et al. 2004).

The past extinctions of giant tortoises and the current threatened status of Madagascan chelonians should not be treated as separate problems. The current declines of Madagascan species are only the latest stage of a much longer-term mass extinction process (see Crowley 2010). In this context, knowledge of their natural history and response to historic threats reveals much about their vulnerability to current threats. Over the last 4000 years of human impact on Madagascar, the ranges of Madagascan chelonians have been greatly reduced, many populations have been lost and
fragmented, and have declined in abundance and distribution. Understanding the natural history of Madagascan chelonians is thus an essential component of any successful conservation strategy for these species.

**Natural History of Madagascan Endemic Chelonians**

**Body Size.** — Madagascar was previously inhabited by two of the world’s largest tortoises, *Aldabrachelys granddidieri* (125 cm straight line carapace length; SCL) and *Aldabrachelys abrupta* (115 cm SCL) (Bour 1994). The island also hosts one of the world’s smallest tortoises, *Pyxis arachnoides* (11 cm SCL). Large body size is a preadaptive trait for long transoceanic drifting that allowed the ancestors of these tortoises to initially colonize Madagascar. It is also an adaptation to a broad range of environmental conditions. However, the selective harvest of giant tortoises by humans indicates that size indirectly confers a vulnerability to extinction (McKinney 1997). The largest extant species of Madagascan tortoise is *Astrochelys yniphora*, which can attain nearly 50 cm SCL (Pedrono and Markwell 2001) (Table 1). *Astrochelys radiata* is slightly smaller than A. *yniphora*. Interestingly, subfossil *A. radiata* from the Morondava region were larger than living members of this species (Bour 1994). Both *A. yniphora* and *A. radiata* exhibit sexual size dimorphism, with males attaining a larger body size than females (Smith et al. 2001; O’Brien 2002). Adult female *P.

**Table 1.** Biometric measurements of extant endemic Madagascan chelonians; means and ranges.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Adult body mass (kg)</th>
<th>Adult straight-line carapace length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Astrochelys yniphora</em></td>
<td>male</td>
<td>10.30 (7.20–18.90)</td>
<td>41.5 (36.1–48.6)</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>8.80 (5.50–12.00)</td>
<td>37.0 (30.7–42.6)</td>
</tr>
<tr>
<td><em>Astrochelys radiata</em></td>
<td>male</td>
<td>6.70 (4.50–10.50)</td>
<td>33.4 (28.5–39.5)</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>5.50 (3.10–10.20)</td>
<td>30.5 (24.2–35.5)</td>
</tr>
<tr>
<td><em>Pyxis planicauda</em></td>
<td>male</td>
<td>0.36 (0.30–0.41)</td>
<td>12.6 (11.4–13.4)</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>0.42 (0.34–0.67)</td>
<td>13.2 (12.0–14.8)</td>
</tr>
<tr>
<td><em>Pyxis arachnoides</em></td>
<td>male</td>
<td>0.19 (0.10–0.30)</td>
<td>11.1 (8.0–14.4)</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>0.20 (0.08–0.40)</td>
<td>11.0 (8.6–15.4)</td>
</tr>
<tr>
<td><em>Erymnochelys madagascariensis</em></td>
<td>male</td>
<td>5.10 (1.75–9.80)</td>
<td>35.2 (27.5–45.8)</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>4.90 (1.75–9.60)</td>
<td>34.5 (28.0–43.0)</td>
</tr>
</tbody>
</table>

Figure 1. Radiated Tortoise, *Astrochelys radiata*, in its natural habitat. Photo by Miguel Pedrono.
planicauda are on average larger and heavier than adult males (Bloxam and Hayes 1991; Rakotozafy 2009), whereas male and female P. arachnoides are about the same size. There is no difference in average SCL between the three subspecies of P. arachnoides (Pedrono 2008). Male and female E. madagascariensis are similar in body size (Kuchling 1988; Garcia 2006) (Table 1).

**Reproduction.** — Age at sexual maturity in Madagascan chelonians differs among species and is related to body size, and thus to individual growth rates. Like other chelonians, the medium-sized species (Astrochelys spp.) have extremely long development times; A. yniphora and A. radiata reach sexual maturity at 17–22 yrs and 16–21 yrs, respectively (Table 2). These species also have a relatively low annual reproductive potential. Mean clutch size of A. yniphora is 3.2 and the species lays an average of 2.4 clutches per year (Pedrono et al. 2001) (Table 2). Astrochelys radiata produces up to 3 clutches of 1–5 eggs per year (Leuteritz and Ravolanaivo 2005). The small Madagascan tortoise species (Pyxis spp.) are characterized by relatively early sexual maturity (9–13 yrs). However, both P. planicauda and P. arachnoides have a very limited reproductive output; each produces 1–3 clutches of a single egg per year (Razandrimilafinarivo et al. 2000; G. Hofstra, pers. comm.). Hence, their intrinsic population growth rate is extremely low. Female E. madagascariensis attain sexual maturity at 18–25 yrs (G. Kuchling, pers. comm.) and produce 2–3 clutches of 13 eggs per breeding season (Garcia 2006) (Table 2).

For all Madagascan chelonians, sex is determined by environmental conditions in the nest, but the sex ratio at hatching in the wild seems to approach parity. All species produce multiple clutches, which may be an adaptation to reduce the risk of nest predation. For all the Madagascan species there is variation in reproductive output among individual females, which is related to female body mass. Both clutch frequency and mean clutch mass are correlated with maternal body mass. Hatchling body mass is also strongly correlated with egg mass. On average, each reproductive female Astrochelys spp. produces around four hatchlings per year, compared to only about one hatchling per year for female Pyxis spp. Erymnochelys madagascariensis has the highest reproductive output of all the living species of Madagascan endemic chelonians, with roughly 17 hatchlings per year, although females probably only produce eggs every two years (Kuchling 1988, 1993). The length of the incubation period is variable (Table 2), and is determined by the length

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**Table 2.** Reproductive parameters of extant endemic Madagascan chelonians; means and ranges, * = in captivity.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maturity (years)</th>
<th>Incubation (days)</th>
<th>Clutch Size</th>
<th>Clutch Frequency</th>
<th>Egg mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Astrochelys yniphora</td>
<td>17–22</td>
<td>237 (197–281)</td>
<td>3.2 (1–6)</td>
<td>2.4 (1–4)</td>
<td>36.2 (20.0–54.0)</td>
</tr>
<tr>
<td>Astrochelys radiata</td>
<td>16–21</td>
<td>(263–342)</td>
<td>2.5 (1–5)</td>
<td>(1–3)</td>
<td>39.0 (28.0–55.0)</td>
</tr>
<tr>
<td>Pyxis planicauda</td>
<td>9–13</td>
<td>(254–343)*</td>
<td>1</td>
<td>(1–3)</td>
<td>19.7 (15.4–22.2)</td>
</tr>
<tr>
<td>Pyxis arachnoides</td>
<td>9–13</td>
<td>(247–324)*</td>
<td>1</td>
<td>(1–3)</td>
<td>17.4 (11.0–22.0)</td>
</tr>
<tr>
<td>Erymnochelys madagascariensis</td>
<td>18–25</td>
<td>77 (58–109)</td>
<td>13 (6–32)</td>
<td>(2–3)</td>
<td>14.8 (5.0–22.0)</td>
</tr>
</tbody>
</table>

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**Figure 2.** Ploughshare Tortoise or Angonoka, Astrochelys yniphora. Photo by Lora L. Smith.
The duration of time between oviposition and the beginning of the rainy season. Eggs of Madagascan testudinids probably undergo diapause during the cool dry season. Increasing incubation temperatures in the wet season may reverse the diapause, embryonic development is completed and hatchlings emerge from the nests during the rainy season.

**Activity Patterns.** — Activity in Madagascan chelonians is closely tied to seasonal rainfall. Tortoises are more active during the warm wet season (from November to May, when virtually all of the annual rainfall occurs), than during the cool dry season (from June to October). For *Astrochelys* spp., juveniles are largely dormant in the dry season when they stay hidden beneath leaf litter. Adults continue to feed during the dry season, although to a lesser degree than during the wet season (Smith 1999; Leuteritz 2002). Both adults and juveniles of both species of *Pyxis* are inactive during the extended dry season in southern Madagascar, when they seek shelter under the sandy soil, leaf litter, or preferentially, under shrubby vegetation (Bloxam and Hayes 1991; Walker et al. 2007). Thus, these tortoises conduct nearly all of their biological activities in just the 5–6 rainy months of the year. *Pyxis* spp. also shelter beneath leaves during the hottest part of the day during the wet season. Madagascan tortoises are particularly active on rainy days. *Astrochelys radiata* and *P. arachnoides* exhibit a bimodal activity pattern, avoiding any activity during peak temperatures, and are active only in the morning (0630–1000 hrs) and late afternoon (1500–1830 hrs) (Leuteritz 2002). The total daily activity period of *P. arachnoides* is short, on average 2–4 hrs a day when it is not raining (Pedrono 2008). Madagascan tortoises are often found basking in the early morning or after rain in open, sunny places. The aquatic species *E. madagascariensis* is also more active during the warm wet season than during the rest of the year; however, it feeds year round (Garcia 2006).

**Habitat and Home Range.** — Many chelonians occur in naturally high population densities as a result of their low energy requirements. However, most populations of extant Madagascan species are allopatric and densities are artificially low due to overharvesting and poaching. Remaining habitat also is fragmented and declining from harvest of trees for firewood and charcoal production, uncontrolled bush fires, and encroachment for cultivation.

*Astrochelys yniphora* occurs in second growth habitat with bamboo (*Perierbambos madagascariensis*), shrubs (*Terminalia boivinii* and *Bauhinia pervillei*), palm (*Bismarckia nobilis*) savannah, and forest edges around Baly Bay in western Madagascar (Smith 1999). *Pyxis planicauda* occurs in dry deciduous forests, as well as more open degraded habitat in the Menabe region north of Morondava in western Madagascar. It prefers secondary forests mixed with open areas over natural undisturbed forests (Rakotombololona, 1998). *Astrochelys radiata* and *P. arachnoides* are found in xerophytic spiny forests in southern Madagascar.

Adult tortoises of all Madagascan species are highly sedentary and exhibit some degree of site fidelity; it is common to find an individual in the same location in the same period during consecutive years. *Erymnochelys madagascariensis* occurs in rivers and lakes in western Madagascar and also is largely sedentary, although it can migrate across dry land if environmental conditions become too unfavorable. Home range size in *E. madagascariensis* varies according to sex, age, time of year, and probably also by population density (Garcia 2006).
Astrochelys yniphora is the only species of Madagascan chelonian for which detailed home range size data are available, but similar patterns are expected for other Madagascan testudinids. Male A. yniphora have a much larger home range than females and the size of the home range is greater in the wet season than in the dry season. Males have an average home range of 21 ha in the rainy season compared to 7 ha in the dry season, and females have an average home range of 13 ha in the rainy season and 4 ha in the dry season (Smith et al. 1999). Males are particularly mobile in the first rains of November and December, during which they fight with other males for access to females. Females are most active from January through May during the nesting season. Nest forays of greater than 1 km have been observed. Home range size is also strongly influenced by the size and age of individuals. Juveniles are particularly sedentary and have a home range of only 0.1–0.3 ha (Pedrono 2000).

Preliminary data on P. planicauda indicates that adult males and females have minimum home ranges of 0.5 ha and 0.42 ha, respectively. Juveniles of this species also are very sedentary with a minimum home range of only 0.02 ha (Rakotozafy 2009).

**Diet.** — Our knowledge of the diet of Madagascan chelonians is largely anecdotal. Astrochelys spp. feed on grasses (e.g., Aristida congesta and Eragrostis sp.), sedges, and some broad-leaved plants. Tortoises seem to prefer new growth rather than mature growth because of the high protein and low fiber content. The introduced cactus, Opuntia sp., benefits A. radiata since it is one of its preferred foods in the wild; the fruits are particularly appreciated. Occasionally, Astrochelys spp. eat droppings of other animals, pieces of bones and mollusc shells. Such items probably provide calcium and other minerals in the diet (Leuteritz 2003). Astrochelys spp. are able to drink through their nostrils instead of the mouth, although they do not possess a valvular structure like the extinct and living Aldabrachelys spp., allowing it to close its olfactory area. Such capability allows tortoises to exploit shallow, ephemeral puddles of water in arid habitats.

*Pyxis planicauda* eats nearly all types of leaves within reach on the forest floor, as well as fungi and fallen fruits. Occasionally they eat snails, slugs, and insects, and have also been observed scavenging animal corpses when they encounter them (Kuchling and Bloxam 1988). *Pyxis arachnoides* is an opportunistic browser and eats many types of terrestrial invertebrates (e.g., molluscs, Coleoptera, Trichoptera larvae, Odonata, and Ephemeroptera). Adult *E. madagascariensis* become progressively more omnivorous and consume Ficus and Raphia fruits, *Phragmites* shoots and stems, freshwater snails, *Melanoides tuberculatus*, and also scavenge dead animals such as fish. This species is principally opportunistic, with a diet dependent on the seasonal and spatial availability of resources. The proportion of animal prey eaten by adult turtles decreases significantly during the dry season (Garcia 2006).

**Predation and Parasitism.** — As in other chelonians, the annual survival rate of Madagascan turtles and tortoises increases with body size and age. The carapace of large adults provides protection from predators. However, small juveniles, especially tortoises, are extremely vulnerable to predation by diurnal predators, as they are active and forage in open habitats in the wet season, and their shells do not harden for several years. Thus juvenile mortality is very high, with most of the offspring never reaching sexual maturity (Pedrono 2000; O’Brien 2002). The pressure from predators can vary temporally and among populations.

The African Bush Pig (*Potamochoerus larvatus*), which was probably introduced from Africa, is capable of killing juveniles of all species of Madagascan chelonians. However, nest predation by African Bush Pigs seems surprisingly low (around 3% for *A. yniphora*; Pedrono et al. 2001). Other potential predators of young tortoises include the Madagascar Buzzard (*Buteo brachypterus*), the introduced Indian Civet (*Viverricula indica*), and snakes (Lioheterodon spp.). Potential predators of eggs or young *E. madagascariensis* include the African Bush Pig, the Yellow-billed Kite (*Milvus aegyptius*), the Madagascar Fish Eagle (*Haliaeetus vociferoides*), and the Nile Crocodile (*Crocodylus niloticus*); there are no known predators of large adult Madagascar Big-headed Turtles.

While disease has never been observed in wild populations, several species of ticks (i.e., *Amblyomma geochelone*, *A. chabaudi*, *Geckobia enigmatica*) have been found on Astrochelys and *Pyxis* spp. (Bertrand and Pedrono 1999; Durden et al. 2002). These parasites do not appear to cause significant disturbance to the tortoises.

**Conclusions and Conservation Implications**

The unique natural history of Madagascan chelonians presents equally unique challenges as well as opportunities for their conservation. Land tortoises, for example, are closely associated with dry scrub habitats, and bush fires within these habitats are one of the main conservation issues in Madagascar. Tortoises are particularly vulnerable to this threat because of their limited mobility; the long-term impact of bush fires on tortoise habitats is another concern. Bush fires will probably become more frequent in Madagascar as a result of climate change. Changes in temperature, rainfall patterns, and storm frequency and intensity may also directly impact Madagascar’s ecosystems. Over the long term, new assemblages of species will form and create modified or entirely new ecosystems as a result of these changes (e.g., Seastedt et al. 2008). However, having been in existence since before the time of the dinosaurs, chelonians have already survived numerous episodes of rapid climate change in the geological past, and they are possibly less vulnerable to climate change than other animal groups in Madagascar. Although increased temperatures could potentially shift the timing of nesting in chelonians and increase egg incubation temperatures, with an increased production of females,
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freshwater turtles in North America have been found to have some plasticity in timing of nesting and selection of nest sites that produce optimal temperatures for a balanced sex ratio (Schwanz and Janzen 2008). Problems may arise from complex interactions associated with climatic conditions, activity budgets, and body reserves of small Madagascan tortoise species that estivate during the long dry season. The rate of recovery of body reserves during the active wet season will depend upon climatic conditions. For example, if climate change results in a shorter wet season, female Pyxis spp. may find it difficult to restore their body reserves to reproduce or survive aestivation.

By far the most critical factor in conservation of Madagascan chelons is overexploitation. The life history characteristics of chelons render them particularly vulnerable to this threat (e.g., Congdon et al. 1994). This is particularly true of the largest remaining Madagascan species, A. yniphora and A. radiata. The fact that poachers in Madagascar specialize in these species and do not transfer their efforts to more abundant species once chelons populations are driven to low numbers does not leave a chance for recovery. As the number of individuals decreases, a constant level of exploitation represents an increasing proportion of their populations. The moderate annual reproductive output and delayed maturity offset of these species cannot compensate for the loss of adults to poaching. It is thus easy to overexploit Madagascan chelons, even at initially high densities.

The extinction of Madagascan giant tortoises illustrates the size-selectivity of this process, and confirms threats to surviving species that are next on the size scale (A. yniphora, A. radiata, and E. madagascariensis). Typically, highly profitable species are exploited first (McKinney 1997); the consumption of P. arachnoidea in areas where A. radiata has disappeared is symptomatic of this pattern. If one accepts this hypothesis of selectivity, the current status of A. yniphora, which presents an intermediary size between the extinct giant tortoises and extant overexploited A. radiata – is not surprising. For the last few centuries A. yniphora has been in a state of near-extinction, with populations stabilized at extremely low numbers. However, collection of A. yniphora from the wild has greatly accelerated over the past 15 years, resulting in very rapid declines in the already depauperate populations and the species is now very close to total extinction in the wild (Pedrono 2008). A similar pattern of decline is occurring in A. radiata populations, although the effects have been buffered by their wide distribution and high population densities in southern Madagascar. However, the scale of exploitation of this species and the apparent extirpation of populations is alarming (Leuteritz 2002; O’Brien 2002).

Given the current threats to all of Madagascar’s endemic chelons, the design of sound conservation strategies is crucial. There is a need to rigorously assess the potential contributions of different management alternatives based on the best available science (Ferraro and Pattanayak 2006). The recognition that all individuals are not alike is fundamental to this process. The life history characteristics of most chelons indicate that conservation of adults, and adult females in particular, is the most effective means of recovering populations (e.g., Frazer 1992; Congdon et al. 1994). This is because an adult female has a long reproductive life span in which to produce enough offspring to compensate for juveniles that do not survive into adulthood.

With critically endangered species such as A. yniphora, captive breeding to restock wild populations is an important component of a comprehensive conservation program. However, if we want to maintain wild populations, then extensive captive breeding and headstarting programs are inadequate if nothing is done to also address the threats facing the adults in the wild. Ex-situ conservation initiatives should never take priority over in-situ approaches; rather they should be used to supplement them. Ill-conceived conservation strategies may result in even further decline of populations that are already under threat. Of real concern for conservation of Madagascan chelons is what we perceive as the continued emphasis on repatriation and rescue centers for confiscated animals and captive breeding and reintroduction, over a greater needed emphasis on conservation of wild populations. We believe that these ex-situ activities can divert attention and resources from efforts to conserve wild populations that still have a chance to recover (Pedrono 2011). They also have the potential to decrease genetic variability within species and to transmit exogenous pathogens to wild populations.

In our opinion, an increased understanding of the natural history of the Madagascan chelons could significantly improve conservation strategies. Priority should be given to research on the two species of Pyxis for which we have little information on vital demographic parameters such as survival rate or average clutch frequency in wild populations. The same is true for E. madagascariensis, the study of which is complicated by its aquatic habitat. These parameters are needed to produce Population Viability Analysis (PVA) models, which allow the identification of parameters that influence the species’ vulnerability and allow for unbiased evaluation of different conservation options (i.e., in-situ vs. ex-situ approaches) that can be used to define conservation strategies for these species (e.g., Tenhumberg et al. 2004). Ultimately, species-based conservation strategies need to be converted into focused, practical action plans to secure protection for dwindling populations of tortoises and turtles.

One of the major reasons for the long-standing debates between in-situ and ex-situ conservation approaches is the lack of empirical evidence in the definition of these species’ conservation strategies. Astrochelys yniphora is the only Madagascan chelion to have been the focus of a comprehensive PVA process to date (Pedrono 2000; Pedrono et al. 2004). However, its results, specifically the recommendation from population modeling to conserve wild adults, have not yet been effectively achieved, as evidenced by the fact that poaching and smuggling of wild individuals from Baly Bay National Park has unfortunately increased. And although some successes have been achieved in some programs, other aspects of conservation programs for Madagascan chelons have been less effective. We believe that shortcomings in the definition and implementation of these species’ conservation
stratégies may be part of the explanation. More of a focus on conservation of wild chelonians in their native habitats, along with applications of tools such as PVA that consider life history characteristics of Madagascan chelonians, is in our opinion key to preserving these unique species.

RéSUMÉ


LITERATURE CITED


