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A star attraction: The illegal trade in Indian Star Tortoises

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Abstract

We report on illegal international trade in Indian Star Tortoises (*Geochelone elegans*), with a particular focus on India and Thailand.Within India, this species has received protection as a Schedule IV list species of the Wildlife (Protection) Act 1972 for over 40 years. This study documents the illegal trade of 55,000 individuals poached from just one 'trade hub' in India. Although domestic demand persists, these individuals appear to have been primarily sourced to satiate international demand for pets in other Asian countries (e.g. Thailand and China). Since 1975, this species has been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) that regulates all commercial trade. However, an analysis of the CITES trade records relating to Thailand imports (between 2004 and 2013) found large discrepancies indicating potential illegal activity which question the legitimacy of its founding captive stock. Given its role as a major hub of illegal trade activity, both as a consumer and a country of transit, we support calls for Thailand to prohibit private ownership by extending its domestic legislation to also cover non-indigenous tortoise species. In consideration of conservation and animal welfare concerns, we also call for more field research to determine the impacts of illegal trade on wild populations, an updated assessment of its conservation status, increased cooperation between national enforcement agencies, and the implementation of targeted human behaviour change initiatives to help reduce consumer demand for this species.

Keywords

CITES, exotic pet, *Geochelone elegans*, illegal wildlife trade, India, Thailand

Introduction

The illegal trade in wildlife is a big and burgeoning business, with global profits estimated to be worth between $8 – $10 billion US dollars each year (Lawson and Vines 2014). It can have severe negative impacts on wild populations, leading to biodiversity loss, the introduction of invasive species, and disease (Bush et al. 2014). This unregulated activity also represents a particularly severe threat to wild animal welfare during illegal capture, transport, sale and subsequent use (Baker et al. 2013). Increased understanding of the links with other types of criminal activity, including drug trafficking, organized crime, and terrorism is also highlighting how illegal wildlife trade threatens the stability and security of the societies involved (Lawson and Vines 2014).

A substantial component of illegal wildlife trade comprises reptiles and their derivatives or products (Nijman et al. 2012). A recent global analysis of reptile trade indicates an apparent shift away from illegally wild-caught to legal captive-bred sources over recent decades (Robinson et al. 2015). However, despite this trend, INTERPOL seized thousands of live reptiles and products worth more than 28 million US dollars following a global reptile enforcement operation 'RAMP' in 2010 (INTERPOL 2010). More recently, 10% of the 799 international seizure records reported by EU Member States in 2012 involved reptiles (TRAFFIC 2013). Some reptile groups (particularly freshwater turtles and tortoises) are facing disproportionately high extractions and therefore proportionately high extinction risks, with consumer demand for use as food, curios, ceremonies, and pets being a major threat to their survival (Robinson et al. 2015).

The illegal trade in Testudines is arguably nowhere more prevalent than in Southeast Asia (Nijman and Shepherd 2015). Increasing affluence across this region is thought to be stimulating illegal activity (Nijman and Shepherd 2010), leading to steep declines in populations of a large number of species (Nijman and Shepherd 2015). Thailand has long been known as a major hub of this trade (e.g. van Dijk and Palasuwan 2000) where large numbers of many species, both native and non-native, are illegally acquired and traded globally as pets (Chng 2014). For example, a recent study focused on Thai enforcement activity revealed that a total of 18,854 freshwater turtles and tortoises were seized in 53 cases reported between 2008 and 2013 alone (Chng 2014).

Of ongoing and increasing concern from an international illegal wildlife trade perspective (Shepherd et al 2004, IUCN SSN TTSG 2010, Horne et al 2012, UNEP-WCMC 2014), the Indian Star Tortoise (*Geochelone elegans*) is a relatively small and adaptable terrestrial species primarily found in scrub forests, grasslands, and some coastal scrublands of arid and semi-arid regions throughout its wide range (Das 2002). Nesting seasons coincide with the monsoons that vary depending on the geographic location (e.g. (May to June in western India) (March to June and October to January in south-eastern India) Das 2002). This species is famed for the 'star-like' radiating patterns of yellow intermixed with black spots on the pyramidal scutes of its shell that serve as camouflage in the wild (Das 1991) (the literal translation of its local name 'nakshatra tabelu' is 'star tortoise'). However, it is this same patterning that also makes it a popular pet to collectors around the world (Fyfe 2007).

The Indian Star Tortoise was last formally assessed in 2000 and is officially considered as Least Concern on the IUCN Red List as it was not thought to be threatened with extinction in any of its range countries (which include India, Pakistan and Sri Lanka (Das 2002)) at that time (Asian Turtle Trade Working Group 2000). However, given that it may become so unless trade is closely controlled, in 1975, it has been included on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UNEP-WCMC 2011). Consequently, international trade in specimens can take place if an export permit or re-export permit is acquired (CITES 2015). However, to safeguard its wild populations, India had chosen to adopt stricter domestic measures than CITES (WWF 1994). Placed under Schedule IV of the Wildlife (Protection) Act 1972 for over 40 years it has been illegal to possess and commercially trade this species either within or from India (Sekhar 2004).

Despite this legal protection, according to Chng's study (2014) the Indian Star Tortoise was the most frequent illegally traded tortoise seized by Thai authorities between 2008 and 2013 (5966 individuals during 15 cases). Furthermore, this species has also been observed to be the most common openly traded tortoise at the infamous Chatuchak Market in Bangkok, Thailand, during the last decade (653 individuals observed for sale). As a non-indigenous species, it is not currently protected under Thailand's Wild Animal Reservation and Protection Act (WARPA) and enforcement action can only be taken if illegal trade activity is evidenced. However, especially given the possibility of forged trade permits and corruption (TRAFFIC 2008), it can be extremely difficult to identify illegally traded wild sourced individuals and establish the international custody chain once tortoises have been smuggled into the country (Chng 2014). Consequently, there are legitimate concerns that the domestic trade of captive bred Indian Star Tortoises in Thailand represents a 'legal loophole' facilitating illegal poaching from the wild (e.g. Nijman and Shepherd 2015).

Despite increasing concern regarding the illegal international trade in this species, there is a lack of current specific information regarding the number of Indian Star Tortoises obtained via illegal methods, where the traded animals originate from, and the sourcing strategies used to supply them (e.g. Asian Turtle Trade Working Group 2000). To date, there have been four main studies that focussed on the illegal trade in this species from India (Moll 1983, WWF 1994, Sekhar et al. 2004, Anand et al. 2005). One of the most recent peer-reviewed studies conservatively estimated that between 10,000 and 20,000 individuals are being poached from the wild in India each year with authors describing it as 'an erratic localised enterprise' which 'must be contained before it assumes alarming proportions and becomes established' (Sekhar et al. 2004).

Given that the trade in this species was last assessed more than 10 years ago, we conducted fieldwork in India over a 17 month period in order to address the following questions: (1) Where are the current main centres of poaching activity in India? (2) How many tortoises are being (illegally) poached from India each year? (3) What methods are criminal actors using to conduct this illegal trade activity? (4) What are the intended destinations for animals poached from India? We hope that the information gathered will help to guide existing efforts to both preserve remaining wild populations and safeguard the welfare of individual Indian Star Tortoises.

Methods

Illegal trade

To help focus our efforts we collected records of illegal trade from the scientific and grey literature. This semi-systematic review identified the historical occurrence of the illegal trade in 11 (38%) of the 29 states and in one (14%) of the 7 union territory capitals in India over the last 20 years (Figure 1). We identified Andhra Pradesh, Bihar, Delhi, Gujarat, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Orissa, Tamil Nadu, Uttar Pradesh and West Bengal as being historically associated with illegal sale and ownership of this species (Moll 1983; Sekhar et al. 2004; Anand et al. 2004; WWF 1994) (Figure 1). We noted that the cities of Bengaluru (also known as Bangalore), Chennai, Delhi, Hyderabad, Kandla, Kolkata, Lucknow, Mumbai, Pune, Thiruvananthapuram and Vadodara are also all specifically mentioned in this regard (e.g. WWF 1994).

We identified the thorn scrub forests located where the borders of the southern Andhra Pradesh, Karnataka and Tamil Nadu states meet as being historically associated with the sourcing of wild Indian Star Tortoises (WWF 1994) (Figure 1). We

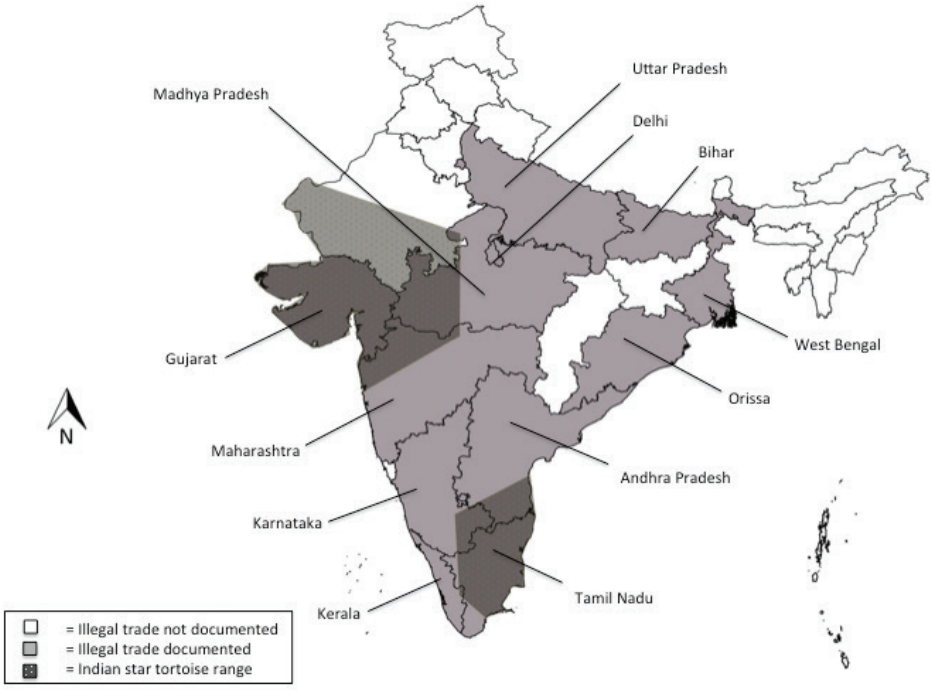

Figure 1. Indian states with documented illegal Indian Star Tortoise trade activity (provided in the existing scientific literature) and the current known geographic distribution of this species within India.

noted that the Saurashtra and Kutch regions of Gujarat are also specifically cited in this regard. We verified this information via concurrent communication with a number of herpetologists and wildlife enforcement officials aware of this issue. Given our specific research objectives (outlined above), we identified the southern state of Andhra Pradesh and the western State of Gujarat as the two sites for our field research.

In Gujarat we focussed our efforts on 16 rural villages and two urban towns surrounding the city of Ahmedabad (referred to hereafter as the 'Gujarat trade hub') (Figure 2). In Andhra Pradesh we focused for US spelling consistency our efforts on eight rural villages around the urban town of Madanapalle, which is located approximately 150 km away from the southern Indian city of Bengaluru, in the state of Karnataka (referred to hereafter as the Andhra Pradesh trade hub) (Figure 2). Between August 2013 and December 2014, we deployed a total of 5 researchers to gather field data. We elicited information, (including footage and stills) from collectors, couriers, consumers and shop retailers regarding source locations (both wild and captive-bred) and intended destinations (both domestic and international). Where possible, researchers documented information regarding the volume and welfare state of the animals involved.

Figure 2. The current domestic and international illegal export trade routes for the Indian Star Tortoise, involving various transport methods (according to this study's fieldwork).

Legal trade

Regulated trade mechanisms can also act as a 'cover' for and facilitate the illegal trade in wild animals (e.g. via false paper work) (TRAFFIC et al. 2008, Dutton et al. 2013). Given existing concerns that 'legal loopholes' are being exploited to sell illegally sourced animals in Thailand (Nijman and Shepherd 2015) we also obtained data from the CITES WCMC (http://trade.cites.org/) to check for any inconsistencies. This database reports all records of import and export of CITES listed species as reported by Parties. Historically there has been some debate amongst taxonomists as to whether this species should be divided into several subspecies or even multiple species (Fife 2007). However, for consistency we included all records referring to '*Geochelone elegans*'. We focus on the live records only, during the period 2004–2013 inclusive, with a specific focus on the numbers reported by both India and Thailand.

Results

Illegal Trade

The Gujarat Trade Hub

With regards to vendors, researchers did not observe any Indian Star Tortoises on open display in this trade hub. However, we found individuals available for purchase upon specific request at the popular 'Dilli Chakla' market in Ahmedabad with seven Indian Star Tortoises (six juveniles and one adult, all in visibly poor health) privately shown to researchers by two vendors during two visits over this period (Figure 2 and Figure 3). Prices ranged from 1,000 to 3,000 Indian rupees (INR) (15 and 50 USD) per animal (Figure 3). Vendors informed researchers that animals sold in Gujarat are typically sourced via contacts based in Bangalore (Figure 2) and are in ready stock in quantities that vary from one to 10. However, larger quantities, if needed, can be supplied with advance payment. They also confirmed that local communities in rural villages surrounding Ahmedabad are also utilised to source wild tortoises from the wild (Figure 2 and Figure 3). The vendors typically operated behind a legitimate facade of dealing in aquariums, exotic birds, and domesticated mammals, such as dogs, cats, rabbits and guinea pigs.

With regards to domestic consumers, despite their legal protection, Indian Star Tortoises are still being openly kept as pets in Gujarat (Figure 4). We observed a total of 107 animals in 17 Hindu households and temples during 36 visits. Owners confirm previous reports (e.g. WWF 1994) that the presence of a tortoise in a household is considered to be a good omen in this particular region of the country. Researchers observed over 100 hatchlings in one urban household on the outskirts of Ahmedabad alone. The owner informed researchers that she was holding these individuals in order to safeguard and prevent their predation prior to subsequent release back into the wild. She was clear to state that, although some were intended for close friends and relatives, none of these animals were intended for commercial sale.

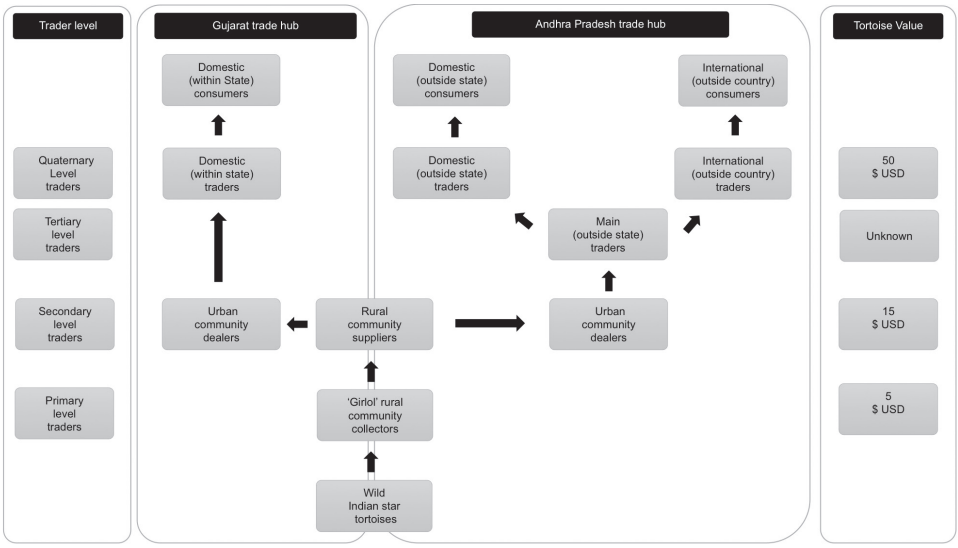

Figure 3. Indian Star Tortoise 'chain of custody' demonstrating the various illegal trade actors and reported market value of individual animals involved in illicit trade activity originating from within India. Tortoise value refers to the maximum observed price (in US dollars) paid to the traders operating at each respective level.

In addition, Indian Star Tortoises are still being openly kept at religious temples for spiritual purposes (Figure 4). We observed a total of 22 animals at three different Shiva temples (with a maximum of 11 individuals observed at one temple) throughout the survey period. We were not permitted access into three additional temples that were reported to house Indian Star Tortoises. Temple representatives confirmed that the tortoise is believed to represent an incarnation of the Hindu God "Vishnu" and as such temple animals are decorated with vermillion marks to symbolize this venerated deity (Figure 4). Animals were reportedly sourced directly from the wild rather than purchased via vendors. Although we were unable to document direct evidence of either the medicinal or subsistence use of Indian Star Tortoises as a source of protein, collectors stated that this activity does still take place.

Previous reports (e.g. WWF 1994) specifically refer to Gujarat as a major organised source of Indian Star Tortoises intended for illegal shipment to the Middle East. However, we found no evidence of any organized illegal transport of Indian Star Tortoises originating from the Gujarat Trade Hub. This is surprising, especially given Gujarat's 1,600 km long coastline, the regular movement of boats to neighbouring Gulf countries, its relatively good transport links (both road and rail) with other large cities in neighbouring states, and the openly observed domestic trade in this species. However, given the relatively short time period of our fieldwork in this geographical area (conducted between August 2013 and January 2014), we acknowledge that further investigation is needed to possibly confirm the absence of illegal transport outside from Gujarat.

Figure 4. A An Indian Star Tortoise at a religious temple near Ahmedabad, Gujarat, India **B** A shopkeeper with a pet Indian Star Tortoise near Ahmedabad, Gujarat, India **C** Indian Star Tortoises kept as pets in a household near Ahmedabad, Gujarat, India **D** An Indian Star Tortoise marked with spiritual 'puja' paint.

The Andhra Pradesh Trade Hub

Unlike Gujarat, in Andhra Pradesh we encountered an organized, large-scale operation engaged in the illegal sourcing of wild Indian Star Tortoises for international consumers (Figure 2, Figure 3). Between January and December 2014 we embedded researchers into a rural hunter-gatherer community known as 'Haki Piki' in Karnataka, 'Yenadi' in Andhra Pradesh and 'Irula' in Tamil Nadu. During this time we observed the collection of at least 55,500 juvenile wild tortoises (a total of 27 consignments, with an average of two per month; Figure 5) by individuals operating from one rural village centre that was collecting tortoises from 15 smaller settlements located along the borders of

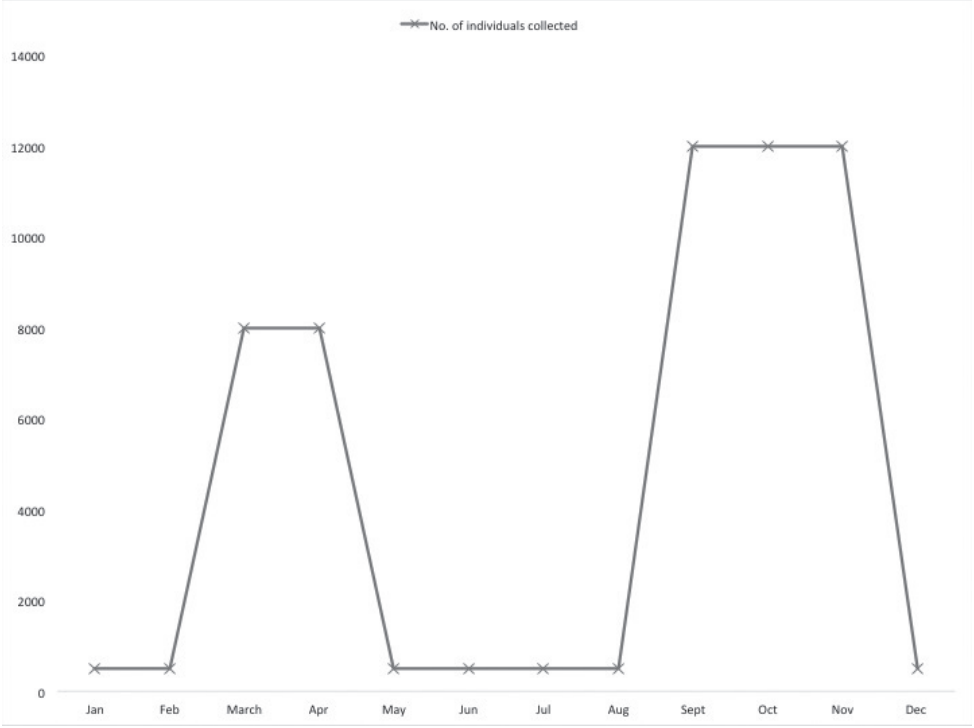

Figure 5. The number of Indian Star Tortoises extracted from one hub 'Madanapalli' in Andhra Pradesh (India) throughout 2014, as observed by this study's field research.

Andhra Pradesh, Karnataka and Tamil Nadu (Figure 2, Figure 6). These secondary level rural traders typically utilize forest dwelling communities like members of the 'Girlol' forest tribal community to collect juvenile tortoises (Figure 3). Collection is predominantly seasonal, taking place after the local monsoon seasons (March and April; and September, October and November) when tortoises tend to emerge out of hiding to feed on fresh sprouting vegetation (Figure 5). Primary collectors tend to pick up specimens that are year-old or older, but collection of sub-adults and adults also takes place.

Between 100 and 150 juvenile tortoises are typically gathered at one time over a period of approximately one week with primary collectors receiving between 50 and 300 Indian Rupees (INR) (1 and 5 USD) per animal from secondary level urban ('middle men') traders depending on the size and health of the animal (Figure 3). Therefore, we conservatively estimate (assuming no mortalities) that the collector engagement in this illegal operation has a collective annual value of up to 16,500,000 INR (263,000 USD) for their impoverished communities. Collectors confirmed they are also often used as couriers to transport these animals to the tertiary level ('main') traders (Figure 3). Animals are often wrapped in cloth and packed into suitcases. However, to avoid detection by enforcement agencies, some are also placed into boxes filled with a top layer 'mask' of other legal produce such as fruit, vegetables, crustaceans and fish.

Figure 6. A: Rural Girlol community collector with wildlife snares; B, C and D; Rural community traders with illegally sourced Indian Star Tortoises (destined for international markets) near Madanapalle, Andhra Pradesh, India.

According to collectors, these tortoises are transported within India to several main traders either by road or by rail (Figure 3, Figure 7). Specifically with regards to this particular trade hub, reference was made to illegal transport along the national highway on the eastern coast of the country joining Chennai (in Tamil Nadu) with Kolkata (in West Bengal) (Figure 7). In addition collectors also made reference to a railway route linking Anantapur and Chittoor (in Andhra Pradesh) to Guwahati (in Assam) via Kolkata (Figure 7). At this stage of the trade chain the main illegal traders are reported to pay between 800 and 1000 INR (12 and 16 USD) per animal (Figure 3). Therefore, we conservatively estimate (assuming no mortalities) that engagement in this operation has an annual value of up to 55,000,000 INR (880,000 USD) for the middlemen involved.

The direct involvement of collectors ends at this point. However, communication with Thai enforcement officials confirmed that cargo boats in Kolkata are used to transport tortoises to other Asian countries including Malaysia, Singapore and Thailand (Figure 7). International passengers also act as couriers taking flights direct from Bengaluru, Chennai, Kolkata and Mumbai (India) or indirect via Dhaka (Bangladesh) into Thailand's Suvarnabhumi International Airport (Anon. Pers. Comm., 2014) (Figure 3 and Figure 7). Alternatively, porous borders are utilised to transport tortoises into Bangladesh (e.g. Dhaka) for further air transport into Thailand (Figure 7). From here, tortoises are also flown on to additional destinations within Southeast Asia including China (predominantly Hong Kong) (Anon. Pers. Comm., 2014) (Figure 7). Throughout our study we found no evidence to suggest that Indian Star Tortoises are being trafficked via Indian from either Sri Lanka or Pakistan.

Legal Trade

Global – CITES Records

Excluding seizure records, CITES reports a total of 211 separate Indian Star Tortoise trade records between 2004 and 2013 (Suppl. material 1). In total, we observed 37,896 individual Indian Star Tortoises reported by export countries during this time. However, during the same time period we also observed a total of 41,014 individual Indian Star Tortoises reported by import countries (representing a discrepancy of 3,118 tortoises). We found that only eleven (5%) of these 211 separate trade transactions have involved wild sourced animals and 198 (94%) of these records have been for commercial use.

India – CITES Records

After analysing the CITES records, we observed no live Indian Star Tortoises (or body parts) exports from India between 2004 and 2013 (Suppl. material 1). During the same time period we found only one import record reported by India (Suppl. material 1). This record relates to 601 wild sourced tortoises that were repatriated following an enforcement seizure made in Malaysia in 2011. These records indicate no legal trade in this species originating from India over the last 10 years.

Thailand – CITES Records

After analysing the CITES records, we observed a total of 2,650 live tortoises imported into Thailand, via seven trade transactions, between 2004 and 2008 (Figure 8; Suppl. material 1). However, we found only 1,100 live individuals reported by exporting countries into Thailand over the same time period (representing a discrepancy of 1,550 tortoises) (Figure 8; Suppl. material 1). We found all of the live imports reported as being sourced via captive breeding programmes for commercial purposes (Suppl. material 1).

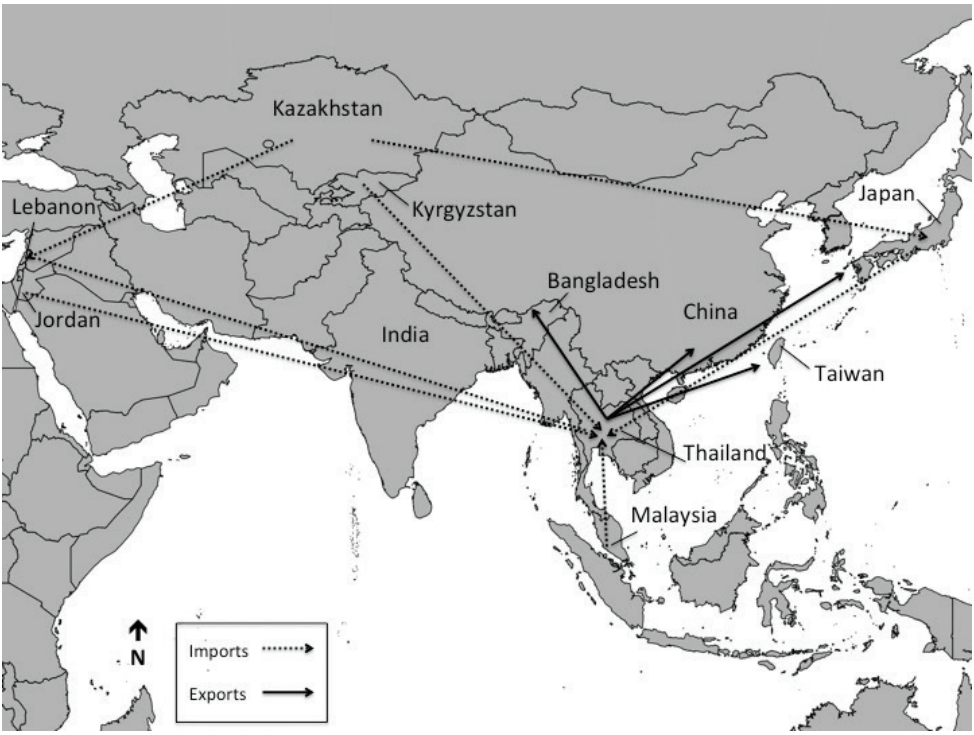

Figure 7. Map to show legal international trade routes for Indian Star Tortoises imported into and exported out from Thailand between 2004 and 2013 (according to CITES WCMC trade database records).

We observed that the majority of import trade transactions into Thailand (43%; *n* =3) came from Lebanon, although imports also came from Jordan (19%) and Japan (19) (Figure 7). We found that Kazakhstan reported to be the country of origin in all records including such data (57%) (Suppl. material 1). Between 2009 and 2013 only one tortoise was imported into Thailand from Singapore, for personal use, from an unknown source (Figure 7; Suppl. material 1).

Between 2004 and 2008 we observed a total of 540 live tortoises exported from Thailand, via ten trade transactions (Figure 9; and Suppl. material 1). However, we found an additional 960 live individuals reported by importing countries from Thailand over the same time period (representing a discrepancy of 420 tortoises) (Figure 9; and Suppl. material 1). We found all of the live exports reported as being sourced via captive breeding programmes (Suppl. material 1).

We observed that the majority of export trade transactions went to Hong Kong (30%; *n* = 3) and Japan (30%), although exports also went to Taiwan (20%) and Bangladesh (20%) (Figure 7; and Suppl. material 1). We found Kazakhstan to be most frequently cited as the country of origin (70%) although Lebanon (20%) and Kyrgyzstan (10%) are also cited with Indian Star Tortoises passing through Thailand for an indefinite period of time (Suppl. material 1). Between 2009 and 2013 we found only three Indian Star Tortoises exported from Thailand to Japan for commercial use from a captive bred source (Figure 7; Figure 9 and Suppl. material 1).

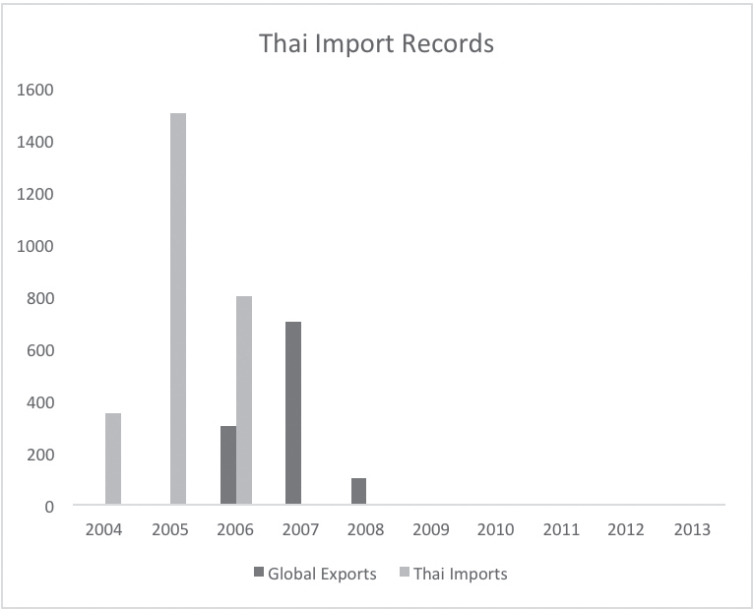

Figure 8. The number of Indian Star Tortoises legally imported into Thailand between 2004 and 2013 according to CITES WCMC trade database records. 'Thai imports' refers to import records reported by Thailand. 'Global exports' refers to export records reported by all other CITES Parties citing Thailand as the intended country of import.

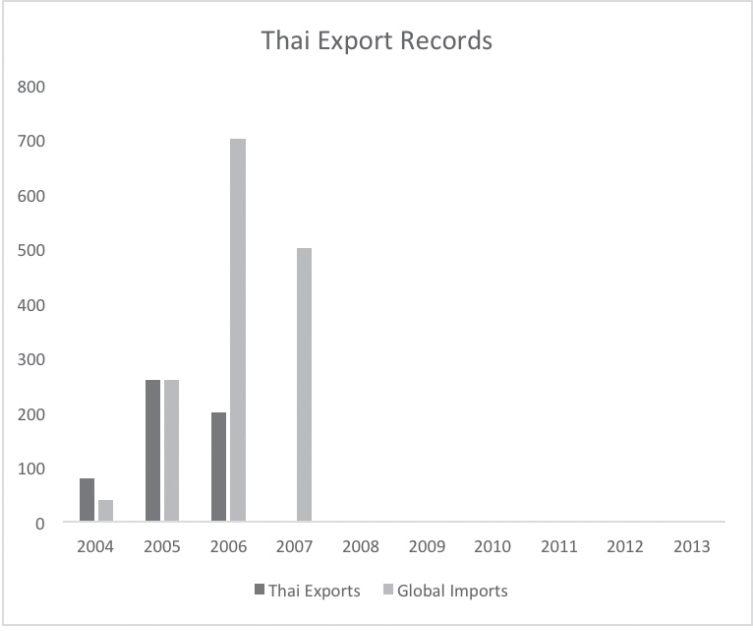

Figure 9. The number of Indian Star Tortoises legally exported out of Thailand between 2004 and 2013 according to CITES WCMC trade database records. 'Thai exports' refers to export records reported by Thailand. 'Global imports' refers to import records reported by all other CITES Parties citing Thailand as the country of export.

Discussion

Conservation and Welfare

The Indian Star Tortoise was last formally assessed for the IUCN Red List fifteen years ago when it was classified as Lower Risk/Least Concern. However, its conservation status is already acknowledged to be in urgent need of updating (Asian Turtle Trade Working Group 2000) and preliminary assessments suggest that a reclassification as 'Vulnerable' may be more appropriate (Horne et al 2012). More detailed field studies regarding the impacts of illegal extraction on wild Indian Star Tortoise populations over time are no doubt required to fully inform this assessment process. However, in cases where there are evident threats to the survival of a species, a threatened listing may be justified even though there may be little direct information on its biological status (IUCN 2015).

We report on the illegal wild removal of at least 55,000 Indian Star Tortoises from just one trade hub in India over a period of one year. This Figure is (three to six times) larger than the 10,000–20,000 individuals previously estimated to be poached throughout the entire range of this species each year (Sekhar et al. 2004). Therefore, despite the current wide distribution of the Indian Star Tortoise, it may be wise to adopt a more precautionary approach to the conservation of this species by providing it with a threatened category status until such detailed information becomes available.

This illegal trade also represents an on-going animal welfare threat (Sekhar et al. 2004, Anand et al. 2005). Physical injury and stress associated with illegal capture, handling and overcrowding can lead to disease and death of traded animals (Warwick 1990; Baker et al. 2013). However, new research also continues to demonstrate that the stress associated with captive conditions during private ownership can also cause detrimental behavioural changes, such as hyperactivity, lethargy and anorexia (e.g. Arena et al. 2012).

Previous studies have raised concerns that Indian Star Tortoises are being smuggled from India into pet markets in Asia, Europe and the United States (e.g. Horne et al. 2012) Although more detailed information is required regarding the consumers involved in this illegal trade chain, our study suggests that many of the Indian Star Tortoises being illegally traded from the Andhra Pradesh trade hub in India appear to be destined for use as exotic pets in Asian countries, such as Thailand and China. As such there are concerns that even if these animals survive capture and illegal transport their welfare may still be compromised as it is currently unclear whether vendors and consumers in these countries possess even a basic understanding of Indian Star Tortoise husbandry requirements (Sekhar et al. 2004, Anand et al. 2005).

An Organized Criminal Network

Ownership of Indian Star Tortoises is likely to have been a long held cultural practice in India (WWF 1994). However, the international commercial trade in this species

appears to be a relatively new and rapidly increasing phenomenon. During an initial survey, Moll (1983) found no evidence of Indian Star Tortoise trade at any of the wildlife markets visited throughout the country and it was not until the mid-1990's (WWF 1994) that initial conservation concerns regarding this illegal activity were first raised. In Gujarat, our findings confirm those of Sekhar et al. (2004) who described an "erratic localised enterprise". Although, commercial trade is clearly taking place, we found no evidence of organised international criminal involvement at this particular trade hub.

Unfortunately, our findings did confirm that the commercial trade in this species has evolved into an international organised criminal operation in other parts of the country (e.g. the Andhra Pradesh trade hub). This type of illegal activity involves a wide range of actors ranging from the rural poor to wealthy urban entrepreneurs (TRAFFIC 2008). It appears that 'middlemen' have built upon the methods to disguise consignments that were first documented more than 10 years ago (Sekhar et al. 2004) to smuggle tortoises internationally via road, rail, air and sea. Even when liberal mortality rates are taken into account, this represents a lucrative business venture worth hundreds of thousands of USD each year to the main criminal actors involved.

Legal Loopholes

Our analysis of CITES records also raises some concerns regarding the current legal trade in this species. We found large discrepancies between imports and exports relating to Thailand that are widely recognized indicators of illegal activity. Historically, Kazakhstan is reported to have been the main supplier into Thailand despite the fact that it is not a range country for this species and a complete lack of import records for any captive breeding stock (Suppl. material 1). The significant involvement of Lebanon (a non-CITES Party until 2013) also calls the legitimacy of Thailand's founding stock into question. Previous calls for CITES Management Authorities to investigate this particular trade route (e.g. Nijman and Shepherd 2010) may be partly responsible for the observed lack of Indian Star Tortoise imports into Thailand over the last five years.

India's Wildlife Protection Act prohibits both trade and private ownership of this species. However, legal domestic trade in other Asian countries appears to be undermining India's efforts to protect this species (Nijman and Shepherd 2015). Specifically, now that the illegal laundering of wild caught animals via legal pathways is subject to increased scrutiny, it appears that illegal reptile traders are increasingly using other more clandestine methods to smuggle these animals into Thailand and on to other target consumer countries, such as China. Once they enter countries that permit legal trade in this species, it is very difficult for the relevant enforcement agencies to distinguish between wild caught and captive bred animals (Nijman and Shepherd 2010).

Consumer demand

With regards to consumers, our study reveals that within India some demand undoubtedly persists for subsistence purposes among members of the rural poor (i.e. as a source of protein). However, on wider assessment, wealth also appears to be an equally strong (if not stronger) driver as domestic demand also extends to 'luxury' use as exotic pets and spiritual purposes. Similarly, although more research is required, international demand for this species throughout South East Asia (particularly Thailand and China) also appears to be driven by demand for use as exotic pets stimulated by increasing affluence across this region (Nijman and Shepherd 2015).

Recommendations

Given the scale of the illegal trade in Indian Star Tortoises uncovered during our study, we recommend that more detailed research should be carried out in order to establish the impact that this unregulated activity is having on wild populations. This information will be required in order to make a fully informed updated formal assessment of the IUCN Red List status of this species. However, while this information is being collected, we suggest that assessors use existing information to inform whether a precautionary approach to the listing of the Indian Star Tortoise is required to help safeguard its survival.

Working together, national enforcement agencies can detect and disrupt the trafficking of wildlife by organised criminal groups, for example by documenting illegal business activities and identifying laws that have been broken in each other's jurisdictions (TRAFFIC 2008). Given the relatively recent development of a highly organised international criminal trade network (involving India, Thailand and other Asian countries such as China) we recommend increased cooperation between relevant national enforcement bodies in collaboration with the Association of Southeast Asian Nations' Wildlife Enforcement Network (ASEAN-WEN).

The legal trade in other Asian countries also appears to be undermining India's efforts to protect the Indian Star Tortoise. As such, we support existing calls (e.g. Nijman and Shepherd 2015) for these 'sink' countries to implement corresponding national bans regarding the commercial trade in this species. In particular, given its concerning current role as a country of transit, extending WARPA to protect non-indigenous species could help to aid Thailand's existing enforcement efforts to address this illegal trade activity.

It is important to note, wildlife laws and enforcement efforts stand little chance of success unless consumer demand for protected wildlife is also addressed (TRAFFIC 2008). Consequently, we recommend that further studies should be carried out to acquire a more detailed understanding of the attitudes and behaviours of Indian Star Tortoise consumers. This information will help to inform existing and any future human behaviour change initiatives focussed on reducing consumer demand for this protected species.

Evidence suggests that a multifaceted approach can be successful in reducing illegal trade in Indian Star Tortoises. For example, a recent market survey has indicated a dramatic drop in the number of Indian Star Tortoises in Malaysian shops over the last 10 years as a direct result of new wildlife legislation, increased enforcement effort and targeted public awareness initiatives (Chng and Bouhuys 2015). As such this type of approach has the potential to yield similar results in other countries of Indian Star Tortoise trade concern such as Thailand.

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Supplementary material 1

Table S1. Table of the Indian Star Tortoise trade transactions (1975–2013)

Authors: Neil D'Cruze, Bhagat Singh, Thomas Morrison, Jan Schmidt-Burbach, David W. Macdonald, Aniruddha Mookerjee

Data type: trade transactions data

Explanation note: Table to show the Indian Star Tortoise trade transactions (1975-2013) as recorded by the Convention on International Trade in Endangered Species of Wild Fauna and Flora World Conservation Monitoring Centre (CITES WCMC) database (http://trade.cites.org/).

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RESEARCH ARTICLE

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Long-term conservation and rehabilitation of threatened rain forest patches under different human population pressures in West Africa

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Abstract

The management schemes of four rain forest patches in southern Benin and south-western Nigeria, which led to the successful protection of numerous threatened plants and animals over the last 20 plus years, are analysed. Since climatic conditions are similar, tree composition depends largely on different availability of water and documented biodiversity mostly on the availability of taxonomic expertise. Management differs according to accessibility and human population pressure, from total closing off of the forest by an international institute near the mega-polis Ibadan to unmarked borders near Lanzron, a remote village in the lower Ouémé Valley, where foreigners are mostly excluded from visiting the site. In Benin, trees and wildlife (antelopes and monkeys) seem best protected where the local vodoun beliefs are adhered to. This is, however, not sufficient and development aid to support and benefit the local population is needed as exemplified in Zinvié. At the Ibadan and Drabo sites, long-term protection is assured by legally-binding land-titles. Since for all of Lanzron and part of Zinvié these are lacking securing them is a priority. In Ibadan, Nigeria, a major rehabilitation effort is concentrated on bringing relatively old grass land and former village sites under forest cover by planting local trees. Rehabilitation in Drabo, in southern Benin, relies on enriching the naturally occurring fallow succession with rare species from nearby threatened sacred forests. We demonstrate that reversing biodiversity loss is possible but requires a long-term commitment. Recommendations for protecting, stabilizing and enhancing similar small hotspots of biodiversity are made.

Keywords
Benin, Nigeria, rainforest, conservation management, sacred forest

Introduction

Today, most West African forests have been destroyed (Poorter et al. 2004, Chazdon 2014). In the so-called Dahomey Gap, which stretches from eastern Ghana to the Republic of Benin, the savannah zone reaches the Atlantic Ocean and rainforests remain limited to pockets characterized by flora and fauna from the Congo block, the Guinea block, or both, with only a few endemics (Robbins 1978, Sinsin and Kampmann 2010). In Benin, rainforest vegetation is restricted to about 1 000 sacred forests, most covering less than 1 ha. These southern forest remnants cover about 1% of the country, yet harbour 64% of critically threatened plant species (USDA 2007, Adomou et al. 2010, Adomou 2011) and numerous endangered animals – almost all outside established nature reserves (Neuenschwander et al. 2011). Most forests in southern Benin, but also those in adjoining south-western Nigeria, are located in highly populated areas (often >200 inhabitants/km^2) embedded in agricultural or peri-urban environments.

Interest in preserving these islands of biodiversity comes first from a widely shared moral imperative. Second, in an ethnographic perspective, these forests have served as worship centres of local belief and/or providers of medicine and food throughout history. Third, in a more practical manner, biodiversity conservation is important to the long-term sustainability of agriculture. A high degree of biodiversity is the basis of organic farming (Pimentel et al. 1997, Mäder et al. 2002, IAASTD 2008), in particular crop protection, varietal development and climate change mitigation. Thus, alternate hosts, shelter and food for natural enemies of pests are important in biological control (Neuenschwander et al. 2003, van Driesche et al. 2010) and wild relatives of crop plants, such as yams, provide genetic resources for adapting crops to climate change (Corlett 2014). Nature reserves must therefore be considered a prudent investment even though knowledge and understanding of their interactions with agriculture are still sketchy and need further research (Wrangham and Ross 2008).

At present, the keepers of these landscapes, small-scale subsistence farmers, are often not or not yet in favour of nature protection in or near their communities (Vodouhê et al. 2010). Increasingly, agriculture and nature protection are, however, seen as complementary (McNeely and Scherr 2001, CGIAR 2015) whereby biodiversity is being preserved in-field by a diversified agriculture as well as in nature reserves (Klein et al. 2014). In Benin, the need to preserve rainforest remnants has been described as the first priority in nature protection (Neuenschwander et al. 2011) whereby benefits should accrue to those living in the vicinity and not (only) to outside operators, as they unfortunately often do. Since the region has no extended virgin forests, rehabilitation of the existing remnants becomes important even if they are small and heavily impacted.

In the present study, we look at four small forests, chosen for different management practices as they are imposed by different human population pressures. The four

forests are reasonably well protected over the timespans of 10 to 30 years that the retrospective analysis covers. We describe the history and ecology of these forests and our efforts to rehabilitate them in order to answer the following questions: 1- Can biodiversity of plants and animals be preserved and augmented sustainably in small humid forest patches? 2- How can interactions with the local populations be managed to assure sustainability? We address the balance between exploitation and protection, and the role of local beliefs. And finally we present our educational efforts at improving the chances for sustainable protection under the predicted and already observed relentless population increase and climate change. For each forest, future trends are divined and activities to cope with them are indicated in an 'Outlook'.

Materials and methods

Study sites

The study describes the conditions and history of four sites:

1) Campus of the International Institute of Tropical Agriculture (IITA) Ibadan, Nigeria. 7°29'N, 3°54'E.

It covers approximately 1000 ha and is situated alongside a major axis north of Ibadan, a fast-growing conurbation whose population exceeds 3 million. The campus is situated in a region of rolling topography at 186 to 240 m, which was acquired by IITA from the Government of Nigeria in 1967 for the establishment of the Institute on a 99 year lease. Roughly rectangular and originally about 10 km outside the city, it consisted of secondary forest and fallow vegetation, 28 villages and smallholder fields interspersed with some cocoa and small areas of grassland created by burning. After the villagers were relocated, the concession was enclosed by a security fence 2.4 m high and 14 km long with access roads on both sides for visibility and maintenance. The Awba River, which runs through the campus, was dammed to form a 2.6 km long reservoir. Land was cleared for housing and fields for agricultural crop research. The remaining area, an estimated 380 ha, was left as a nature reserve.

The reserve is at a 'crossroads' of sub-Saharan forest types, where rainforest meets savannah and at the westernmost limit of the Guinea-Congo forest adjoining the Dahomey Gap. It is fragmented by roads and other land uses. The largest block of forest was more or less intact until the 1980s when an area of 46.6 ha was cleared for alley-cropping and other experiments. After a decade of intensive use, this area was abandoned and became infested with *Leucaena leucocephala* and *Gliricidia sepium*. In 2012 the area was cleared again. An experiment to grow yams on different indigenous tree species occupied a few hectares, serving longer term as reforestation. Another area of forest borders on a derelict Arboretum of 5.9 ha, which was established in the 1990s for agroforestry purposes. The Golf Course and forest belt along the southern perimeter of the campus retain some fine forest trees and act as a wildlife corridor. In the

main forest block, trails of approximately 5 km enclosing an area of 37 ha of varied topography were cut in December 1987. Historically cutting of lianas produced large masses of dead vegetation, which sometimes brought down entire trees. In 2013 more conservative cutting back was introduced and trails were no longer raked, resulting in noticeably more flowers and fruits, and also in litter that protects the trails from erosion. Despite regular disturbance from movement of vehicles and people, and even removal of topsoil for horticultural purposes, the IITA forest is one of the few remaining and best protected patches of forest in south-western Nigeria.

Soils are mostly shallow and acidic. The bedrock is of banded gneiss which weathers to form site-specific soils and saprolite (softened granite or gneiss) with characteristic exposed flattened outcrops. Clay, quartz gravel and sand predominate in uplands, laterite on lower and middle slopes, and poorly drained clayey and sandy soils in valley bottoms. Where trees and vegetation are cleared, organic matter is rapidly lost and soils have low water-holding capacity. Erosion is a major concern on forest access roads, trails, and other exposed areas. Aquifers are rare and groundwater is shallow and localized mostly in faults and troughs in the bedrock (Moorman et al. 1974).

Annual rainfall in the Ibadan area averages 1300 mm and is heaviest in June (190 mm) and September (220 mm), with markedly less in August, and a pronounced dry season from November to March. Turbulent storms with heavy rain occur frequently during the wet season causing severe erosion of exposed soils and laterite roads. Typical daytime temperatures are 26–38 °C while at night the temperature rarely falls below 18 °C, occasionally dipping to 16 °C during Harmattan, which occurs mainly in January when dust-laden air currents flow from the north.

Research on biodiversity and conservation increased incrementally. Though some forest areas had been utilised as a resource for research (Hall and Okali 1978, 1979) and more recently by postgraduate students the strongest conservation efforts were made by two projects. The first (2000–2002), involved an environmental education centre, a biological inventory, and socio-economic characterization of communities and land use. Some propagation and planting of indigenous trees was carried out, but the focus was apparently on supplying farmers with tree crop plants, such as cocoa, citrus, plantain, and teak. The second, the Forest Project (2010–2014), continued maintenance of forest trails, increased security patrols and monitoring of biodiversity, engaged in large-scale reforestation and established an indigenous plant nursery and Ethnobotanical Garden. Up to now, no agreed management plan exists, apart from keeping forest trails clear for hiking and a ban on hunting.

Restoration was an important aspect of the current project. Over 85 tree species and many other indigenous plants were propagated. Most species were recovered from the IITA forest, but a few, such as *Massularia acuminata* and *Picralima nitida* were collected in Cross River State. Surplus seed was stored in the IITA Genetic Resources Centre.

Reforestation was done by planting indigenous species after removal of invasive exotic species. The main area of reforestation was on the east bank of the reservoir. It is approximately 2.6 km long and 30–60 m wide. With the aim of controlling erosion and run-off of nutrients and agrochemicals, over 4400 trees of 45 species were planted

in this degraded farmland, i.e., derived savannah grassland. Ensuring that small trees survive competition from giant grasses (*Andropogon* spp.) required clearing of 1–2 m in diameter around the base of each tree; cut grass was used to mulch the cleared area. In addition, approximately 360 trees of 18 species were planted in gaps on the west bank of the reservoir, including trees that cope with seasonal flooding. Other reforested areas include two former dumpsites where 1120 trees of 18 species were planted and where the soil is contaminated with heavy metals, organic solvents, etc. Within the forest, restoration was carried out successfully in locations that present different challenges. In former village sites planting holes were made in dense bush. Here young trees grew rapidly in soil enriched by organic waste from former human habitation. Patches of *Chromolaena odorata* along trails were cleared before flowering and planted with young trees at the start of the following rainy season. A rock outcrop in the forest was cleared of bush and successfully planted with *Hildegardia barteri*, a species adapted to these extreme conditions. Watering of young trees was seldom done, either at planting or during the dry season, due to difficult access and staff time; only a few within easy reach of the reservoir were watered by hand when obviously stressed.

2) Sanctuaire des Singes, Drabo Gbo, IITA-Benin, Benin 6°30'N, 2°18'E.

The monkey sanctuary of Drabo Gbo was founded in 1995, when the first author bought 2.5 ha of teak forest and agricultural land from the elders of Drabo Gbo, 30 km north of Cotonou, 12 km from the spreading town of Calavi. Up to 2005, more land was bought and today the sanctuary covers a total area of 14 ha of small old forest islands and rehabilitated forest adjacent to the villages of Drabo Gbo, with about 500 inhabitants, Drabo Fanto of the same size, and the still smaller village of Dodja. The sanctuary is reached over unsurfaced, often bad roads. Most parts of the forest edge are protected by a low fence consisting of lines of barbed wire with palm leaves inserted perpendicularly. This is more a marker for people to respect than a protective measure and leaves free access to wildlife.

The forests include the old sacred forest of Dodja (0.7 ha) north of Drabo Gbo which was not touched for over 100 years, but still shows signs of tree felling before this time. Another sacred forest, the Orojamè forest of Drabo Fanto, was created about 80 years ago by delineating a surface of 0.4 ha around an old *Cola gigantea* tree. Additional purchase of land brought this to 0.8 ha. This still is the central site for the regional Oro cult. The rest of the land is covered by fallow of 10–20 years of age. Villagers report that most of the present land was under forest cover 40–50 years ago.

The forests grow on a deep lateritic soil and the water table throughout the area and the adjoining villages is at 25 m. Annual rainfall in Drabo averages 1200 mm spread over two rainy seasons and interrupted by a short dry season in mid-July-August. Early rains are highly irregular. Typical daytime temperatures fluctuate between 26 and 34 °C. Night temperatures rarely fall below 20 °C, but during Harmattan in January temperatures as low as 15 °C have been observed.

Rehabilitation of the forests was initiated by dozens of collection trips in the southern rainforest patches (Ahozon, Dangbo, Ewè, Lama, Niaouli, Pobè: see Neuen-

schwander et al. 2011) during the last 20 years. An estimated several thousand plantlets (1–10 plantlets or seeds per species and collection date) were either planted out in a nursery or directly into what were judged to be the best microhabitats for each species. Hand irrigation in the nursery and frequent mulching in the forest assured that even plants from slightly moister forests could survive in Drabo.

In order to find open space for planting new trees 30–50 oil palms *Elaeis guineensis* are cut every year until all thickets of oil palms will have been removed. Trees are sold to producers of the local alcoholic drink *sodabi*, which is distilled from palm wine. Every year, some teak (*Tectona grandis*), *Senna siamea* and *Acacia auriculiformis* are marked to be cut to satisfy demand by villagers for fire- and construction wood.

At the time of purchase, the trees of each lot, particularly oil palms, were bought separately from the land in order to avoid problems with the sellers or, later, their children. Title deeds were obtained as new land was acquired between 1995 and 2003. All titles (a total of 25) were issued to the owner and registered with the central authorities. For some later land purchases, however, titles have not yet been obtained. In January 2014, the rights to all plots (except for the central house) were handed over in a ceremony to IITA, which accepted the responsibility of maintaining the forest and using it for research while respecting the existing forest cover. The Drabo forest reserve was brought to the attention of the mayor of Calavi, when a new Community Development Plan was developed, which is, however, still not finalized and publicized.

3) Forêt de la Panthère of Kpotomè at Zinvié, Benin. 6°37'N, 2°21'E.

The Forêt de la Panthère, a forest island of 1.4 ha, is the relict of a much larger forest that 100 years ago sheltered the eponymous pair of sacred panthers. It is situated in the Zinvié arrondissement near the village of Kpotomey (in Fon language: 'the panther village'), which has about 600 inhabitants. Initially, this forest belonged to the founder family collective; but about 50 years ago it was given on loan to the lagoon village of Gbodjè, which sacralised the forest and gave it to their vodoun deity. In 2007, as relations between owners and users had become conflict-ridden, the owners demanded that the forest be handed back. A recent decision by the justice recognized ownership by the family collective from Kpotomey against claims by the former users from Gbodjè. Ownership of the Forêt de la Panthère is, however, not yet recorded in any legal document.

This forest is situated on a ferralitic soil with sandy clay. The water table is at only 2–3 m depth. Climatic conditions and rainfall patterns are as in Drabo.

The owners of the forest do not deliberately rejuvenate it and the boundary is not marked by a fence. In order to rehabilitate parts of the forest, CREDI-ONG (French acronym for Non-government Organisation 'Regional Research and Education Centre for Integrated Development') started the creation of a green belt of 1.4 ha by buying up neighbouring lots in 2008. This land is left to develop into mature fallow and is sometimes enriched by planting trees, among them *Ceiba pentandra*, in opportune sites. A recent threat by an expanding quarry is being blocked by the purchase of another piece of land.

4) Forêt de Bahazoun at Lanzron, Benin. 6°38'N, 2°23'E.

The forest of Bahazoun at Lanzron covers 50 ha and is the largest forest island in the community of Abomey-Calavi. Situated in the large floodplain of the Ouémé River, this forest has been, for many generations or over 100 years, in the hands of the same large family. Today, Lanzron (meaning 'rich in jumping wild-life') is a small village of about 100 inhabitants, which is accessible only over rural tracks that are highly degraded during the rainy season.

The Bahazoun forest, with its preliminary plant list by Hèdégbètan (2011), is situated on hydromorphic soil with gleys and alluvial deposits. The forest is inundated from August to November; the rest of the year the water table is at a depth of 2–3 m. The overall climate is similar to the one reported for Drabo, though rainfall is probably slightly higher.

Methods

All four sites are covered by semi-deciduous forests of the Guinea-Congolese zone (Adomou 2011). Drabo is at the edge of the Plateau district, Zinvié and Lanzron in the Ouémé Valley district, and IITA-Ibadan (about 200 km NE of Cotonou) botanically closest to the Pobè district. For Benin, plants are identified according to Akoègninou et al. (2006) and Hawthorne and Jongkind (2006), for Nigeria in addition with Hutchinson and Dalziel (1963), Keay et al. (1964), and comments by R Latchford (Environmental Investigation Agency) and D Ladipo (pers. comm. on *Milicia excelsa*). Taxonomic positions are updated with reference to http://www.theplantlist.org/ (Table 1). For mammals see Kingdon (1997), for birds see Borrow and Demey (2001) plus for Benin F Dowsett-Lemaire and R Dowsett (2009, unpublished results) and for Nigeria Adeyanju et al. (2014); for lizards and chameleons Trape et al. (2012); for butterflies Larsen (2005) and Sáfían Szabolcs (unpubl. results) for Nigeria and Goergen et al. (2011) for Benin (all insects, incl. for Nigeria). New vertebrate species of Benin are mentioned in Neuenschwander et al. (2011). The conservation status (following IUCN-criteria) has been updated for Benin (Neuenschwander et al. 2011) with EW = extinct in the wild, CR = critically endangered, EN = endangered, VU = vulnerable. For Nigeria, it is given according to the slightly outdated official IUCN list. It applies a ranking that is often one step lower than the Benin list, though exceptions like *Millettia warneckei*, *Pararistolochia goldieana* and *Synsepalum brevipes* exist where the Benin ranking is lower.

By necessity, human interactions are reported as anecdotes. Throughout, comparisons between the different sites are presented in Table 2 with semi-quantitative scores to be further evaluated in the discussion. Score 1 indicates worst, score 5 best conditions; where this is not applicable, score 1 indicates historically earlier, score 5 recent conditions.

Results

1) Forest Reserve of the International Institute of Tropical Agriculture (IITA)

Biodiversity conservation and restoration

Small areas of this forest have a high diversity of plant species, providing a snap-shot of mature Guinea-Congo forest, but the general picture is one of secondary forest and 'bush' with few large trees. Being isolated and no longer bound together by lianas, such trees are prone to storm damage, setting back forest regeneration. Though village sites were abandoned 45 years ago they remained devoid of trees as tree seedlings could not establish in dense bush. The trees that were planted on dump sites gave mixed results; some failed to thrive, perhaps because they are sensitive to certain contaminants, while others like *Alstonia boonei*, *Antiaris toxicaria*, *Bombax buonopozense*, *Ceiba pentandra*, *Cleistopholis patens*, and *Triplochiton scleroxylon* flourished. In other sites where young trees have been planted into bush and kept clear of climbers, regeneration is rapid. After three years, some trees reached heights of 3–7 m. These include *Bombax buonopozense*, *Cola gigantea*, *Entandrophragma angolense*, *Pterocarpus santalinoides*, *Pterocarpus soyauxii*, *Terminalia superba*, and *Triplochiton scleroxylon.* Nevertheless, the initial estimate of 75–100 years for the entire forest to attain maturity seems unlikely.

Despite the general degradation, over four decades of protection have ensured the survival of a great diversity of plants and animals. Loss of surrounding forests during this period adds to the importance of this refuge for numerous species that are becoming scarce in south-western Nigeria. It has become a stronghold for several taxa that have been assessed by the IUCN as of priority for conservation. There are also mature rainforest trees outside forest areas, particularly iroko (*Milicia excelsa*), which are sacred to the local Yoruba people. As a result, the entire campus has conservation value and is reputedly the last stronghold of iroko in south-western Nigeria

Currently, the checklist of flora stands at 509 species, including approximately 150 species of trees. The majority of species are indigenous; but also included are some exotics that have become naturalized, including large stands of giant bamboo (*Bambusa vulgaris*), which was introduced to West Africa from Asia long ago. It now occupies many hectares, especially along watercourses. Being virtually impossible to eradicate it poses a major challenge to conservation and regeneration of the forest. The most common trees are listed in Table 1. Endangered tree species include *Afzelia africana* VU, *Afzelia bipindensis* VU, *Albizia ferruginea* VU, *Entandrophragma angolense* VU, *Entandrophragma cylindricum* VU, *Garcinia kola* VU, *Guarea cedrata* VU, *Khaya grandifoliola* VU, *Khaya senegalensis* VU, *Mansonia altissima* EN, *Nauclea diderichii* VU, *Nesogordonia papaverifera* VU, *Parkia bicolor* EN, *Strombosia pustulata* EN, and *Terminalia ivorensis* VU.

In addition to IUCN Red List species, local knowledge indicates that the following species are in steep decline: *Alstonia boonei*, *Milicia excelsa*, *Pterocarpus erinaceus* and *Triplochiton scleroxylon*.

Table 1. List of scientific plant names, according to www.plantlist.com. Red List status for Benin see Adomou et al. (2010) and for Nigeria see IUCN International List (VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild); + = not threatened, but mentioned in text for at least one forest. Status: July 2015.

Species	Ibadan	Drabo	Zinvié	Lanzron
Acanthus montanus (Nees) T. Anderson (Acanthaceae)	+	CR		
Acacia auriculiformis A. Cunn. (Leguminosae)		+		
Acridocarpus alternifolius (Schum. & Thonn.) Nied. (Malpighiaceae)		EN	EN	EN
Acridocarpus smeathmanii (DC) Guill. & Perro (Malpighiaceae)	EN	EN		
Afzelia africana Pers. (Leguminosae)	VU	EN		
Afzelia bipindensis Harms (Leguminosae)	VU			
Albizia adianthifolia (Schumach.) W.F.Wright (Leguminosae)		+	+	+
Albizia glaberrima (Schum.) Thonn. & Benth. (Leguminosae)	+	+	+	+
Albizia ferruginea (Guill. & Perr.) Benth. (Leguminosae)	VU	VU		VU
Albizia zygia (DC.) J.F. Macbr. (Leguminosae)	+	+	+	+
Alstonia boonei de Wild. (Apocynaceae)	+			
Antiaris toxicaria Lesch (Moraceae)	+	+	+	+
Bambusa vulgaris Schrad. ex Wendel (Poaceae)	+	+		+
Barteria nigritiana Hook.f. (Passifloraceae)		CR		
Berlinia grandiflora (Vahl) Hutch. & Dalziel (Leguminosae)	+	+		+
Blighia sapida Koenig (Sapindaceae)	+	+	+	+
Blighia unijugata Bakker (Sapindaceae)	+	+	+	+
Bombax buonopozense P.Beauv. (Malvaceae)	+	+		
Caloncoba echinata Engl. (Flacourtiaceae)		CR		
Ceiba pentandra (L.) Gaertn. (Malvaceae)	+	+	+	+
Celtis prantlii Priemer ex Engl. (Celtidaceae)	+	+		
Celtis zenkeri Engel. (Celtidaceae)	+	+		
Chromolaena odorata (L.) R.M. King & H. Rob. (Asteraceae)	+	+	+	+
Chrysophyllum albidum G.Don (Sapotaceae)	+	+	+	
Cleistopholis patens (Benth.) Engl. & Diels (Annonaceae)	+	+		+
Cola gigantea A. Chev. (Sterculiaceae)	+	+	+	
Cola millenii K.Schum. (Sterculiaceae)	+	+	+	
Craterispermum cerinanthum Benth. (Rubiaceae)		+	+	+
Dactyladenia barteri Hook. f. ex Oliv. (Chrysobalanaceae)	+			
Dennettia tripetala Baker f. (Annonaceae)	VU	CR		
Dialium guineense L. (Leguminosae)	+	+	+	+
Distemonanthus benthamianus Baill. (Leguminosae)		EN		
Elaeis guineensis Jacq. (Arecaceae)	+	+	+	+
Entandrophragma angolense C.DC (Meliaceae)	VU	CR		
Entandrophragma cylindricum (Sprague) Sprague (Meliaceae)	VU			
Euclinia longiflora Salisb. (Rubiaceae)		EN		
Ficus exasperata Vahl (Moraceae)	+	+	+	+
Funtumia elastica (Preuss) Stapf.(Apocynaceae)	+			
Garcinia kola Heckel (Clusiaceae)	VU	EW		
Guarea cedrata (A Chev.) Pellegr. (Meliaceae)	VU			
Gliricidia sepium (Jacq.) Kunth. ex Walp. (Leguminosae)	+	+		

Species	Ibadan	Drabo	Zinvié	Lanzron
Hildegardia barteri (Mast.) Kosterm. (Malvaceae)	+	+		
Holarrhena floribunda (G.Don) Durand & Schinz (Apocynaceae)	+	+	+	+
Homalium le-testui Pellegr. (Flacourtiaceae)		EN		
Khaya grandifoliola C. DC. (Meliaceae)	VU	EN		
Khaya senegalensis (Desv.) A Juss. (Meliaceae)	VU	EN	EN	EN
Lecaniodiscus cupanioides Planch, ex Benth.(Sapindaceae)	+	+	+	+
Leucaena leucocephala (Lm.) de Witt (Leguminosae)	+	+	+	+
Maerua duchesnei (DeWild.) F.White (Capparaceae)		EN		
Mansonia altissima (AChev.) A. Chev. (Sterculiaceae)	EN	CR		
Maranthes robusta (Oliv.) Prance ex F.Wright (Chrysobalanaceae)	+	+		+
Massularia acuminata (G. Don) Bullock ex Hoyle (Rubiaceae)	+			
Milicia excelsa (Welw.) C.C. Berg (Moraceae)	VU	EN	EN	EN
Millettia warneckei Harms (Leguminosae)			+	+
Mimusops andongensis Hiern. (Sapotaceae)	VU	EN		EN
Monodora myristica (Gaertn.) Dunal (Annonaceae)		EN		EN
Napoleonaea vogelii Hook. & Planch. (Lecythidaceae)		+	+	+
Nauclea diderrichii (De Wild.) Merr. (Rubiaceae)	VU	EN		
Nesogordonia papaverifera (A.Chev.) Capuron (Malvaceae)	VU	CR		
Pararistolochia goldieana (Hook f.) Hutch. & Dalziel (Aristolochiaceae)	VU	+		
Parkia bicolor (Jacq.) R.Br.ex G.Don (Leguminosae)	EN	EN	EN	
Picralima nitida (Stapf) T.Durand & H.Durand (Apocynaceae)	+	+		
Piptadeniastrum africanum (Hook f.) Brenan (Leguminosae)		VU	VU	
Psilanthus mannii Hook f. (Rubiaceae)		CR		
Pterocarpus erinaceus Poir. (Leguminosae)	+			
Pterocarpus soyauxii Taub. (Leguminosae)	+			
Pouteria alnifolia (Baker) Roberty (Sapotaceae)	+	+	+	+
Senna siamea Lam. (Leguminosae) Caesalpiniaceae)	+	+		
Spathandra blackeoides (G.Don.) Jacq.-Fel. (Melastomataceae)		+	+	+
Spondias mombin L. (Anacardiaceae)	+	+		+
Sterculia tragacantha Lindl. (Sterculiaceae)	+	+	+	+
Strombosia pustulata Oliver (Olacaceae)	VU	EN		EN
Synsepalum brevipes (Baker f.) T.D.Penn (Sapotaceae)		+		+
Synsepalum dulcificum (Schum. & Thonn.) Daniell. (Sapotaceae)	+	EN	EN	EN
Tectona grandis L. (Verbenaceae)	+	+	+	
Terminalia ivorensis A. Chev. (Combretaceae)	VU			
Tricalysia coriacea (Benth.) Hiern (Rubiaceae)		CR		
Trichilia monadelpha (Thonn.) J.J.de Wilde (Meliaceae)	+		+	+
Trilepisium madagascariense DC. (Moraceae)	+	+		
Triplochiton scleroxylon K.Schum. (Meliaceae)	+	EN		
Turraea heterophylla J.B.Hall (Meliaceae)	+	EN		
Xylopia aethiopica (Dunal) A.Rich. (Annonaceae)	+	VU	VU	
Zanthoxylum zanthoxyloides (Lam.) Zep. & Timb. (Rutaceae)	+	VU	VU	VU
Zanthoxylum gilletii (De Wild) P.G.Waterman (Rutaceae)		EN		

The most spectacular plant in the forest is *Pararistolochia goldieana* VU, a liana with massive trombone-shaped blooms measuring some 60 cm long and 30 cm across at the gaping mouth. It is known from lowland rainforest in Cameroon, Bioko (Equatorial Guinea) up to Sierra Leone. The population in the IITA forest is possibly the largest remaining in south-western Nigeria.

The checklist of birds for IITA currently stands at 269 species. The Ibadan campus was designated as a globally Important Bird Area (IBA) in 2002 by BirdLife International and re-registered in 2014. It includes a wide range of habitats for both resident and migratory species. Among Guinea-Congo species are Baumann's greenbul (*Phyllastrephus baumanni*), a West African endemic, and the rare Ibadan malimbe (*Malimbus ibadanensis* EN), which is restricted to small patches of dense vegetation in and around the Ibadan area. Most areas where it was once recorded have been reduced or have disappeared with urbanization, increasing the importance of the IITA forest in the conservation of this species.

The checklist of butterflies has 236 species. Of particular note is the indigenous *Charaxes boueti* (Nymphalidae), a formerly rare butterfly feeding on exotic bamboo. Beetles of special interest are: *Taurhina nireus* (Scarabaeidae, Cetoniinae) a very infrequent and strongly seasonal species not previously known from Nigeria, and the localized subspecies *Pachnoda cordata camerounensis* (Scarabaeidae, Cetoniinae).

The provisional list of mammals includes 46 species. Eleven species of bats have been recorded to date and they are probably the most numerous mammals in forest areas; at certain times of the year when trees such as iroko and mango are fruiting, hundreds of thousands of straw-coloured fruit bats (*Eidolon helvum*, Pteropodidae), converge on the campus and roost in such large numbers that they damage and occasionally kill trees. Nine species of squirrels (Sciuridae) have been recorded, to which may be added Lord Derby's flying squirrel (*Anomalurus derbianus* EN, Anomaluridae). Due to urbanisation and poaching no resident troop of monkeys has been recorded in the IITA forest for over a decade though occasional unconfirmed sightings are made. Gambian mongoose (*Mungos gambianus*), marsh mongoose (*Atilax paludinosus*), and flat-headed cusimanse (*Crossarchus platycephalus*, Herpestidae) are documented. Western tree hyraxes (*Dendrohyrax dorsalis*, Procaviidae) are seldom seen but often heard at night, and there are occasional encounters, often in car headlights, of African civets (*Civettictis civetta*, Viverridae). The largest mammal, and a favourite with poachers, is the bush duiker (*Sylvicapra grimmia*, Antilopidae), one of three species of duiker recorded in the forest.

A preliminary survey of reptiles recorded 20 species. Observations indicate that populations are decreasing due to persistent slaughter by farm and garden staff and through more intensive use of land. There is a single record of green mamba (*Dendroaspis* sp.) and the presence of python (*Python* spp.) has been confirmed; but forest cobra (*Naja melanoleuca*) and spitting cobra (*N. nigricollis*, Elapidae) are common, the latter perhaps becoming more common as a result of deforestation and consequent spread of grassland.

Sustainable people management

In 1970 villagers were relocated but allowed continued access for the purposes of collecting firewood, oil palm, and kola nuts until compensation was paid. Though compensation was paid many years ago, villagers are still allowed to collect materials as a goodwill gesture. From an ecological standpoint, large amounts of biomass are removed annually that could be recycled or sold to support conservation of the forest. In terms of relationships, the arrangement perpetuates an attitude that local people have rights to exploit resources within the campus, especially as these resources–bush-meat, timber, wild fruits and vegetables, and medicinal plants–are now in extreme short-supply in surrounding areas and can provide the basis for commercial enterprises rather than for domestic consumption.

Until recently gunshots could be heard at any time of the day and night and little could be done by unarmed Forest Project staff against armed poachers. Forest Rangers are now employed by the Security Unit with powers to arrest poachers and hand-over to police for prosecution. Theft of plants/plant parts, fuel wood etc. is treated more leniently with a warning and on-the-spot education.

Protection of the forest arguably owes more to the high level of campus security than to its perceived importance for conservation. There is, however, no doubt about its value to IITA staff and visitors who enjoy forest walks and commemorative tree planting, to schools and universities which benefit from environmental education, and to local people in terms of resources they once took for granted. Most people in surrounding areas still live on less than $1 a day, depend on medicinal plants for health care, prefer bush-meat to meat from domestic animals, and have little or no education; they are therefore unaware of issues such as unsustainable use of natural resources, loss of biodiversity, or climate change.

Outlook

To protect a forest on the campus of an international institute that is dedicated to agricultural research yet surrounded by comparatively poor people who want to profit from this forest is a challenge. Public relations at local, state and federal level, and a better understanding of the importance of such a refuge of biodiversity among campus residents, staff (including low-literate employees, such as casual workers) and visitors, will be crucial for its survival. Protection of the forest and campus as a Science Park in perpetuity is also vital to ward off interest by developers. In addition to conservation of biodiversity, the new IITA Forest Unit aims to reduce pressure on forest resources by cultivating useful fruits, vegetables, mushrooms, and medicinal plants, and farming of bush meat, such as grass cutters and snails. Partnerships with other NGOs and/or relevant university departments to co-manage the forest are being considered and a new Tree Heritage project (2015–2018) will build on these *in situ* and *ex situ* resources.

2) Sanctuaire des Singes, Drabo Gbo

Biodiversity conservation and restoration

In Dodja, huge (30–40 m high) trees of *Cola gigantea*, *Celtis* spp. and *Antiaris toxicaria* are probably several hundred years old. A few big trees also exist in Drabo Gbo. Over 90% of today's Drabo forests are, however, the results of fallow development over 20 years through low bush to what is now young secondary forest. The introduction of species from older forests and the freeing of trees from climbers sped up this succession. Since most land had been under forest cover before, quick regrowth leading to a 20 m high canopy was assured. Even trees planted as seeds or seedlings 20 years ago reached this height.

As a result of the long-lasting effort in introducing plantlets and seeds from other forests of the region the list of plants registered on this land now comprises over 600 species including 200 species of trees. The forest has become a sanctuary for rare rainforest species, some from unique and unprotected stands in Benin. A total of 50 threatened species (out of the Red List Benin total of 100 in these categories) are found in Drabo i.e., 15 VU, 24 EN, 9 CR, and 2 EW). We cite here only those that are critically endangered (CR): *Mansonia altissima*, *Nesogordonia kabingaensis*, and *Dennettia tripetala* from the threatened, unprotected forest of Ewè, *Caloncoba echinata* and *Entandrophragma angolense* from Niaouli, *Barteria nigritiana* and *Tricalysia coriacea* from Ahozon, *Psilanthus mannii* from Dangbo and *Acanthus montanus* from Porto Novo. Some interesting endangered species (EN) that in Benin occur in only one or two locations are also listed in Table 1. As only a few specimens of some of these species occur in Drabo their survival is not yet assured.

The forest harbours some rare insects, among them *Euschmidtia congana* VU (Euschmidtiidae), a small, wingless grasshopper, and the blue leaf butterfly (*Junonia cymodoce* VU, Nymphalidae, both rain forest species could have survived only in the small remnant forests like Orojamè; but have now been observed in the regrown forest parts of Drabo.

The Drabo forest has a rich bird fauna, which also includes rainforest species, the most spectacular being Narina's trogon (*Apaloderma narina*) and black-shouldered nightjar, (*Caprimulgus pectoralis nigriscapularis*). Black-throated coucal (*Centropus leucogaster*) was also observed in Drabo. Among the reptilians, *Varanus exanthematicus* and *V. niloticus*, *Chamaeleo gracilis* and *C. necasi*, a recently discovered species, have been found. Throughout the years, the once rare *Chamaeleo* spp. have become abundant. Eight species of snakes were observed in the vicinity of the house, among them *Python regius* and *P. sebae*, which have become less and less abundant during the last few years. The green mambas, *Dendroaspis* spp., are uncommon, not clearly identified, but probably underreported species, while the two cobras, *Naja melanoleuca* and *N. nigricollis* remain common despite being fiercely persecuted by the population.

Among the mammals, three species of squirrels, among them *Funisciurus substriatus* EN (Sciuridae), but also grass cutter (*Thryonomys swinderianus*, Thryonomyidae),

the recently described duiker (*Philantomba walteri*, Antilopidae), and the mongooses *Mungos gambianus* and *Galerella sanguinea* are common. The primates are represented by the potto (*Perodicticus potto*, Loridae) and *Galagoides thomasi* (Galagonidae), which survived in the sacred forest Orojamè, from where they spread throughout the forests, as well as by mona monkey (*Cercopithecus mona* VU) and green monkey (*Chlorocebus aethiops tantalus*, Cercopithecidae). The star attraction of this forest is, however, the endemic red-bellied monkey (*Cercopithecus erythrogaster erythrogaster* CR). In the early 1990s, the first author received a few of these animals from the Ouémé Valley and their progeny have since developed into a wild-living group of about 20–25 freely reproducing and free-living monkeys. Because of its usual shyness this monkey is difficult to observe in the few localities in the Ouémé Valley and the Lama forest, where less than 1 000 individuals survive. It can, however, be observed easily in the Drabo sanctuary and is largely tolerated by the villagers.

Sustainable people management

In the beginning, the local population was allowed to use the forest for gathering fuel wood and medicinal plants. This was, however, not a sustainable solution as every first finder of a medicinal plant would uproot and destroy it completely. Similarly, trees were being prepared by trespassers through ringing so that they would topple and offer fuel wood. Around the village, small mammals were, and still are, severely hunted and some newcomers from Cotonou made it known that they would only eat animals they shot themselves. In view of the small size of the forest, it was therefore agreed that all hunting, felling of trees, gathering of fuel wood and medicinal plants would only be allowed in the presence and with the accord of the owner. This agreement, though violated occasionally, was generally respected.

Then, in an incident that demonstrated the possible negative effects of local beliefs, over 60 trees were felled because a seer (*bokonon*) proclaimed that a bad spirit responsible for a murder in a neighbouring village resided in this particular lot. Subsequent discussions with elders and the young led to a deal whereby the elders together with some younger men offered to guard the forest from intruders for a monthly fee of $30 by severely punishing any trespassers. This deal has held for over two years. The abundance of red-bellied monkeys and duikers, otherwise a highly prized game, is testimony to the successful implementation of this arrangement.

This deal was only possible because the first author had been introduced into the local cults of the *zan gbetos*, the hunters of the night, as well as the Oro cult, for whom he maintains the sacred forest Orojamè in Drabo Fanto, and, lately, to the newly established revenant cult. For their celebrations, these groups have free access to the corresponding parts of the forest. Since almost all males of Drabo Gbo and the surrounding villagers are adepts of these cults there is a certain coherence and social pressure. All three cults are secret male societies (separate female societies exist) with

elaborate induction ceremonies led by chosen elders. Some of the festivities, particularly the dances by the 'paillottes', tent-like ornate covers, are performed by day and can be seen by visitors.

At present, trespassers are mainly reported by casual observation rather than by actively posting guards. However, if somebody is caught felling trees or cutting bark and lianas fines imposed by the council of elders are substantial (in the order of $100-$200, paid in kind). While villagers severely punish crop damage by roaming pigs or goats to maize or other crops, no sanction is possible when these animals sometimes penetrate the forest.

In Drabo, roads are bad and are mostly maintained by the villagers themselves. Electricity has only recently been brought to a neighbouring village, from where haphazard private lines now extend over 1 km to the sanctuary. All water comes from private wells, which provide abundant water of the best quality. All villagers (except PN) survive below the internationally accepted minimum daily income of $1 or $2 per person per day. Income sources are highly varied but all are derived in part from subsistence farming. Most farmers in Drabo have sold land to Beninois who live in Cotonou and eventually intend to build a modest house on it. Meanwhile, this land is continuously farmed by the previous owners with little respect to soil conserving measures, such as fallow and crop rotation. Most villagers are part-time artisans and quite a few are motorbike taxi drivers working in the nearby town of Calavi, while the majority of women work at home. Nobody suffers from chronic hunger, though diets are simple. Why then would such poor people respect the forest?

The villagers sometimes approach the first author for help to pay school fees, medical bills, or apprenticeships, etc. Few people in the village outside the small circle of immediate friends would tolerate the forest if it were not for this assistance. Benefits like more abundant and more regular rains, refuge for organisms beneficial in agriculture, refuge for medicinal plants and game, etc., are regularly explained to the villagers, but traditional viewpoints persist, i.e., land is there to be farmed. As the village is being encroached upon by the expanding town of Calavi, some villages like Drabo Fanto and Dodja already sold their traditional sacred forests. The recent creation of a small ethno-botanical garden for useful plants accessible on demand and the negative experiences of neighbouring villages where all old trees had been cut are, however, starting to swing the opinion in the younger men, provided the financial support is maintained.

Outlook

Most villagers had never seen a live monkey before the red-bellied monkeys of the sanctuary started reproducing and interacting with the population, particularly with children. Local people now take a certain pride at having these monkeys as a speciality of the village. Damage mostly by the associated green monkeys, which are much more aggressive crop raiders than the red-bellies, must, however, be compensated for.

Apart from being a prime site for ecological research, the sanctuary is also an important site for nature protection in a region where natural forests are mostly unprotected. As a consequence, a mild ecotourism has developed thanks to the website posting of the forest by NGOs active in ecotourism (http://www.ecobenin.africaweb.org; www.credi-ong.org; http://www.naturetropicale.org). This activity is viewed by the villagers with some interest though the unreliable and small income from ecotourists will benefit only a few.

Regular visits by university students and schools also create interest and provide evidence that perhaps, in the future, this sanctuary could be beneficial to the surrounding population. Many of the taxonomists, who visit the famous insect collection of IITA-Benin to set up collaborative projects, also come to Drabo to collect specimens.

In view of the many threats to sustainability, IITA has signed an agreement to maintain the forest; but social upheaval is always a possibility and might result in an enraged populace destroying the forest. At present, the deal with the local cults works well; but revelation churches fiercely opposed to these beliefs are gaining ground. Also, we do not know whether urbanization will bring with it a better understanding for nature protection or instead a fear of unknown dangers lurking in forests. Equally insidious is the potential impact of climate change, especially reduced rainfall. This will particularly affect some of the rare species from more northerly, already threatened habitats such as Ewè. The predicted increase in storms might increase tree fall, which in such a small forest could lead at worst to the destruction of the forest.

3) Forêt de la Panthère, Zinvié

Biodiversity conservation and restoration

The forest contains old trees of a rare beauty. The main species are huge *Piptadeniastrum africanum* VU, *Milicia excelsa* EN and *Xylopia aethiopica* VU (others see Table 1). A dendrometric study by CREDI-ONG in 2013 counted 57 trees with a mean diameter of 94 cm. The maximum diameter was 238 cm with a height of 32 m. Other threatened plant species include *Acridocarpus alternifolius* EN, *Khaya senegalensis* EN, *Parkia bicolor* EN, and *Synsepalum dulcificum* EN, plus *Zanthoxylum xanthoxyloïdes* VU. Since the forest is left as it is and there are no forest management practices the understory is dense and only few tree seedlings are capable of sprouting in the resulting darkness.

Despite its small size, the forest harbours green monkeys (*Chlorocebus aethiops tantalus*), potto (*Perodicticus potto*), and galago (*Galagoides* sp.), *Funisciurus substriatus* EN, civet cats (*Civettictis civetta*), spotted genet (*Genetta tigrina*), and Walter's duiker (*Philantomba walteri*).

Recently, *Papilio phorcas* CR (Papilionidae), which in Benin had only been known from one locality, was observed, which gives hope that this beautiful butterfly persists also in other forests of the Ouémé Valley.

Sustainable people management

Involvement in the Forêt de la Panthère by CREDI-ONG started when the deities were removed and the forest became desacralized. This allowed a first visit by the managers of this NGO, who were duly enchanted by this ancient forest. The owners, on the other hand, wanted to cut the trees for sale. CREDI-ONG succeeded in convincing them to preserve the forest and to exploit it in the framework of eco-touristic activities.

From 2008 onward, CREDI-ONG paid $100 per year to the owner family in order to have free access to the forest with its visitors. In 2012, savage tree cutting in the understory forest was observed. The family and village collectives decided to re-sacralise the forest by handing it over to the *zan gbeto* cult. Once this was done in 2013, the owner family decided to return $20 on received rent to the village association responsible for the protection of the environment. At present, no wood collection and no hunting are allowed. Since trespassers know they face severe punishment by the *zan gbeto* cult no further intrusions have been observed. Since 2013, visits to the forest require prior authorization from the heads of the *zan gbeto* cult, but CREDI-ONG kept its visiting permit. Tourists primarily come to see the mini-zoo, before they venture into the nearby forest.

The village of Kpotomey today has electricity, running water, is linked with good roads to nearby Zinvié, where medicinal facilities and schools are available. At present, CREDI-ONG has an annual income by visitors to the forest representing 28 person-days, which is used to employ villagers as assistants and tour guides. Group and social activities abound and the trainees from collaborating NGOs in Europe and local schoolchildren are taught the importance of sustainable nature conservation.

Outlook

Since several externally funded projects of CREDI-ONG are strictly community-oriented and offer better lives to numerous people this model of nature conservation has a good chance of surviving increased population pressure. At present, the reserve is being expanded along the Sô River, with the plan to make the 'Sitatunga Valley' a new national park with benefits for adjacent communities through ecotourism and merchandising of local foods and crafts.

4) Forêt de Bahazoun at Lanzron

Biodiversity conservation and restoration

The forest has never been seriously degraded. Throughout it has a relatively low, but dense 10–15 m high canopy. A total of 139 species of plants has been identified, but the final list is probably considerably longer. *Berlinia grandiflora* is the dominant tree,

Synsepalum brevipes is frequent (others see Table 1). Threatened species include *Acridocarpus alternifolius* EN, *Khaya senegalensi*s EN, *Milicia excelsa* EN, *Mimusops andongensis* EN, *Monodora myristica* EN and *Zanthoxylum xanthoxyloïdes* VU.

The fauna has never been studied in depth as the villagers keep the forest closed most of the year. Civet cats (*Civettictis civetta*), spotted genet (*Genetta tigrina*), Walter's duiker (*Philantomba walteri*) and bushbuck (*Tragelaphus scriptus*) occur regularly; but the outstanding species is the sitatunga (*Tragelaphus spekii* EN, Antilopidae). This large, marsh-dwelling antelope is of wide distribution in Central Africa, but has only relict populations in West Africa.

Sustainable people management

The Bahazoun forest is privately owned and not protected by any legal document. The local administration in Abomey-Calavi does not seem to be aware of its presence and the forest is not listed in the official Community Development Plan.

Management of the Bahazoun forest is entirely in the hands of the family, who are fiercely opposed to any interference by the forest administration. Access is strictly controlled by the inhabitants of Lanzron, who view any person showing interest in the fauna and flora with suspicion because they fear to be dispossessed of their forest. Only a small portion is dedicated to *zan gbeto*, the rest is managed according to the rules defined by the chief of the family. Only men are authorized to cut some trees for constructions, but any sale of wood is forbidden. Collection of dead wood is organized once every two to three years on a decision by the elders, and the opening and closing of the forest are confined to the vodoun *zan gbeto*. Firewood at present is sold at $1 per bundle. This allows the women to gain up to $160 each time the forest is opened. All unauthorized gathering of wood is strongly punished by the *zan gbeto*, the fine to be paid in kind or as cash. Hunting by the local population, by contrast, is not regulated.

CREDI-ONG is allowed to perform certain activities such as ornithological visits in the vicinity of the forest, always accompanied by somebody from Lanzron. So far, not all team members have been initiated into the vodoun cult.

The villagers of Lanzron are generally poor subsistence farmers without access to electricity. Roads are extremely bad and access to medical services is at a considerable distance. The forest plays an important role in their daily lives, providing medicinal plants, firewood, timber for construction, and income through hunting.

Outlook

Since the villagers are proud of their forest the perspectives for its survival are good, provided some action is taken. The first requirement is a legally binding written management plan with safe title deeds; otherwise the land-grabbing observed in other parts of the Calavi community and the installation of big farms by rich absentee landlords

will destroy this old management through elders. At present, CREDI-ONG is helping to improve prospects by providing water pumps, employment for rangers, and training according to the principles they developed in their fief in Zinvié.

Discussion

Despite a low ecological footprint until recently (van Vuuren et al. 1999) pressure on natural resources in Benin is growing rapidly and the decline of biodiversity, a measure for quantifying this pressure, has reached crisis status (Wilson and Peter 1988, Laurance 2006). Protection of the remaining rainforest in the Dahomey Gap and southwestern Nigeria is therefore urgent. In southern Benin, these are naturally small pockets, most of them sacred forests, which have been studied before (Sokpon and Akpo 1999, Nagel et al. 2004, Adomou et al. 2010, 2011, Agbani et al. 2012). The present study is, however, the first to relay the experience of the managers of such forests over a time span of 10 to 30 years, to describe rehabilitation of the forests and to take into account the threat-status of organisms (Table 2).

Though all four forests are under practically identical climatic conditions, underlying bedrock and soil influence species composition and resistance of the forests against storms and dry spells. Because biodiversity inventories are still local and rare, documented species richness is mainly dependent on how well these forests have been studied; Ibadan has the longest records and the highest number of visiting specialists, while Lanzron is mostly inaccessible to visitors.

For the preservation of biodiversity, nature reserves with expensive security measures like IITA-Ibadan might represent the future. Despite this huge effort, which is not paid for out of any funds allocated to forest management, wildlife is still threatened. Nevertheless, the venerated iroko (Ouinsavi et al. 2005) and the spectacular *Pararistolochia goldieana* are well protected. The forest is possibly the last refuge for the Ibadan malimbe, Nigeria's rarest endemic bird (Manu 2001, Manu et al. 2005) and has been designated an Important Bird Area (IBA) in 2002 by BirdLife International (Fishpool and Evans 2001). In Drabo, the troupe of habituated red-bellied monkeys has the potential to attract tourists. Many other animals are also protected; but they are far less conspicuous, as are the threatened plant species that now thrive in the restored forest. In Zinvié, the key-attraction is the mini-zoo together with the exemplary village development schemes; for visitors they far outshine the rich flora. Similarly, in Lanzron it is the elusive sitatunga that attracts attention, though it is only rarely seen. Since an adult male sitatunga can fetch from $200 to $600 (Kissira 2014) the species is still subjected to hunting by the villagers (Alladayè 2011). It is encouraging to see that insects of the rainforest or mammals like potto and others survived. The observed sustained protection of flora and fauna in the four forests thus demonstrates the value of even tiny refuges, provided these are well managed.

Benin and Nigeria have big parks in the thinly populated North: the Complex WAP World Heritage Centre of the UNESCO, i.e. three contiguous parks, namely

Table 2. Conditions and management of four rainforest patches in a gradient from 1 to 5.

Criterion	Location			
	Ibadan	Drabo	Zinvié	Lanzron
Location: 1-remote from town, 5- surrounded by city	5	3	4	1
Ownership of the land: 1- uncertain, group ownership, 5- private ownership with title	5[1]	5	3	1
Protection: 1- none, 5- securely fenced	5	3	2	1
Soil: 1- unstable swampy or rocky, 5- deep soil, allowing for quick growth and stable conditions.	1-3	5	4	2
Forest succession: 1- fallow, 5- old forest.	1-5	1-5	1-5	5
Rehabilitation: 1- not needed, not envisaged, 5- on most of the land	3	5	2	1
Presence of threatened plant species: 1- no concern, 5- threatened species introduced	3	5	2	1
Presence of wildlife: 1- nothing particular, 5- attractive protected species	5	5	5	5
Use of forest: Firewood and construction wood: 1- no collection allowed, 5- organized use	1	3	3	5
Hunting: 1- not allowed, 5- free, but organized	1	1	1	4
Stealing wood, medicinal plants: 1- tolerated, 5- severely punished	3	4	3	4
Poaching (shooting/trapping animals): 1- tolerated, 5- severely punished	5[2]	5	3	4
Cost of protection/guards: 1- none, 5- high costs	5	2	1	1
Involvement with local customs: 1- none, 5- full integration in local cults	1	5	4	5
Condition of local population: 1- uniformly poor, 5- inhabitants rich, urban and influential	1-5[3]	2	2	1
Management by local population: 1- none, 5- organized governing structures	1	2	5	4
Importance of ecotourism: 1- none, 5- important with well-organized distribution channels	2	2	5	3
Outside donors: 1- none, 5- projects are actively sought	3[4]	2	5	2
Personal involvement: 1- anonymous protection, 5- highly involved champion	5	5	5	3
Education of users and neighbours: 1- none, 5- highly developed curriculum	3	2	5	3

[1] Land owned by Nigerian Federal Govt., on 99-yr lease to IITA.

[2] Offender is arrested and handed over to local police for prosecution

[3] Staff of the international institute vs. inhabitants of surrounding city (few poor farmers – increasingly middle class, including IITA employees)

[4] Currently no donor for forest as such

Parc W in Niger, Arly in Burkina Faso, Parc Penjari in Benin of about 10 000 km^2 constitute the largest fully protected area in tropical West Africa. In southern Benin and south-western Nigeria, national parks are, however, almost totally absent. Protect-

ing and restoring small refuges, as in the case of the four forests, is therefore justified and important.

Management and interactions with the populations living in the vicinity of these forests is deeply influenced by the accessibility to towns: IITA-Ibadan is now completely engulfed by a large city, sequestered by its high security fence from the surrounding population, which nevertheless assumes it still has rights to exploit the forest. The Forêt de la Panthère lies near Zinvié, a relatively small centre, and Drabo will be surrounded by modest habitations in the near future. Only in Lanzron is there a homogeneous population of subsistence farmers far away from a town. Better access demands higher security measures and enclosures, but offers better possibilities for education in ecology as well as ecotourism.

Surrounding populations are differently integrated in the management of the forests. In Drabo, the manager/owner of the forest lives in the forest and his integration into the local cults assures protection in an arrangement called 'working with people' (Sodeik 1998). CREDI-ONG initiated official associations with commonly agreed rules and remuneration with its villagers. Moreover, this NGO, supported by international donors, created many sources of income through well-organized ecotourism, fish-farming, and ecological agriculture benefitting the village. This approach of 'talking with people' (Sodeik 1998) includes full political power and, purportedly, a better chance for sustainability. The same approach has not yet been implemented in Lanzron. In IITA-Ibadan, commercialization of forest products will increasingly benefit local populations.

Engaging with traditional beliefs in Drabo has up to now protected the forest, where monkeys and duikers abound despite their value on the market. Yet, Christian revelation churches have been successful in fiercely opposing traditional beliefs. By contrast, the Catholic Church has adopted and adapted these traditions. The managers from Zinvié have stimulated the village associations to re-sacralise their forest in order to add some measure of protection. It must, however, be remembered that sacred forests have not been created for the purpose of nature conservation and that their sacred status alone is often insufficient to protect them from destruction (Siebert 2003, Juhé-Beaulaton 2008). In Lanzron, traditional protection and modest exploitation of the forest seem to be working well. The long-term problem lies in the fact that ownership is not secured. As the community becomes more heterogeneous it risks attracting rapacious entrepreneurs, even from within the village, who can eventually derail all communal efforts. Defining and securing landownership, followed by boundary fencing, is therefore their first priority. In Benin in general, maintaining good public relations with local dignitaries and politicians has been a continuous uphill struggle taxing the managers; in IITA-Ibadan the same struggle must be fought, though it is mostly internal.

While the government of Benin has signed all relevant international treaties and the laws to protect the forests are in place (Republic of Benin 2012) rigorous implementation of these rules has not always been a priority. In fact, most southern forests are not adequately protected, which calls for new nature reserves to be established

(Neuenschwander et al. 2011). Such an effort is now under way, led by CREDI-ONG, to develop a new national park in the so-called 'Sitatunga Valley' adjacent to the Forêt de la Panthère. Eventually the education effort made by the government, universities and various NGOs might lead to a change in attitude (Sokpon and Akpo 1999, Nagel et al. 2004, Adomou et al. 2011, Agbani et al. 2012); but since this is a slow process the champions of the presently well-guarded forests of this study will have to use all means to train youths, promote eco-tourism and environmental education at all levels, but also to define the necessary obligations for the local populations including, in the case of Benin, vodoun dignitaries.

The presence of flagship species such as the red-bellied monkey, sitatunga, or IBA ranking provide highly desired incentives for support at all societal levels including governmental to preserve forests. Though not necessarily easily available, opportunities for financial support exist, for instance within BirdLife International, which promotes champions for sites or species, IUCN, or specialized foundations (Mohamed bin Zayed Species Conservation Fund, IPSI Satoyama Initiative, etc.). In most instances this involves the transfer of substantial resources from North to South (Balmford and Whitten 2003). Our experience in protecting and rehabilitating precious forest ecosystems of small size might also stimulate universities, managers of industrial and touristic sites, and private land owners to create similar forests on their own land. In the Sahel zone in Burkina Faso, e.g., many such forests have been created with strict rules for use by the local population by NewTree (http://newtree.org). A biodiversity assessment is still largely lacking, but might be included according to the experiences made in our four forests. We have demonstrated that reversing biodiversity loss is possible even in the highly populated south of Benin and south-western Nigeria, though at great costs, not only in money, but in management and personal involvement.

The following major recommendations for other conservation efforts in the region can be extracted: a) Ownership of the forest must be vigorously defended against other interests from outside, but also from inside the local community, by clearly defining, within a well-defined managerial and political structure, purpose, rights and obligations. Ownership must include not only the plot, but also the trees growing on it. Managing forests for somebody else, by contrast, is not likely to be sustainable; b) Support to the community is needed by creating interest in the reserve, but only as long as established rules are respected; c) Such support should be accompanied by education at all levels, a recommendation that probably also applies to big reserves established and maintained by governments; d- In theory, these conclusions are all not new, but implementation needs champions and funding. Where these are lacking, reserves risk existing only on paper as is the case for many Forêts Classées in central and northern Benin or the Gambari Forest Reserve in Nigeria. At least in the case of Benin, which is still among the 20 poorest nations of the world despite efforts of successive democratic governments, outside funding and further education are probably the only means to assure protection of its biodiversity.

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RESEARCH ARTICLE

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Morphological shifts in populations of generalist and specialist amphibians in response to fragmentation of the Brazilian Atlantic forest

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Abstract

Changes in morphological traits, such as body size, body condition, and leg length, are important indicators of changes to life history or habitat quality, which can affect the performance of individuals and therefore the persistence of populations under environmental change. Only very few studies assessed the effect of fragmentation on morphological traits. The few available studies on anurans found that in landscapes with less forest cover body size decreased. Therefore, we predict that body size should also be smaller in fragments compared to continuous forest. Body condition is a further trait closely related to individual performance and thus should decline with more adverse conditions, as is expected in fragments. We tested these hypotheses using snout-vent length, body mass, body condition, and tibia length as response variables. We collected data of a habitat generalist (*Rhinella ornata*) and a habitat specialist (*Ischnocnema guentheri*), both leaf-litter amphibian species, from three sites in a fragmented landscape (two isolated and one connected site) and one site in a contiguous part of the Atlantic Forest of Southeast Brazil. In the generalist species, snout-vent-length (SVL) and body mass were significantly lower in fragments compared to the contiguous forest control, whereas tibia length and body condition

did not differ among sites. In contrast, SVL, body mass, and tibia length of the specialist species did not differ among sites, but body condition was marginally different among sites, being relatively low in one but not the other isolated fragment. The results indicate that different processes affect the morphology of the two species following habitat fragmentation.

Keywords
Fragmentation, habitat loss, amphibians, body size, body condition, Brazilian Atlantic forest

Introduction

Habitat loss and fragmentation are a major cause of biodiversity loss (Sarre et al. 1996, Pimm and Raven 2000, Sala et al. 2000, Funk and Mills 2003, Henle et al. 2004). Most studies examining their effects focused on community composition, patch occupancy patterns, population viability, and the genetic variability of selected species (e.g. Tocher et al. 1997, Wiegand et al. 2001, Bell and Donnelly 2006, Dixo et al. 2009, Tucker et al. 2014). In contrast to the large volume of literature for oceanic islands (e.g. Kramer 1951, Losos 2009), very few studies addressed changes in morphological parameters following habitat fragmentation. However, habitat loss leads to major changes in abiotic and biotic conditions and morphology is known to respond to abiotic and biotic conditions (Wade 2004). Exemplarily, Smith et al. (1997) found that differences in vegetation structure between African rainforest and the rainforest-savanna ecotone led to different selection regimes causing morphological changes in rainforest birds.

Changes in morphological factors are important indicators of changes in life history or habitat quality (Palkovacs 2003, Buckley et al. 2005, Lowe et al. 2006, Lomolino and Perault 2007). Snout-vent-length, body condition, and body proportions are important phenotypic factors that affect the performance of individuals in terms of their reproductive output and survival in numerous organisms (Stearns 1976, Roff 1992). In amphibians, smaller snout-vent length and lower body condition often translate into reduced survival probability (Altwegg and Reyer 2003) and cause maternal effects, such as poor clutch quality (Reading 2007), smaller clutch size (Funk and Mills 2003), and smaller egg size (Kaplan 1992, Laugen et al. 2002). These factors in turn lead to a lower number of hatchlings and metamorphosing individuals (Berven and Gill 1983, Semlitsch et al. 1988) and affect the size at metamorphosis (Pakkasmaa et al. 2003, Räsänen et al. 2005), maturity, and fecundity (Smith 1987, Semlitsch et al. 1988). As a consequence of their important influence on demographic traits, body size and body condition may ultimately determine the ability of species to persist under changed environmental conditions.

Various environmental factors are known to influence morphology and body condition. In amphibians, resource availability, predation risk, and temperature during larval development have been frequently identified as major determinants of body size and body condition. An increase in resource availability can lead to better body condition and a larger body size (e.g., Du 2006, Jessop et al. 2006, Wu et al. 2006). Due to the costs of anti-predator behaviour, higher predation pressure can lead to early hatch-

ing, lower growth and developmental rates, and thus to a smaller size at emergence or metamorphosis (e.g., Ball and Baker 1996, Laurila et al. 2002). In amphibians this further negatively affects limb dimensions and locomotor performance (Goater et al. 1993, Buckley et al. 2005). Warmer temperatures accelerate developmental processes and usually lead to an earlier metamorphosis, smaller size at metamorphosis, smaller size at maturity, and therefore overall a smaller adult size (Smith 1987, Semlitsch et al. 1988, Beachy 1995, Ståhlberg et al. 2001).

Habitat loss and fragmentation create changes in the abiotic and biotic environment, therefore leading to changes in the quality of the remaining habitat (Saunders et al. 1991) that can result in changing selective pressures on morphology (Thomas et al. 1998, Ewers and Didham 2006). Thus, changes in morphology may serve as an early and easy to measure indicator for negative effects of fragmentation on species (Sumner et al. 1999). Finding suitable early indicators of environmental stress (Helle et al. 2011) is important in order to apply effective conservation measures prior to severe declines of populations and of the species at the landscape level (Leary and Allendorf 1989). However, the contribution of habitat loss and fragmentation to phenotypic changes is poorly known, in particular in amphibians. Neckel-Oliveira and Gascon (2006) showed shifts in the body size of a habitat generalist (*Phyllomedusa tarsius*) in fragments, regrowth forest, and pasture compared to continuous forest, with larger individuals in the latter, and explained these shifts with changes in habitat quality. Leg-length in relation to snout-vent length was also affected by the degree of retained forest in one Neotropical frog species (Delgado-Acevedo and Restrepo 2008). Likewise, the prickly forest skink (*Gnypetoscincus queenslandiae*) of tropical Australia was smaller and had lower mass (corrected for differences in snout-vent-length) in fragments compared to continuous forests (Sumner et al. 1999).

Body condition declined and the level of stress hormones increased with the number of forest fragments in a study of the common toad (*Bufo bufo*) (Janin et al. 2011). Likewise, yellow-bellied toads (*Bombina variegata*) from forest ponds showed better body condition than those from ponds in the agricultural matrix (Scheele et al. 2014). In contrast, Püttker et al. (2008) found a negative relationship between body condition and patch size in two tropical forest small mammal species that are habitat specialists and no significant relationship in four species that are habitat generalists. The mechanism(s) driving these patterns remain unclear but likely involve multiple factors.

Since previous studies found that in more disturbed habitats and landscapes with less forest cover body size decreased in anurans (Pyastolova and Vershinin 1999, Neckel-Oliveira and Gascon 2006, Delgado-Acevedo and Restrepo 2008), we predict that body size should also be smaller in fragments compared to continuous forest. Due to the strong link among morphological characteristics, we further predict that leg length and body condition should be reduced in forest fragments compared to continuous forest. Here, we test these hypotheses. Moreover, habitat specialists are particularly sensitive to changes of microhabitat quality in fragmented habitats and are consequently more prone to extinction in the fragmented landscape than generalists (Margules 1996, Henle et al. 2004), we therefore assume a stronger response regarding the morphological shifts of habitat specialist species compared to generalist species.

Material and methods

Study area

The study was carried out in the Mata Atlântica, Brazil, in continuous forest of the Morro Grande Reserve and a fragmented landscape surrounding Caucaia do Alto (both approx. 23°40´S, 47°01´W), located 40 km southwest of São Paulo in the municipalities of Cotia and Ibiúna, Brazil. The forest reserve and the adjacent study area are located on the Atlantic Plateau of São Paulo at an altitudinal range of 860-1075 m above sea level (Metzger et al. 2006). The original forest of the study region is classified as lower montane rainforest and forms a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest (Oliveira and Fontes 2000). All study sites, including the control site, were characterised by secondary forest and have remained undisturbed for at least 50 years. The fragmented landscape presented approx. 31% of remaining, highly fragmented forest that was surrounded by urban areas and rural installations (15%) and open areas (i.e., agriculture, pasture, fallow lands, areas in early successional stages; 39.3%) (see Dixo et al. 2009).

We selected four sites: two isolated small forest fragments (Carmo Messias and Dito, referred to in the following as “iso1” and “iso2”, respectively), one small forest fragment (Alcides, referred to in the following as “connect”) connected by a forest corridor to a larger forest area, and a control site (“control”) within the continuous forest. Forest fragments covered an area of 5 ha each and contained no permanent/larger water bodies within the forest area or within a radius of 200 m outside the forest fragment. The continuous forest was about 9,400 ha in size. There was no permanent/larger water body present at the control site within a radius of 200 m.

Selected species

We chose two leaf-litter dwelling forest species for comparison. We selected *Rhinella ornata*, a bufonid species, as a habitat generalist due to its high tolerance to matrix habitats. This species is distributed throughout the Atlantic Forest in the states of São Paulo and Rio de Janeiro (Haddad et al. 2008) and can be found in undisturbed continuous forest areas as well as in disturbed forest fragments (Heyer et al. 1990). It breeds in temporary and permanent ponds within forests and open areas (Izecksohn and de Carvalho-e-Silva 2001, Haddad and Prado 2005). Reproduction starts at the end of the dry season in late July and at the beginning of August (Dixo 2005).

We selected *Ischnocnema guentheri* for comparison. This species is distributed over large parts of the Mata Atlântica (Haddad et al. 2008) and occurs only within forest habitats although it can sometimes be encountered in vegetation close to the forest edge (Heyer et al. 1990). Thus, it has a more specialised habitat requirement. Females deposit egg clutches terrestrially, hidden below tree trunks and stones (Kwet and

Di-Bernardo 1999, Izecksohn and de Carvalho-e-Silva 2001). Frogs develop directly within the egg capsule (Heyer et al. 1990, Izecksohn and de Carvalho-e-Silva 2001).

Sampling

We established three parallel transects of 100 m each on each site. We sampled frogs by hand during the rainy seasons October 2003 until March 2004 and November 2004 until March 2005. We surveyed each site for five consecutive nights (21:00 – 01:00 local time) before sampling the next site. Once all sites had been sampled, the next round of sampling started again at the first site. The total search effort was 25 nights per site (2003/2004 15 nights per site, 2004/2005 10 nights per site).

We measured snout-vent-length (SVL) and tibia length (TL) of all captured individuals using a calliper with an accuracy of ±0.1 mm. We measured tibia length for the left body side. We weighed individuals using digital scales with an accuracy of ±0.1 g. We used photographical individual identification to eliminate data points of recaptured individuals. As juveniles were seldom captured, we only included the data of subadult and adult individuals in the analysis (*R. ornata* with a SVL ≥ 27 mm; *I. guentheri* with a SVL ≥ 10 mm). As knowledge on natural history of both species is scarce, we could not further separate subadult from adult individuals. Unless calling, sexes cannot be separated by external morphology in both species.

Data analysis

Opinions about which body condition index (BCI) to use are controversial in the literature (Jakob et al. 1996, Schulte-Hostedde et al. 2005, Peig and Green 2009). The most common approaches are to use the residuals from a regression of mass on the third power of length or of *ln* mass on *ln* size. Peig and Green (2009) developed a scaled mass index (SMI) which standardizes body mass at a fixed value of body size based on the scaling relationship between mass and body size using major axis regressions. This new index better reflects changing relationships between mass and body size considering different growth curves at different ages than alternative indices (Peig and Green 2009, 2010). We used the SMI and additionally the more frequently used residuals of the regression of *ln* mass on *ln* size for consistency assessment.

We assessed differences in SVL, body mass, and BCI among sites by using an analysis of variance (ANOVA), after testing the assumption of normality of all variables used (Kolmogorov-Smirnov-Test: $D = 0.5 – 0.7$, all $\alpha > 0.05$). For tibia length, we used an analysis of covariance (ANCOVA) to remove a potential influence of SVL in the comparison of sites. For significant results, we used the post-hoc Tukey's Honestly Significant Difference test (Tukey's HSD) for multiple comparisons to assess differences among individual sites.

Results

We captured a total of 499 individuals of the selected species, comprising 116 *R. ornata* and 383 *I. guentheri*. After removing juvenile individuals from the data, 54 and 376 individuals respectively were kept for the analyses. An overview of captures and measurements per species and site is given in Table 1.

In *R. ornata* snout-vent-length (SVL) and mass differed significantly among sites (ANOVA: $F = 5.03$, $\alpha < 0.01$; and $F = 5.7$, $\alpha < 0.$, respectively). Both were highest for the control site, with the difference to "iso1" being statistically significant in a Tukey's HSD ($\alpha < 0.01$) and that to "iso2" being marginally significant ($\alpha = 0.09$) for SVL and significant ($\alpha = 0.05$) for mass. Both were intermediate in the connected small site. Tibia length (TL) did not differ among sites when accounting for differences in SVL (ANCOVA: $F = 0.41$, $\alpha = 0.7$). BCI calculated as SMI did not differ among sites (ANOVA: $F = 0.726$, $\alpha = 0.5$). The same was the case when using residuals of the regression of *ln* mass on *ln* SVL as BCI (ANOVA: $F = 0.64$, $\alpha = 0.9$).

Snout–vent length and body mass of *I. guentheri* did not differ significantly among sites (ANOVA: $F = 1.35$, $\alpha = 0.26$ and $F = 0.84$, $\alpha = 0.47$, respectively). Likewise, TL did not differ significantly among sites when the effect of SVL was accounted for (ANCOVA: $F = 0.84$, $\alpha = 0.5$). BCI based on SMI was highest in the control site and one isolated site and lowest in the other isolated site (Table 1), but the difference among sites was only marginally significant (ANOVA: $F = 2.00$, $\alpha = 0.11$). When using the residuals of the regression of *ln* mass on *ln* SVL as BCI, qualitatively results were very similar though BCI was highest in the control site (data not shown). The difference among sites was marginally significant ($F = 2.67$, $\alpha = 0.09$), but all comparisons between pairs of sites were not significant (Tukey's HSD; all $\alpha > 0.05$).

Table 1. Mean ± one standard deviation (SD) of morphological traits of the studied species in the four study sites. Abbreviations: control = control site, connect = connected site, iso1 and iso2 = isolated site one and two; BCI: body condition; N: sample size; SVL: snout-vent-length; TL: tibia length. [BCI calculated as SMI]

	N	SVL (mm)	TL (mm)	BCI	Body mass (g)
I. guentheri					
control	18	20.0±2.4	13.9±1.5	0.78±0.10	0.74±0.24
connect	60	21.4±4.4	15.0±3.1	0.75±0.20	0.94±0.49
iso1	136	20.2±5.1	14.0±3.9	0.70±0.22	0.84±0.62
iso2	162	19.6±7.0	13.4±5.5	0.78±0.33	0.94±0.86
R. ornata					
control	9	57.8±22.2	26.5±9.2	6.46±0.54	19.9±19.1
connect	6	51.2±12.5	23.9±6.3	6.65±0.72	11.3±5.9
iso1	26	39.4±8.5	18.3±4.0	7.04±1.30	5.3±4.0
iso2	13	44.4±12.2	20.1±6.2	6.61±1.42	8.2±8.0

Discussion

Our results partly support the predicted effects of fragmentation on phenotypic characteristics (smaller snout-vent-length, shorter legs, and lower body mass, and body condition in fragments compared to continuous habitat). Individuals of the generalist species *R. ornata* were smaller in fragmented habitats compared to the control site, while body condition did not differ among sites. For the specialist species *I. guentheri* body condition differed marginally significantly among sites and was highest in the control site and in one isolated fragment but lowest in the other isolated fragment. The other morphological traits did not differ among sites. Thus, the habitat generalist and the habitat specialist showed different morphological responses to habitat fragmentation.

The reduced body size in *R. ornata* and the lower body mass of *I. guentheri* in the most severely affected (small isolated) site(s) are in line with previous studies in lizards and amphibians that found a reduced body size in landscapes with low forest cover, in fragments, and in disturbed compared to undisturbed habitats (Pyastolova and Vershinin 1999, Sumner et al. 1999, Neckel-Oliveira and Gascon 2006, Delgado-Acevedo and Restrepo 2008). Neckel-Oliveira and Gascon (2006) assumed, but did not test, that the morphological difference was environmentally induced during development due to changes in the habitat quality of the larval habitat. A smaller size at metamorphosis frequently translates into a smaller adult body size in anurans (Smith 1987, Semlitsch et al. 1988) although data from tropical species are not yet available. This explanation may also apply to the observed morphological shifts in *R. ornata*, as it also undergoes development in aquatic habitats.

In fragments that do not retain suitable aquatic habitats eggs have to be deposited in water bodies in the matrix. Eggs and aquatic larvae have to deal with changes in biotic and abiotic parameters of reproduction ponds within the matrix. Ponds inside and outside of forests usually will differ in physical conditions (Becker et al. 2007). Ponds within the matrix will receive more insolation and should therefore generally be warmer than forest ponds. Warmer temperatures accelerate developmental processes and usually lead to an earlier metamorphosis, smaller size at metamorphosis, smaller size at maturity, and therefore overall a smaller adult size (Smith 1987, Semlitsch et al. 1988, Beachy 1995, Ståhlberg et al. 2001, Wells 2007).

For frogs with a direct development much less is known about the factors that determine development and the morphology of hatchling and subsequently adult anurans than for pond breeding anurans. Delgado-Acevedo and Restrepo (2008) found smaller individuals of two directly developing *Eleutherodactylus* species – a genus closely related to *Ischnocnema* – in disturbed and fragmented compared to undisturbed and unfragmented habitats. They further found an influence between the level of remaining forest cover in the landscape and the allometric change of leg length in one of the species. We did not find a change in snout-vent-length, leg length, or body mass in *I. guentheri*. Delgado-Acevedo and Restrepo (2008) did not provide an explanation for their observations but laboratory studies in *Eleutherodactylus coqui* showed that froglets from eggs that hatched early had relatively smaller legs than froglets in the control

group (Buckley et al. 2005). More studies on directly developing frogs in fragmented landscapes are required before a clear pattern on morphological changes can emerge and mechanistic explanations can be derived.

The results for body condition suggest that the quality of the terrestrial habitat was not negatively affected for the habitat generalist *R. ornata* despite body mass being significantly lower in isolated fragments. For the habitat specialist *I. guentheri* habitat quality seems to have been negatively affected in one but not the other isolated fragment. This suggests that the study sites differed in food resource quality or physiological stress that translate into energetic costs for the latter species in some fragments but not in others. While fragmentation of tropical forests has a large effect on species composition and abundance in invertebrates (Didham et al. 1998), the majority of anurans are rather opportunistic in their food choice (Toft 1985). However, the study of Didham et al. (1998) suggested that in tropical forests common invertebrate species seem to be more sensitive to fragmentation than rarer species; and edges alter the trophic structure of communities (Laurence et al. 2011). Whether these changes translate into different overall abundances of invertebrates that are suitable as food for medium sized frog species, whether abundance changes differs among fragments and may depend on the matrix, and whether these changes differ for habitat generalists and specialists remain to be studied.

Edge effects on abiotic conditions, such as an increase in temperature and a decrease of humidity, affect a larger fraction of a small than a large patch or continuous forests (Saunders et al. 1991). Habitat generalists that are matrix tolerant may be better adapted to deal physiologically with such changes than forest habitat specialists that are intolerant to the matrix. This may explain why in our study body condition decreased in one isolated fragment in the habitat specialist *I. guentheri* whereas it was not affected in the matrix tolerant *R. ornata*. Similarly, Scheele et al. (2014) explained the higher body condition in the yellow-bellied toad (*Bombina variegata*) in forest ponds compared to ponds in pastures by a combination of higher resource availability, more humid micro-climatic conditions and greater water availability.

In conclusion, the effects of fragmentation on size and body condition differed between the habitat generalist and the habitat specialist. This suggests that the two species are affected by different processes driving morphological shifts in the wake of habitat fragmentation, and that for specialists these processes may differ among fragments. The observation that in the same study region as ours habitat specialists among small mammals showed an increase in body condition with fragmentation (Püttker et al. 2008) further corroborates that fragmentation may affect ecological processes that result in unexpected morphological shifts in species-specific ways. Further studies of morphological shifts of small vertebrates in fragmented landscapes and the processes that drive such shifts are required to improve our understanding of subtle effects of habitat fragmentation that in the long-run may lead to different levels of species sensitivity to extinction.

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