

### West African slender-snouted crocodile Mecistops cataphractus



Compiler: Emmanuel Amoah

Contributors: Claudia Louise Gray and Rikki Gumbs

Suggested citation: Amoah et al. A Survival Blueprint for the conservation and management of the West African slender-snouted crocodile, *Mecistops cataphractus* in the Jimi River (Obuasi) and Tano River (Tanoso), Ghana. An output from the EDGE of Existence fellowship, Zoological Society of London, 2019.



#### 1. STATUS REVIEW

#### 1.1 Taxonomy:

The Taxonomy of African slender-snouted crocodiles (*Mecistops spp.*) has been the subject of debate among crocodilian researchers for decades. While some have reported *Mecistops* as a true crocodile belonging to the genus *Crocodylus*, others have argued it belongs to a genus of its own. Recent DNA and morphological studies provided enough evidence to suggest that the African slender-snouted crocodile is different from the genus *Crocodylus* and consequently placed it in a unique monotypic genus *Mecistops* (McAliley *et al.*, 2006). This finding has been corroborated by all subsequent phylogenetic studies (e.g., Hekkala *et al.*, 2011; Meredith 2011; Oaks 2011; Shirley *et al.*, 2013). *Mecistops* has recently been split into two divergent species based on morphological and genetic data (Shirley et al., 2018). There are now two species of *Mecistops* recognised: the West African slender-snouted crocodile (*M. cataphractus*) and the Central African slender-snouted crocodile (*M. leptorhynchus*) (Shirley et al. 2018).

#### 1.2 Distribution and population status:

As the name suggests, the West African slender-snouted crocodile is endemic to West Africa (Shirley et al., 2018), and the geographic range of this taxon is reported to be decreasing (Shirley, 2007). The extent of occurrence in the north of this species' range has already declined drastically due to aridification and human encroachment and it is projected that this species will likely be lost from the areas that are not naturally forested (i.e., the wooded, gallery savanna areas in the north) of West Africa in the next 10–20 years, if it has not already (Shirley *et al.*, 2014). Throughout its range, the population has reduced between 70–90% over the past three generations (75 years) due to loss of range and suitable habitat, direct exploitation and lack of commitment to enforce existing laws (Shirley et al. 2018; Shirley, 2014). Across West Africa, subpopulations outside protected areas have already been reduced to the point where even small perturbations will result in localized extinctions (Shirley, 2014).

#### 1.2.1 Global distribution:

Country	Population estimate (plus references)	Distribution	Population trend (plus references)	Notes
Benin	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Burkina Faso	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Côte d'Ivoire	Not estimated	Taï and Comoé National Parks and scattered populations outside protected areas	Declining (Shirley et al., 2009; M. Shirley, unpub. data)	
Gambia	Not estimated	The River Gambia national park	unknown	
Ghana	Not estimated	Obuasi Municipality, Tanoso, Mole National Park, River Offin	Declining (Shirley et al., 2009; E. Amoah, unpub. data)	
Guinea	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Guinea- Bissau	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Liberia	Not estimated	unknown	unknown	
Mali	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Senegal	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct
Sierra Leone	Not estimated	unknown	unknown	
Togo	Not estimated	unknown	Highly depleted (Shirley, 2014)	Possibly extinct

#### 1.2.2 Local distribution:

Country	Region / province	Site	Level of Protection	Population size	Reference(s)	Notes
Ghana	Ashanti Region	Jimi River (Obuasi Municipality)	Community forest	Not estimated	E. Amoah, unpub. data	The Jimi River harbours good numbers of <i>M. cataphractus</i> . During this study we recorded 6 nests (3 old and 3 active)
Ghana	Northern Region	Samole Stream	Mole National Park	Not estimated	Shirley et al., 2009	Only 2 individuals have been recorded
Ghana	Northern Region	Mognori River	Mole National Park	Not estimated	Shirley et al., 2009	Only 2 individuals have been recorded
Ghana	Ashanti Region	Offin River	Barekese Dam. It's a restricted zone for Ghana Water Works	Not estimated	Shirley et al., 2009	Only 1 individual was recorded
Ghana	Brong East Region	Tano River (Tanoso)	Traditional protection	Not estimated	E. Amoah, unpub. data	This site contains probably one of the highest concentrations of <i>Mecistops</i> in the whole of West Africa

#### 1.3 Protection status:

The African slender-snouted crocodile (*M. cataphractus*) is classified as Critically Endangered by IUCN due to the rapidly decreasing population across its range (Shirley, 2014). It is nationally protected by Ghana Wildlife Law. However, enforcement of wildlife laws is generally weak in Ghana making the species prone to illegal hunting even sometimes in the wildlife protected areas. There are some very small numbers of individuals inside protected sites, as mentioned in the table above. However, the only two known significant population of West African slender-snouted crocodiles in Ghana are all found in areas (Tanoso and Obuasi) outside the wildlife protected areas network. This means that protection of these populations will require significant community awareness, support and investment in the conservation of the species.

#### 1.4 Ecology, behaviour and habitat requirements:

The West African slender-snouted crocodile is a medium-sized crocodile that could reach a maximum of 4 m (Brazaitis, 1973), however, due to hunting and other related disturbances it is now difficult to see individuals over 3-3.5 m (Shirley, 2014). It is a typical forest species which inhabits forested rivers and other densely vegetated bodies of water (e.g. reservoirs and freshwater lagoons). Nevertheless, individuals have also been found in sparsely vegetated, gallery habitats within savanna woodland (Waitkuwait 1989, Shirley et al. 2009).

The slender-snouted crocodile is a mound nester. Limited information is available on the average clutch size from wild populations. Waitkuwait (1989) reported an average clutch size of 16 ±7 eggs from six nests from the Taï National Park. We also found an average clutch size of 21±4 eggs (range: 16-25 eggs) from 4 nests from Obuasi and Tanoso. Nesting starts from the beginning of the annual wet season (late March-August) at the fringe of aquatic habitats. Where conditions are favourable, nests are typically constructed at the base of trees at the edge of undisturbed forested wetland habitats, though some nests have also been encountered in cacao plantations in Côte d'Ivoire (Shirley 2007) and grassland in Ghana (E. Amoah pers. obs.). The nesting season broadly overlaps with that of the sympatric dwarf crocodile (*Osteolaemus* sp.), though there appears to be partitioning of nest habitat between the two species, and *M. cataphractus* has a more restricted nesting season (Waitkuwait, 1989). Females lay a small clutch of very large eggs, relative to female body size, and hatchlings tend to be larger than those of other crocodile species (Waitkuwait 1985, 1989; Thorbjarnarson 1996).

Like most crocodilians, juveniles feed primarily on small fish and a variety of invertebrates. Adult animals are primarily piscivorous, though they have been observed to consume mammals (Pauwels et al. 2003, 2007; E. Amoah pers. obs.), turtles and birds (M. Shirley pers. obs.). While there is nothing specific documented in the literature, *M. cataphractus* is known to be a very vocal species, perhaps indicating a much more structured social hierarchy or breeding ethology than is presently known (Shirley, 2014).



#### 1.5 Threat analysis:

Threat	Description of how this threat impacts the species	Intensity of threat (low, medium, high, critical or unknown)
Habitat loss/modification	One of the serious threats impeding the population recovery of <i>Mecistops cataphractus</i> is anthropogenic modification of its habitats (Shirley, 2014). The species is typically forest dependent and relies heavily on forest vegetation for nesting. Unfortunately, the everincreasing human population and the associated demand for agriculture expansion is rapidly modifying the habitat for this species. Furthermore, illegal alluvial gold mining is polluting waterbodies and seriously affecting the species. <i>M. cataphractus</i> is very sensitive to human presence and may abandon nests after the slightest disturbance (E. Amoah pers. obs). At both Tanoso and Obuasi, remnant forest patches serving as nesting habitats are being cleared at a rapid rate for agriculture. At Obuasi we have recorded 4 failed nests (2017 and 2018 nesting seasons) that resulted from habitat disturbances.	Critical
Human- Crocodile Conflicts	This threat stated is localised and happening at Obuasi, one of my EDGE project sites, though may be occurring throughout the remaining range of the species. Here there is increasing tension between fish farmers and the species as farmers complain of fish raiding by the species. Several individuals have been killed upon sightings in fishponds.	High
Illegal hunting	The species is hunted across West Africa for food. Hunting is a major contributor of the species' depleted population. Unregulated hunting has resulted in a lot of localised extinctions outside protected areas throughout the species' range and where it still occurs, subpopulations have been seriously depleted to the extent that even small perturbations are likely to result in localized extirpation (Shirley, 2014).	Medium

Subsistence and small-scale fisheries	Depletion of prey resources and incidental catches of crocodiles arising from fishing is negatively affecting the population of the species	Medium
Weak law enforcement	Although the Ghana Wildlife Laws offer complete protection, enforcement of these laws is weak making the species prone to illegal harvesting	medium

#### 1.6 Stakeholder analysis:

Country	Stakeholder	Stakeholder's interest in the species' conservation	Current activities	Impact (positive, negative or both)	Intensity of impact (low, medium, high or critical)
Ghana	Ghana Crocodile Research Team	Ecological research, awareness and long-term conservation	The team is currently conducting ecological studies, raising awareness and initiating various programmes to promote long-term conservation of the species	Positive	Critical
Ghana	Ghana Wildlife Division	Enforcement of wildlife laws	No activity	Neutral	Low
Côte d'Ivoire	Rare Species Conservatory Foundation (RSCF) NGO of Dr. Matthew Shirley)	Ecology and population protection	Dr. Matthew Shirley provided training for our team in crocodile capturing, handling, radio tagging and tracking	Positive	High
Ghana	Locals of Obuasi Municipality and Tanoso	Protection of species against hunting (the case of Tanoso) and	We currently engaging the fish farmers on means to	Both	high



		control of fish raiding (obuasi)	reduce and if possible halt fish raiding by the slender-snouted crocodiles		
Ghana	Ghana Water Resources Commission (GWRC)	There are water treatment plants at both Tano and Jimi River. GWRC offers some form of restrictions around its treatment plants. This in a way limit the amount of disturbances that will have occurred in those areas	This project will partner with GWRC to protects the watersheds of the two rivers	Positive	low
Ghana	Department of Wildlife and Range Management, KNUST	Research on the ecology and conservation of the species	The department provides technical advice on wildlife conflicts management and other stakeholder involvements when the need arises	Positive	Medium
West and Central Africa	West and Central Africa Crocodile Specialist group, a subgroup within the IUCN/SSC Crocodile Specialist Group	The group is interested in establishing the population and threat status of the species throughout its range	The group provides advice on various aspect of the project.	Positive	Medium
Ghana	Municipal Assemblies	The municipalities have interest in protecting the water bodies that occurs under their jurisdiction	They are enforcing laws to protect the rivers	positive	low





#### 1.7 Context and background information that will affect the success of any conservation action for this species:

	Description	Threats	Opportunities
Socio-cultural effects and cultural attitudes	Ghanaians have divergent views about crocodiles and this has much influence on how a community behaves towards crocodiles.	At Obuasi, locals perceive crocodiles as dangerous and destructive animals and mostly resort to lethal methods when spotted around their residence or fishponds. This perception threatens the long-term survival of the species in the municipality.	At Tanoso, the Tano River is regarded as sacred and all its aquatic creatures are prohibited from consumption. This tradition promotes prey availability and also prevents hunting of crocodiles. Such tradition is likely to help secure the long-term protection of crocodiles in the river.
Economic implications	<ul> <li>Illegal mining activities</li> <li>Alternative livelihood programmes</li> <li>Capacity building programmes</li> <li>Illegal hunting</li> </ul>	The Obuasi study site is prone to illegal gold mining activities. Such activities affect the water quality, destroy the river channel and reduce prey availability. Control of illegal miners involves a lot of risk and logistics. At Obuasi, <i>M. cataphractus</i> is hunted for food. The hunting is mainly done at subsistence scale and not sold in commercial markets. This makes it more difficult track	<ul> <li>Training locals in livelihood programmes will help reduce pressure on the species' habitat</li> <li>Building the capacity of fish farmers in non-lethal methods to control crocodiles against fish raiding will reduce the species' mortality as a result of conflict with farmers.</li> </ul>





		number of individual being hunted	
Existing conservation measures	At Obuasi, there are no existing conservation measures but at Tanoso there is an indirect conservation measure.	There is the possibility that the traditional beliefs may fade away with years as immigration and emigration continues and people become more involved in Christianity and Islam. This could negatively affect the protection offered to the species by tradition beliefs.	The existing traditional beliefs at Tanoso offer an incredible form of protection to this rare and Critically Endangered species. We will continue to work closely with traditional leaders to promote the sustainability of these beliefs.  At both sites, we see the opportunity to develop community based protection approaches.
Administrative/political set-up	There are national laws which offer complete protection to the West African slender-snouted crocodiles  Community Resource Management Areas (CREMA) Techiman Municipal Assembly	There is a low level of commitment from the Ghana Wildlife Division towards law enforcement and research on this species. This apathetic behaviour threatens long-term protection of the species.	The existing laws which offer protection for the species can be enforced to promote long-term conservation.  CREMA as an initiative has help controlled illegal hunting of wildlife in communities where it being carried out. It presents good opportunity to protect the species through community involvement







			The assembly has provided us with permits to work in the municipality. The assembly is in charge of waste management in the municipality. There is possibility for us to collaborate to control pollution in the river.
Local expertise and interest	The Ghana Crocodile Team consists of just four individuals. We have also trained 12 local volunteers and two graduate students.	The current number of crocodile experts is very low. This makes it very challenging to adequately respond to the threats of the species.	The crocodile Team can train graduate students and more community volunteers to help address the current human resources challenges.
Resources	Funds and logistics are needed to conduct thorough countrywide surveys to determine the status of the species in Ghana. Further resources are needed to raise awareness and also build local capacity for the species' conservation.	It is difficult to raise adequate funds to implement conservation initiatives for crocodilians.	We are currently partnering with ZSL, Segre Foundation, Mohammed Bin Zayed, Columbus Zoo and Aquarium, Mohammed Conservation Fund and RSCF in diverse ways. We will continue to partner with funding agencies and other collaborators with similar interest to raise funds and secure resources needed to protect <i>M. cataphractus</i> .





#### 2. ACTION PROGRAMME

Vision (30-50 years)  Discover and protect all the remnant subpopulations of West African slender-snouted crocodiles in Gha	na
Goal(s) (5-10 years)	IIIa
Protect the remnants of West African slender-snouted crocodile in Ghana by mitigating threats through approach	a collaborative
Objectives	Prioritisation (low, medium, high or critical)
1.Conserve critical nesting areas of West African slender-snouted crocodile subpopulations at Obuasi and Tanoso	Critical
2.Survey the extents of Tano and the Jimi watershed to estimate the populations of West Africa slender-snouted crocodiles	Critical
3.Initiate long-term population monitoring across known habitat of the species	High
4.Conduct ecological studies necessary for the species' conservation in Ghana	Critical
5.Create community-based protected areas such as Community Resources Management Areas (CREMA) across critical habitats of the species in Ghana	Critical
6. Strengthen and build local capacity (e.g. local volunteers, traditional leaders etc.) to enhance the species' conservation	High
7. Initiate and promote sustainable community-based ecotourism	High
8.Continuously promote public awareness to mitigate threats of the species	Critical







Activities	Country / region	Priority (low, medium, high or	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Objective 1: C	onserve criti	cal nesting	areas of West A	 Africa slend	er-snouted croco	dile subpopulations	at Obuasi and	Land/water management
Identification of all nesting sites along Tano watershed and Jimi River	Ghana	Critical	£50000/year	10 years	Ghana Water Resources Commission, Environmental Protection Agency(EPA), Local government authorities, traditional leaders, land owners, farmers	Data on nesting sites across the two habitats  Map of all the nesting sites across the two habitats	Difficult to raise sufficient funds to survey the entire drainage systems of Tano and Jimi	Land/water management
Restoration of degraded nesting areas along Tano drainage and Jimi River	Ghana	High	£10000/year	25 years	Local communities, farmers, Ghana Water Resources Commission	Rehabilitated nesting sites	It is difficult to convince local farmers to leave buffers along waterbodies during their land preparations	Land/water management





Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Safeguard critical nesting areas against anthropogenic disturbances eg. Farming, illegal mining etc.	Ghana	Critical	£5000/year	15 years	Farmers, traditional leaders, community volunteers	Nesting sites secured against farming	Farmers may not be willing to corporate with the idea of protecting nesting sites.  Illegal miners do not value conservation and may show not concern towards protecting the species	Land/water management
Objective 2: S	•		Γano and the J	imi draina	ge to estimate the	he populations of W	lest Africa	Improving Knowledge
Population surveys in the Tano River and Jimi River	Ghana	high	£20000/year	5 years	community volunteers	Data on population of the species in Tano drainage and the Jimi River	Difficulty in detecting the extremely shy <i>M. cataphractus</i> Challenges in raising adequate funds for surveys	Improving Knowledge
Objective 3: In	nitiate long-te	erm populat	ion monitoring	across kno	wn habitat of the	species	,	Improving Knowledge







Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Develop monitoring transects across the identified habits of the species for population surveys and nest search	Ghana	High	£10000/5years	Beyond 50 years	Ghana crocodile team and trained volunteers	Data on transects developed across the species' range	It may be difficult to secure funds to develop the survey transects	Improving Knowledge
Regular (every 5 years) countrywide population and threats surveys	Ghana	High	£60000/5year	Beyond 50 years	Ghana crocodile team and trained volunteers	Data on population monitoring	It may be difficult to secure funds to conduct the stated monitoring	Improving Knowledge
	onduct ecolo	gical studie	es necessary for	the specie	s' conservation in	Ghana		Improving Knowledge
Investigate the nesting ecology of the <i>M.</i> cataphractus	Ghana	Critical	£10000/year	10 years	Ghana Crocodile Team	Data on nesting ecology of the species	We may not find adequate nests	Improving Knowledge







Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Study M. cataphractus habitat preferences and responses to human disturbances	Ghana	Critical	£20000/year	25 years	Ghana Crocodile Team and other herpetologists	Documents M. cataphractus habitat preferences and responses to disturbance	It may be difficult to raise the said amount annually	Improving Knowledge
				such as Co	mmunity Resour	ces Management Are	eas (CREMA)	Land/Water protection
Survey and	Ghana	Critical	£30000	10 years	The project	Number of	Some land	Land/Water
identify all areas that qualify for the creation of Community Resource Management Areas (CREMA)				,	team, local government agencies and traditional leaders	CREMAs that will be created	owners may not be willing to release their lands for the creation of CREMA	protection







Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Stakeholder consultations on creation of CREMA	Ghana	Critical	£10000/year	10 years	The project team, indigenes, local government agencies and traditional leaders	Number of stakeholders meetings organised	Some stakeholders may not show commitment to the creation of CREMAs	Land/Water protection
Objective 6: S conservation.	•	d build loca	I capacity (eg lo	ocal volunte	ers, traditional lea	ders etc.) to enhan	ce the species'	Capacity Building
Organise regular community volunteer trainings for indigenes around critical habitats of the species	Ghana	High	£3000/year	20 year	Project team and local volunteers	Number of people trained	Difficulty in raising such funds to conduct the trainings	Capacity Building
	litiate and pr	omote susta	ainable commur	nity-based e	cotourism	1	1	Livelihood, Economic & Other Incentives







Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Conduct feasibility study on potential community- based ecotourism sites across the species' range	Ghana	High	£20000/year	10 years	Project team	Number of feasibility studies conducted	Difficulty in raising such funds to conduct the studies	Livelihood, Economic & Other Incentives
Establish and promote community-based ecotourism sites	Ghana	high	£50000/year	20 years	Project team, Ghana Tourism Authority, Ghana Water Resources Commission and	Number of community-based ecotourism sites that will be established across the species' in Ghana	Difficulty in raising funds  Some communities may not support the idea of ecotourism	Livelihood, Economic & Other Incentives
Objective 8: C	ontinuously p	romote publi	c awareness to mi	itigate threa	ts of the species	I	<u> </u>	Education & Awareness







Activities	Country / region	Priority (low, medium, high or critical)	Associated Cost	Time scale	Responsible stakeholders	Indicators	Risks	Activity type
Regularly organise awareness campaigns to enhance the species' protection	Ghana	High	£5000/year	Beyond 20 years	Ghana Wildlife Division, The project team and community volunteers	<ul> <li>Number of people reached during campaigns</li> <li>Pre and post awareness assessmen to evaluate changes in attitude towards the species</li> </ul>		Education & Awareness





#### 3. LITERATURE CITED

- Brazaitis, P. (1973). The identification of living crocodiles. Zoologica 53(3-4): 59-101.
- Hekkala, E., Shirley, M.H., Amato, G.D., Austin, J.D., Charter, S., Thorbjarnarson, J.B., Vliet, K.A., Houck, M.L., Desalle, R. & Blum, M.J. (2011) An ancient icon reveals new mysteries: mummy DNA resurrects a cryptic species within the Nile crocodile. *Molecular Ecology*, 20, 4195-4215.
- McAliley, L.R., Willis, R.E., Ray, D.A., White, P.S., Brochu, C.A. & Densmore, L.D. (2006) Are crocodiles really monophyletic? Evidence for subdivisions from sequence and morphological data. *Molecular Phylogenetics and Evolution*. 39, 16-32.
- Pauwels, O.S.G., Mamonekene, V., Dumont, P., Branch, W.R., Burger, M. and Lavoue, S. (2003). Diet records for Crocodylus cataphractus (Reptilia: Crocodylidae) at Lake Divangui, Ogooue-Maritime Province, southwestern Gabon. . *Hamadryad* 27(2): 200-204.
- Pauwels, O.S.G., Barr, B., Sanchez, M.L. (2007). Diet and size records for Crocodylus cataphractus (Crocodylidae) in south-western Gabon. *Hamadryad* 31(2): 360-361.
- Shirley, M.H., Carr., A.N., Nestler, J.H., Vliet, K.A., and Brochu, C.A. (2018). Systematic revision of the living African Slender-snouted Crocodiles (Mecistops Gray, 1844). *Zootaxa* 4504 (2): 151–193
- Shirley, M.H. (2014). Mecistops cataphractus. The IUCN Red List of Threatened Species 2014: e.T5660A3044332. <a href="http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T5660A3044332.en">http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T5660A3044332.en</a>. Downloaded on 11 February 2019.
- Shirley, M. H., Oduro, W., and Beibro, H. Y. (2009). Conservation status of crocodiles in Ghana and Côte-d'Ivoire, West Africa. *Oryx*, 43(1), 136-145.
- Shirley, M.H. (2007). Crocodile Conservation in West Africa: Planning for the Future. Final Report to the Wildlife Division of the Forestry Commission, Ghana and the Wildlife Directorate, Ministry of Water and Forests. Côte-d'Ivoire.
- Thorbjarnarson, J.B. (1996). Reproductive characteristics of the Crocodylia. *Herpetologica* 52(1): 8-24.
- Waitkuwait, W.E. (1985). Investigations of the breeding biology of the West African slender-snouted crocodile Crocodylus cataphractus Cuvier, 1824. *Amphibia-Reptilia* 6(4): 387-399.
- Waitkuwait, W.E. (1989). Present knowledge on the West African slender-snouted crocodile, Crocodylus cataphractus Cuvier 1824 and the West African dwarf crocodile, Osteolaemus tetraspis Cope 1861. Crocodiles. Their Ecology, Management and Conservation. A Special Publication of the IUCN-SSC Crocodile Specialist Group, pp. 259-275. IUCN, Gland, Switzerland.