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Original Research Article

Assessing the spatiotemporal dynamics of endangered mammals through local ecological knowledge combined with direct evidence: The case of pangolins in Benin (West Africa)

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ABSTRACT

Although pangolins are considered to be one of the most trafficked wild mammals in the world, their conservation status remains uncertain through most of their ranges, and notably in western Africa. Using local ecological knowledge in combination with direct occurrence evidence, we assessed the distribution and abundance of the white-bellied pangolin (*Phataginus tricuspis*) and the giant pangolin (*Smutsia gigantea*) in Benin over the last two decades (1998–2018). We organised focus groups with local hunters in 312 villages within sampling units of 25 km × 25 km covering the whole country. Participatory maps of past and current geographic ranges of pangolins combined with direct evidence (96 collected scales) suggested that the white-bellied pangolin had a wide distribution and reached higher latitudes than previously known, whereas the giant pangolin could be restricted to a single forest and has been absent from the northern part of the country over at least the last two decades. Local hunters perceived a significant decline of the white-bellied pangolin (range contraction = 31% in 20 years) and almost unanimously an extirpation of the giant pangolin (93%), the latter being restricted to the Alibori forest reserve (northern Benin). Protected areas were identified as the main potential occurrence zones for pangolins: 77 and 100% of the potential geographic ranges of the white-bellied and the giant pangolins, respectively, overlapped partially or totally with the protected area network of Benin. Using a generalized linear model, we showed that the probability of reporting recent observations of the white-bellied pangolin was significantly higher for villages near protected areas and distant from main roads. The forests perceived as having sustainable populations of white-bellied pangolins were the Lama Forest reserve (southern Benin) and the complex comprising Monts Kouffé - Wari Maro - Ouémé supérieur (central Benin), a view that was supported by the great number of direct occurrence evidence collected in those areas. Overall, our study highlights an important geographic range contraction of the white-bellied pangolin and a possible entire extirpation of the giant pangolin over the last two decades in Benin.

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1. Introduction

Pangolins (Pholidota, Mammalia), or scaly anteaters, are one of the most trafficked wild mammals in the world (Challender and Waterman, 2017; Heinrich et al., 2017). They are facing unprecedented levels of harvesting to supply local bushmeat market networks (Mambeya et al., 2018) and, more importantly, to feed the ever-increasing demand from the Chinese Traditional Medicine market (Challender et al., 2015; Boakye et al., 2016; Heinrich et al., 2016; Mwale et al., 2017; Ingram et al., 2019). Because of a recent decline of the Asian pangolin populations, an illegal, international trade sourcing from Africa into Asia has emerged (Baker, 2014; TRAFFIC/WWF-UK, 2018; Challender et al., 2020), likely facilitated by the increasing economic ties between East Asia (China) and many African countries (Ingram et al., 2019). These trafficking routes probably follow the same criminal networks as the ivory trade (TRAFFIC, 2019).

Globally, around 895,000 pangolins were trafficked since the early 19th century (Challender et al., 2020) and the Gulf of Guinea is one of the main hub of the trade (Ingram et al., 2019). Although recent investigations using CITES trade data (Challender et al., 2015; Heinrich et al., 2016), bushmeat and traditional medicine market surveys (Boakye et al., 2016; Ingram et al., 2018, 2019; Mambeya et al., 2018) and DNA profiling of seized scales (Zhang et al., 2015; Mwale et al., 2017) have shed light on the extent of the pangolin trade in Africa, the ecology, distribution and population trends of the four species occurring across the continent remain poorly studied.

Understanding spatiotemporal changes in distribution and abundance, and their drivers is a prerequisite for implementing successful wildlife conservation actions (Parry and Peres, 2015). Such investigations have been carried out in part of the ranges for *Manis pentadactyla, M. crassicaudata, and M. javanica* in China and Bangladesh (Nash et al., 2016; Trageser et al., 2017) and *Smutsia temminckii* in southern African (Pietersen et al., 2016). Ingram et al. (2019) highlighted the need of baseline ecological data for African pangolins in West Africa to inform policy makers and implement efficient conservation efforts. As such, investigating the spatiotemporal dynamics of African pangolins can help design effective conservation strategies at the country and continental scales.

Two species of pangolins are reported to occur in Benin: the white-bellied pangolin (*Phataginus tricuspis*) and the giant pangolin (*Smutsia gigantea*). The white-bellied pangolin is considered Endangered on both the IUCN Red List and the Red List for Benin, whereas the giant pangolin is considered Endangered on the IUCN Red List and Critically Endangered on the Red List for Benin. A certain number of discrepancies exist between the geographic range delineated for each species on the Red List for Benin (Akpona and Daouda, 2011) and the global IUCN Red List assessments (Pietersen et al., 2019; Nixon et al., 2019). Indeed, the IUCN Red List suggested the uncertain presence (i.e. possible extinction, no recent observations) of the giant pangolin in northern Benin (citing Akpona and Daouda, 2011) and a latitudinally limited (6°10′-10°0′ N) distribution of the white-bellied pangolin, whereas the Red List for Benin showed a widespread distribution of both species in the national parks and forest reserves from southern to northern Benin.

In West Africa, pangolins are used for nutritional, medicinal and spiritual purposes, those having constituted drivers of population decline since the last three decades (Soewu et al., 2020). There is an urgent need to re-assess the distribution and population trends of the two species occurring in Benin, given the human-induced pressures that pangolins are facing, which combine agricultural activities and road infrastructure development (Mama et al., 2013; Alohou et al., 2017) and the local trade for bushmeat and traditional medicine (Codjia and Assogbadjo, 2004; Akpona et al., 2008; Djagoun and Gaubert, 2009; Djagoun et al., 2012; S. Zanvo, unpublished data). In addition, the international trafficking network has probably reached pangolin populations in Benin, with 513 kg of pangolin scales recently seized at the international airport of Cotonou (March 2018; Ingram et al., 2019). So far, only one local-scale study has investigated the ecological aspect of the white-bellied pangolin in Benin (in the Lama forest reserve; Akpona et al., 2008).

Large-scale (here, countrywide) assessments of species' distribution and population trends are especially challenging for nocturnal and elusive species such as pangolins (Thompson, 2004; Pillay et al., 2011). The lack of country-scale and long term data in Benin hampers a literature-based analysis, which can provide an alternative to surveys in countries where there is a paucity of research (Mota-Vargas and Rojas-Soto, 2012). In this context, the use of local ecological knowledge (LEK) represents a cost-effective, reliable approach for monitoring past and current species distribution and population trends at large scales (Silvertown, 2009; Turvey et al., 2014). LEK has received growing interest in ecology over the last two decades (Brook and McLachlan, 2008; Bélisle et al., 2018). This approach is especially appropriate in tropical regions where people depend mainly on natural resources (Pardo de Santayana and Macía, 2015) and where collection of biological data is scarce (Lima et al., 2017; Martinez-Levasseur et al., 2017), such as in Benin (Gaillard, 2010). LEK has been recommended for studying the distribution and population trends of cryptic and threatened species (Turvey et al., 2014), and has been used to study the distribution and conservation status of pangolins in Asia (Nash et al., 2016; Trageser et al., 2017) and southern Africa (Pietersen et al., 2016).

Our study combines LEK with sampling of direct occurrence evidence to assess over the last two decades (1) the distribution of the white-bellied and giant pangolins in Benin, (2) the perceptions of local hunters on their population trends, and (3) the landscape drivers influencing the current geographic distribution of pangolins.

2. Material and methods

2.1. Study area

The study was conducted from April 2018 to March 2019 in the Republic of Benin, at a countrywide scale. Benin is located between latitudes 6°10' - 12°25′ N and longitudes 0°45' - 3°55′E (Fig. 1). The country covers 114,673 km^2 with an estimated population of c. 10 M inhabitants (INSAE, 2013). Benin is subdivided into three ecological regions (White, 1983): 1) the

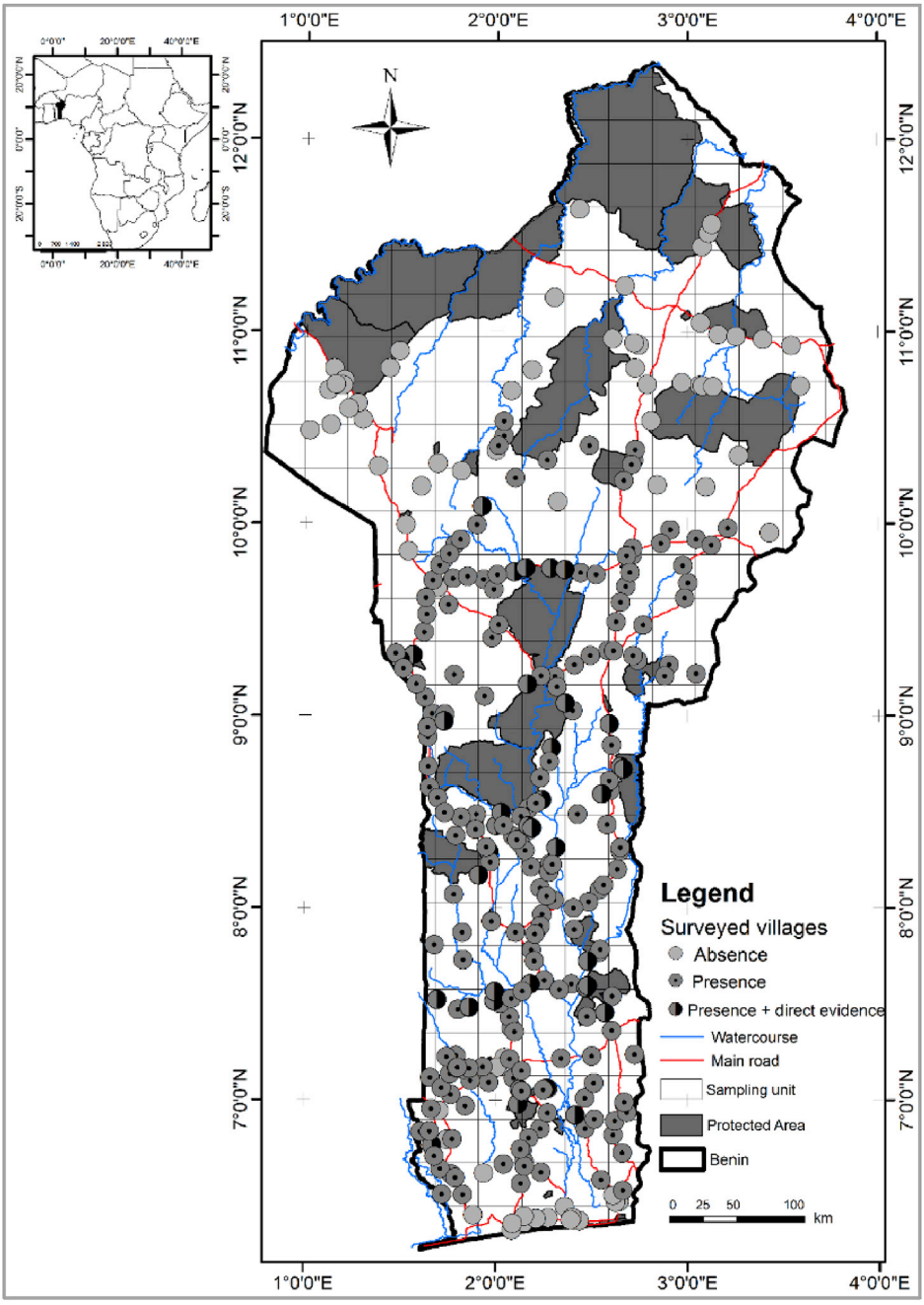

Fig. 1. Location of the 312 villages in which the focus groups were held with local hunters from April 2018 to March 2019 in combination with direct evidence collection. Grids (sampling units) are 25 × 25 km. 'Absence': villages in which focus group participants mentioned the absence of pangolins; 'Presence': villages in which focus group participants mentioned the presence of pangolins without providing direct evidence (scales); 'Presence + direct evidence': villages in which focus group participants supported their statement with direct evidence (scales).

Guineo-Congolian region located 6°10' - 7°15′ N and characterized by bimodal rainfalls, 2) the Sudano-Guinean region extending 7°15' - 9°45′ N, and 3) the Sudanian region between 9°45' - 12°25′ N, both characterized by unimodal rainfalls. Benin shows a highly human-dominated landscape with mosaics of natural vegetation including savannah and forest patches (White, 1983). Natural vegetation represents 26% of total land area with 23.3% of protected areas patchily distributed across two national parks and 56 forest reserves (CENAGREF/PAPE, 2013). Forests are classified into two groups according to the national forest legislation: forest reserves, protected and managed by public forest agents and community forests managed by local communities (CENAGREF/PAPE, 2013). White-bellied and giant pangolins have been reported to occur in most of the Beninese forest reserves and in some community forests (Akpona and Daouda, 2011). The white-bellied pangolin has been confirmed through scientific investigation exclusively in the Lama forest, southern Benin (Akpona et al., 2008), whereas the giant pangolin was documented over three decades ago in the hunting zone of the Pendjari Biosphere Reserve, northern Benin (Sayer and Green, 1984).

2.2. Sampling design and data collection

Benin was subdivided into 228 grids of 25 km × 25 km using ArcMap 10.1 (ESRI Inc.) (Fig. 1). At this grid size, 80% of the sampling units included a core of natural or semi-natural vegetation (potential hunting zones) with human presence, essential for collecting LEK. Forty-six grids were not considered due to the absence of villages within their boundaries. In southern, central and a part of northern regions, grid-based surveys were conducted within 122 grids. This sampling approach was not carried out for the remaining 48 grids in northern Benin and two incomplete grids (i.e. a small portion of grid cell without any potential habitat) in central Benin. We restricted our grid-based sampling efforts in northern Benin since we were able to gather grid level data for these areas from the Pendjari and W National Parks staff, in addition to professional hunters' associations (wildlife hunting management organizations, AVIGREF and professional hunter organizations from the departments of Borgou and Alibori, ACPBA) and former poachers. These structures (AVIGREF and ACPBA) are affiliated to the two National Parks (Pendjari and W respectively). The two small portions of grid located in the central were covered by discussions in neighbouring grid cells.

We gathered information on the past and current occurrence of pangolins on the basis of key-respondent surveys in villages surrounded by habitats potentially favourable to pangolins (forest, tree and shrub savannah, gallery forest, wetland, swamped forest and old plantation). Target villages were selected using the source origins of the pangolins found in 49 bushmeat and traditional medicine markets (S. Zanvo, unpublished data) and the potential habitats identified during meetings with stakeholder groups (and sometimes through informal interviews when we did not detain any prior information). At least one village per grid was sampled, except in the northern region where we were able to collect data for many grids from a reduced grid number. The sampling efforts varied from a grid to another according to the spatial extent of hunters' LEK, potential habitat diversity and size, and the presence of direct evidence. We used a focus group technique to collect data with different stakeholder groups (hunters, rangers and former poachers), except the wildlife-monitoring officers with whom we performed individual interviews before starting data collection in the Pendjari and W National Parks. Focus group technique is a cost effective approach that has been widely used for addressing biodiversity conservation issues, notably in surveys of local communities with a similar hunting background to ours (Nyumba et al., 2018). Such an approach was relevant in the Beninese context where local hunters are likely to avoid giving their opinion individually, fearing negative repercussions from forest management authorities (S. Zanvo, pers. obs. March 2018). Moreover, hunting fraternities are known to exist across Benin, with memberships following well-defined internal rules to keep secrets and knowledge (Kougniazondé et al., 2014).

Focus group participants were identified through informal interviews with villagers and mediated by local community leaders and/or gatekeepers (the authorities of particular divinities 'Vodoun' or a secret organizations in villages) whom assisted us during exchanges but not as respondents. Single focus groups (8–15 persons) were organised in 312 villages. Respondents selected to participate in the focus groups were local hunters, at least thirty years old generally, volunteers and having long-term (>10 years) residency in the area (Kotschwar Logan et al., 2015). However, in some villages, twenty years old hunters were also involved in the focus groups because they were strongly recommended as knowledgeable persons for recent observations of pangolins. They have just provided information on the frequency of observing/harvesting pangolins and potential habitats during the last five years. Snowball sampling approach (Berg, 2001) was used to collect additional, potential occurrence sites of pangolins with non-participants (i.e. people not included in the focus groups) who provided us direct evidence at the end of focus groups. A local translator was used in some villages, generally a student able to speak French in order to facilitate discussion with participants. All participants were guaranteed confidentiality and anonymity before starting discussion. Groups of participants were all composed of adult males, with at least one experienced hunter (over 50 years old) able to give us accurate trends on species dynamics over the last two decades. We started surveys in southern Benin around two reference habitats close to our home institution: the forest reserves of Pahou (unknown absence/presence) and Lama (confirmed presence). These first two 'pilot' focus groups allowed us to validate our protocol before the countrywide survey.

A colour poster and an identification guide comprising the four African pangolin species were used to guide the debate during the focus groups (Beaudreau et al., 2011; Kotschwar Logan et al., 2015). The poster comprised nine photographs of native mammals, with two photographs of pangolins, and three photographs of non-native mammals. The combination of native and non-native mammals on the poster was necessary to be sure that local hunters were able to genuinely identify pangolins, in order to avoid any social desirability bias (Krumpal, 2013). For each pangolin species, the identification guide showed the different parts (head, belly, tail and scales) of the animal in order to optimize identification by participants.

Discussions were conducted following three steps: 1) identification of mammalian species by respondents on the poster; 2) identification of pangolin species occurring in the local environment (and based on the identification guide); 3) answer to a short questionnaire. During the focus groups, participants were asked to identify the mammals that occur in their local environment and give their local names. If pangolins were included in the list, participants were asked to spot the species they refer to among the four African species on the identification guide. When the species was accurately identified, participants were asked to give their perceptions on the abundance trends over the past 20 years (2018, 2013, 2008 and 1998), and to list the drivers of these trends and the potential occurrence sites within the grid extent. The proposed response options for characterizing the abundance trends were defined as follows: 'missing'- probability of observing an individual at the target period is zero in the local environment; 'scarce'- probability of observing an individual at the target period is near to zero in the local environment; 'medium' high probability of observing an individual every month in the hunting season for the target period; and 'abundant' high probability of observing many individuals every month in the hunting season at the target period in the local environment. Questions on drivers and potential habitats were open. We delimited a period of two decades in order to avoid the bias related to the probable loss of LEK with time (Saynes-Vásquez et al., 2013; Aswani et al., 2018). The geographic coordinates of each village were recorded. For each step, the consensual decision of participants was recorded, except for questions about drivers of abundance trends and potential habitats where we recorded all responses.

The presence of pangolins determined during the focus groups was confirmed by the collection of direct evidence −whenever possible− when respondents evoked opportunistic encounters with a recently deceased animal or when scales collected some time ago were said to be kept in the village. The 'snowball' technique allowed us to collect the scale samples from both participants and non-participants of focus groups, when the latter were recognized by participants as possessing the scales. Three to five scales were collected in a plastic zip bag on which the provider's code, harvesting year and habitat were recorded. The scale samples were deposited in the collections of the Laboratory of Applied Ecology, University of Abomey-Calavi, Benin. A monthly collection of direct evidence was conducted during the dry season (January, February and March) in the villages where the presence of pangolins was declared by local hunters during focus groups without providing direct evidence.

2.3. Data analysis

In order to build the distribution maps of the white-bellied and giant pangolins, we considered the geographic coordinates of all the villages ($N = 235$) where focus group participants successfully and in a consensual manner (100% of participants when there is no direct evidence) agreed on a pangolin species presence, with or without collecting direct evidence (scales). Whenever the above conditions were not met, the species were considered absent from the village. As such, only the villages where respondents reported pangolins to be "scarce", "medium" or "abundant" for a given time period were considered as valid occurrences. We used ArcMap 10.1 (ESRI Inc.) to generate superimposed layers (25 km $\times$ 25 km grids) representing each period/species, where the grids containing villages reporting the presence of pangolins were considered as occupancy areas of the targeted species. Occupancy area is here defined as the probability that a grid was occupied at a given time period (over the past 20 years) by a pangolin species (see Latif et al., 2016). For each reported potential habitat with or without direct evidence collection, the total area was calculated using the recent shapefile in ArcMap 10.1 (ESRI Inc.). The management modality for each forest and its national classification were extracted from official documents (FAO, 2010; CENAGREF/PAPE, 2013; DGEFC, 2017).

In order to assess local people's perceptions about trends in the abundance of the white-bellied and giant pangolins over the last two decades and identify factors causing these trends, each focus group was considered as an independent observation. R version 3.5.1 (R Core development team) was used for all the statistical analyses. Local hunters' perceptions regarding pangolin abundance level (missing, scarce, medium and abundant) were plotted for each species using the cumulative barplot in the ggplot2 R package for four different periods (2018, 2013, 2008 and 1998). Differences among abundance levels across time periods were tested with the Pearson's χ^2 test for the white-bellied pangolin and the Fisher exact test for the giant pangolin due to low observation numbers. The drivers of pangolin declines as extracted from the respondents were classified into the six following categories, for which frequencies of citations were calculated: wood energy harvesting (deforestation), hunting, agriculture, transhumance (livestock), fire and urbanization.

In order to understand the landscape characteristics that may influence the current geographic distribution of the white-bellied pangolin, we computed in ArcMap the Euclidean distances from villages to the nearest (i) protected areas (*DistAP*), (ii) permanent watercourses (*DistWater*), and (iii) main roads (*DistRoad*). For all the villages considered ($N = 235$), focus group participants were hunters with similar hunting background. So, we assume an equal understanding of the white-bellied pangolin distribution in the local areas among villages. Only 2018 was considered and presence/absence data were defined as described above, and were modelled with these landscape variables (*DistAP, DistWater and DistRoad*) using a generalized linear model. We did not model the current distribution of the giant pangolin because only two villages reported its presence in 2018, without any direct evidence of occurrence.

3. Results

Focus groups gathered 3282 respondents (hunters, rangers and former poachers), 291 local community leaders, 21 gatekeepers. The average age per focus group varied between 33 and 52 years old and all the participants were men. All the

collected pangolin scales (96 samples) belonged to the white-bellied pangolin with 6, 38, 15 and 47% harvested respectively in 2016, 2017, 2018 and 2019 by local people.

3.1. Geographic range over the last two decades

The geographic distribution of the two species of pangolins as extrapolated from the focus groups extended between 6°10′ and 11°00′ N, with the giant pangolin being restricted to 10° 20′-11°00′ N (Fig. 2a and b). Our investigations suggested that the white-bellied pangolin over the last two decades (from 1998 to 2018) underwent a 31% (14,169 km^2) contraction of its occupancy area while that of the giant pangolin was reduced by 93% (15,955 km^2) (Table 1).

In total, c. 77 and 100% of the occupancy areas (Table 1) of the white-bellied pangolin and the giant pangolin, respectively, were partially or totally included in protected areas in 2018, against c. 60% two decades ago (1998). Twelve forest reserves and two game ranches out of the 23 forest islands cited by local hunters are the current potential habitats of the white-bellied pangolin with only one out of 23 forests cited by local hunters for the giant pangolin (Table 2). These forest reserves and ranches are managed as wildlife reserves and for wood energy harvesting (Table 2). Forest reserves and ranches (protected areas) supplied 76% of the pangolin scales collected as direct evidence (66% from wildlife reserves and 10% from wood energy forests). The wildlife reserve complex constituted by Monts Kouffé, Wari-Maro and Ouémé supérieur in the central part of Benin provided 46% of the scale samples and the Lama forest in southern Benin provided 13%.

3.2. Abundance trends according to respondents

Respondents perceived a decline in the abundance level of the white-bellied pangolin in Benin (Fig. 3a), and their perceptions depended significantly on time periods ($\chi^2 = 126.7$, $p < 0.001$) over the last two decades. The species was seen as abundant for 37% of the focus groups in 1998, in comparison with 4% in 2018. Inversely, its extirpation (missing) was mentioned in 33% of the focus groups in 1998 against 54% in 2018. The extirpation of the giant pangolin was perceived almost

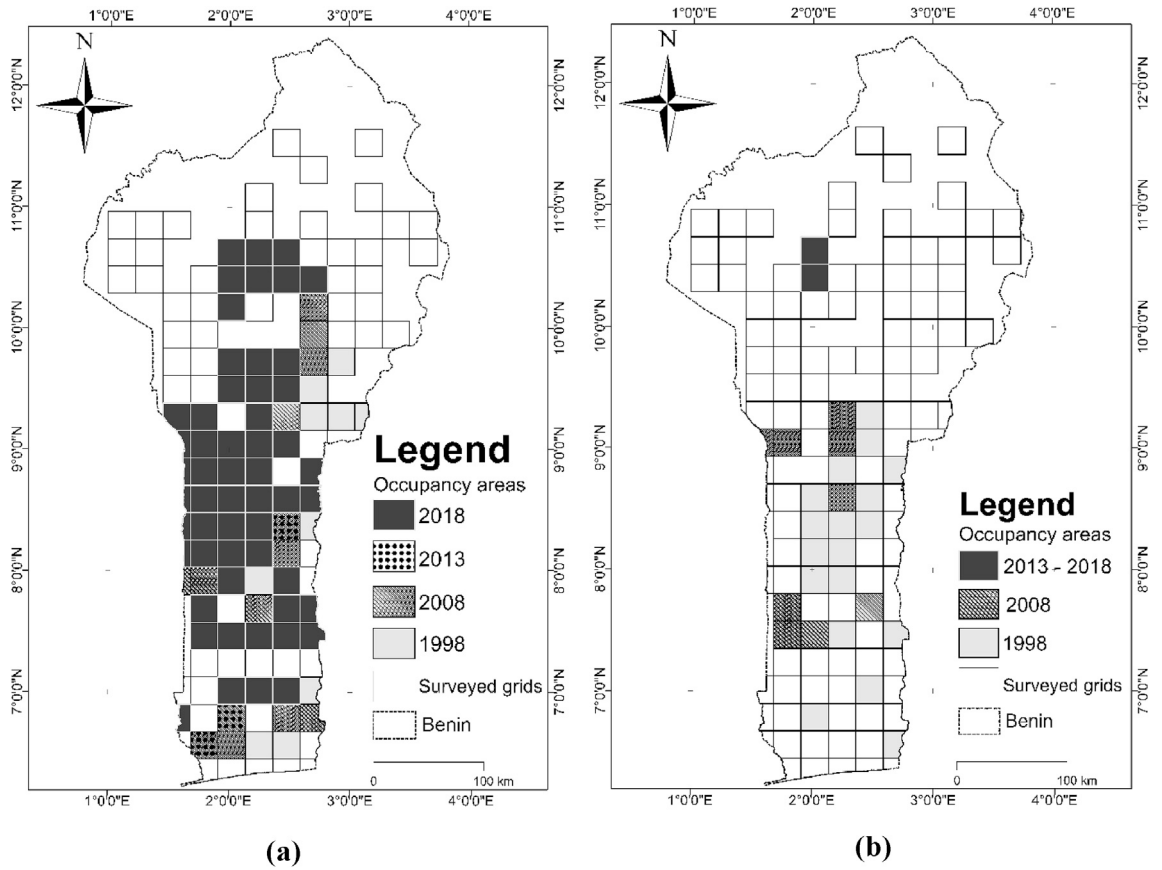

Fig. 2. Geographical range dynamics of (a) the white-bellied pangolin and (b) the giant pangolin in Benin from 1998 to 2018. Each grid cell represents an occupancy area for one or several time period(s) by overlaying sampled units (grids) and responses of focus groups. During this period, no new colonization and recolonization events have been mentioned by participants. Thus, the time of occupancy of a grid cell implies that the species has been present since 1998.

Table 1
Twenty-years temporal trend in occupancy areas (global and protected) between the two species of pangolins in Benin, as expressed by the focus groups.

Year	Phataginus tricuspis		Smutsia gigantea	
	Occupancy area (km^2)	Occupancy area including a protected area (km^2)	Occupancy area (km^2)	Occupancy area including a protected area (km^2)
2018	30960.797	23820.235 (77%)	1250	1250 (100%)
2013	32813.046	24445.235 (74%)	–	–
2008	39693.748	26945.235 (68%)	6443.909	3943.909 (61%)
1998	45129.603	27934.588 (62%)	17205.278	10540.684 (61%)

unanimously over the last period of our study (2013–2018; Fig. 3b), and this perception was also related to time periods ($p < 0.001$).

Respondents perceived wood energy harvesting (81.5%), hunting (77.08%) and agriculture (70.84%) (Table 3) as the major drivers of the white-bellied pangolin's decline, and hunting (91.2%) as mainly driving the extirpation of the giant pangolin.

3.3. Drivers of geographic distribution of the white-bellied pangolin

GLM analysis revealed that distance from, villages to protected areas (*DistAP*) and villages to main roads (*DistRoads*) were the main landscape variables explaining the current distribution of the white-bellied pangolin (Table 4). The probability that hunters made recent observations of the white-bellied pangolin increased when villages were (i) closer to protected areas and (ii) further away from main roads.

4. Discussion

Our national-scale study offers an unprecedented reassessment of the distribution, population trends and landscape occupancy drivers of pangolins in Benin. Such a detailed level of investigation on pangolins at the regional or country-scale have so far only been done in Asia (Nash et al., 2016; Trageser et al., 2017) and southern Africa (Pietersen et al., 2016) on other species.

Our approach combining LEK and direct evidence of occurrence (pangolin scales) yielded a reliable assessment of the current ranges of pangolins in Benin, and likely improved the accuracy of the current ranges delineated in global or national red lists that serve as references for the community involved in wildlife conservation (Akpona and Daouda, 2011; Nixon et al., 2019; Pietersen et al., 2019). From the respondents and direct occurrence evidence collected in this study, it appears that the ranges of both the white-bellied and giant pangolins probably never occurred beyond a latitude of 11°00′N, at least within the last 20 years. The national parks occurring beyond that latitude are the Biosphere Reserve of Pendjari and the Transboundary Park W, where wildlife biomonitoring done in recent years (camera traps and wildlife census, 2012–2015) by park managers has failed to report any sightings of pangolins (S. Zanvo, pers. obs. December 2018). Unanimously, the oldest hunters, together with rangers and former poachers stated that the two species of pangolins had never occurred in the National Parks of Pendjari and W, and their surrounding areas, contradicting what was suggested in the Red List for Benin on the basis of vague assumptions without photographic evidence or voucher specimen (Akpona and Daouda, 2011). This contradiction is equally observed with the IUCN Red List (Nixon et al., 2019), which listed the giant pangolin as "probably extant" in those two national Parks (citing Akpona and Daouda, 2011; but the supposed record from Pendjari comes from Sayer and Green, 1984). Although LEK may be subject to erosion through time (Saynes-Vásquez et al., 2013; Aswani et al., 2018), we believe that the absence of the giant pangolins from those two national parks is plausible since such northern latitudes may represent unfavourable climatic conditions for the species. Our study suggests that the giant pangolin was subject to a rapid decline and total extirpation from southern and central Benin, representing 93% of range contraction in the last 20 years. In the last five years, the giant pangolin was only mentioned by a focus group from the Alibori forest reserve, showing a very restricted potential range in Benin (10°20' - 11°00′ N; c. 259,000 km^2). No direct occurrence evidence (scales) from giant pangolin was retained by villagers confirming the rarity of the species in the country as reported in other parts of its range (Bräutigam et al., 1994), but is at odds with the relatively widespread occurrence of the species in Benin suggested by Akpona and Daouda (2011).

Our survey suggested a more stable distribution dynamics of the white-bellied pangolin over the past 20 years from southern to north-central Benin (6°10′ N to 11°00′ N), although the species was identified as undergoing an important contraction of its range (31%) over the last two decades. Our survey indicates that the white-bellied pangolin is likely present in at least 23 Beninese forests, and this was confirmed by direct occurrence evidence in 17 (74%) of the cases (Table 2). The current distribution of the white-bellied pangolin as delineated from our interviews shows a more fragmented range in southern and central Benin, and demonstrates the occurrence of the species at higher latitudes, increasing the range exposed by the IUCN Red List (reaching approximately 10°20′ N in Pietersen et al., 2019 *versus* 11°00' N in the present study).

Globally, the two species of pangolins in Benin were seen as undergoing a significant decrease of their distribution range over the last 20 years (see above), associated with an increase in the proportion of their existing range falling in protected areas, reaching 100% (one reserve) in the case of the giant pangolin. Such a pattern of range loss and "refugial" occupancy into protected areas is typical of populations undergoing rapid extirpation due to habitat deterioration and targeted hunting activities (Bauer et al., 2015). Our survey also suggested an important decrease in the abundance of the two pangolin species

Table 2
Characteristics of the current forests potentially housing the white-bellied and the giant pangolins, with frequency of collected scales (direct evidence).

Forest/Habitat	Management modality	Classification objective	Total area (km^2)	Number of collected scales
Agoua*	Forest reserve	Wood energy	67052.18	5
Agrimey*	Forest reserve	Wood energy	3056.877	0
Alibori supérieur**	Forest reserve	Wood energy	259135.158	0
Atchin*	Community forest	Social service	37.992	1
Bassila*	Forest reserve	Wood energy	3040.771	0
Djaloukou	Game ranch	Wildlife reserve	3880	0
Dévé*	Community forest	Social services	3.83	2
Dogo*	Forest reserve	Wood energy	31630.365	4
Felea*	Community forest	Social services	42.759	0
Gbadagba	Game ranch	Wildlife reserve	1415	2
Gnanhouizoun*	Community forest	Social services	6.261	8
Ikpokporo*	Community forest	Social services	32.368	0
Kouvizoun*	Community forest	Social services	529.588	2
Lama*	Forest reserve	Wildlife reserve	17604.197	13
Lokoli*	Community forest	Social services	2942.103	1
Monlouvé*	Community forest	Social services	18.382	2
Monts Kouffé*	Forest reserve	Wildlife reserve	191652.549	27
Ouémé Boukou*	Forest reserve	Wildlife reserve	22437.079	4
Ouémé supérieur*	Forest reserve	Wildlife reserve	184768.521	12
Penessoulou*	Forest reserve	Wood energy	5247.062	1
Toui-klibo*	Forest reserve	Wildlife reserve	44131.032	2
Wari-Maro*	Forest reserve	Wildlife reserve	117615.512	7
Gallery forests*	NA	Soil and water protection	NA	8

(*) white-bellied pangolin (**) white-bellied and giant pangolins.

over the last two decades in Benin, as perceived by local hunters. For the giant pangolin, 100% of the focus groups declared the species either rare (15%) or missing (85%) ten years ago, with the species being reported as missing in 2018 by 98% of the groups. Such perceptions are consistent with general population trends for the species, again supporting the view that the giant pangolin is generally rare and declining throughout its range (Nixon et al., 2019). In Benin, traders from traditional medicine markets also confirmed this trend (S. Zanvo, unpublished data). A decrease in abundance was also perceived in the white-bellied pangolin over the last two decades, the species being declared abundant in 1998 by 37% of the focal groups but only by 4% in 2018. Although the species is considered the most common African pangolin (Pagès, 1975; Angelici et al., 1999; Gaubert, 2011), it is believed to be declining in Ghana and Guinea, and to near extinction in Rwanda (Pietersen et al., 2019). Soewu and Ayodele (2009) also reported that 92% of the traditional practitioners in the nearby Ogun State, Nigeria, stated that the abundance of white-bellied pangolin was continuously decreasing. Although a previous study from the Lama Forest Reserve in southern Benin reported a density of 0.84 individuals per km^2 (Akpona et al., 2008), our study suggests that such relatively high density estimates may not be common or reflective of the current situation in the country. Khwaja et al. (2019) suggested that degraded habitats could lead to a greater detection probability of the white-bellied pangolin, amplifying its time of activity on exposed parcels. So, in the current context of highly degraded forests in Benin, the general decline perceived by local communities over the last two decades could be considered as a genuine representation of the population trends in pangolins.

Nixon et al. (2019) associated the decline of the giant pangolin to habitat alteration and unsustainable exploitation for bushmeat and traditional medicine, feeding both local and international markets (Djagoun et al., 2012; Heinrich et al., 2016; Ingram et al., 2019). Its large size, low reproductive rate and terrestrial habits make it particularly vulnerable to over-exploitation (Kingdon et al., 2013). In Benin, the major cause for the species' depletion was identified as hunting by c. 91% of the focus groups, followed to a lesser extent by habitat alteration (45–60%), in agreement with Akpona and Douada (2011). Because the species is restricted to forested habitats (Gaubert, 2011), deforestation and agricultural activities might have played a significant role in its local extinction and range fragmentation in Benin. Despite almost one year of survey at the country scale, no direct occurrence evidence (scales) of giant pangolin could be collected (whereas 96 items were collected for the white-bellied pangolin). We posit that the giant pangolin, which was already considered rare in Benin 20 years ago, is now at best restrained to the forest reserve of Alibori and is facing high extinction risk, especially since its former presence in southern and central forest reserves did not prevent from its rapid extirpation. Field investigations using camera trapping (Khwaja et al., 2019; Morin et al., 2020) are urgently needed to confirm the existence and status of the remaining populations and to investigate their habitat use in order to propose concrete solutions for the conservation of the giant pangolin in Benin.

Pietersen et al. (2019) linked the decline of the white-bellied pangolin across its range to habitat alteration, wood plantation and unsustainable hunting. In Benin, the major causes of decline were identified as deforestation (81%), agriculture (70%) and hunting (77%). Although the species predominantly occurs in moist tropical lowland forests, it can also be found in dense woodlands and secondary growth forests such as abandoned oil palm or even teak plantations (Sodeinde and Adedipe, 1994; Angelici et al., 1999; Akpona et al., 2008; Gaubert, 2011), thus suggesting a certain level of adaptability to human-induced habitat transformation. However, severe fragmentation of forested habitats by intense agriculture activities,

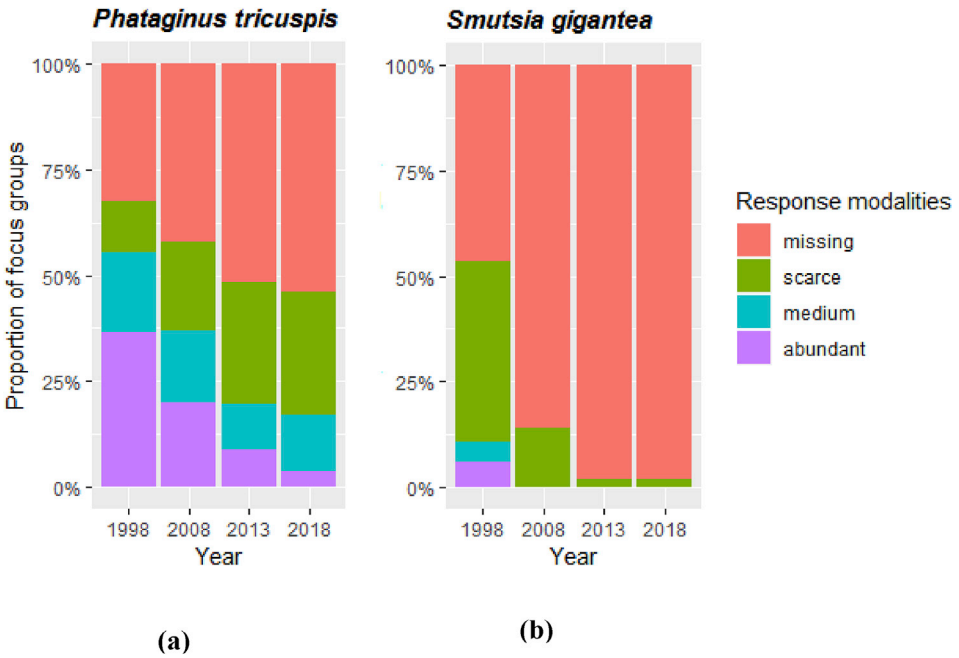

Fig. 3. Focus group representations of abundance trends of pangolins in Benin over the last two decades (1998–2018).

Table 3
Local hunters' perceptions about the drivers of pangolins' decline ($N = 235$ focus groups).

Threats	Frequency of citations (%)	
	P. tricuspis	*S. gigantea*
Deforestation (wood energy)	81.25	59.88
Hunting	77.08	91.2
Agriculture	70.84	45.05
Transhumance	45.83	55.36
Fire	29.16	3.16
Urbanization	8.33	–

Table 4
Relative importance of landscape variables associated by local hunters to the recent observations of the white-bellied pangolin in Benin.

Variables (m)	Estimate	*p-value*
DistAP	−0.0001	0.0000 ***
DistRoad	0.0001	0.0000 ***
DistWater	−0.000031	0.1419

growing urbanization and forest exploitation for wood energy (FAO, 2010; Alohou et al., 2017) are likely to significantly reduce the coverage of suitable habitats for the white-bellied pangolin in Benin. The species is subject to intense exploitation across its range for bushmeat and traditional medicine, and is the most represented pangolin species in bushmeat markets (Djagoun and Gaubert, 2009; Djagoun et al., 2012). The important quantity of direct occurrence evidence (96 samples of scales) collected during our survey showed that hunters stored pangolin scales in their houses either as trophies or for uses in traditional medicine (Akpona et al., 2008; Djagoun et al., 2012), and possibly for supplying traditional medicine markets.

The expanding scale of the illegal international trade towards Asia (Challender and Hywood, 2012; Xu et al., 2016) is likely contributing to the depletion of white-bellied pangolin populations. In Benin, international trafficking has been confirmed by a recent seizure of 513 kg of pangolin scales at the airport of Cotonou (Ingram et al., 2019). This potentially highlights an extension of the western African pangolin trafficking network towards Asia, which was so far preeminent in Sierra Leone, Ivory Coast, Ghana, and Nigeria (Xu et al., 2016). Our study suggested that the white-bellied pangolin in Benin mostly occurred far from the road network and near or within protected areas, emphasizing avoidance of the most disturbed human-dominated landscapes by road networks (Shanley and Pyare, 2011) and the crucial role played by protected areas for the

survival of the species. The road networks would have facilitated defaunation from impacted areas due to the good access to pangolin's habitats for hunting activities. However, the high percentage (76%) of scales collected from protected areas is a token of the ongoing poaching pressure within those reserves. Besides, the classification objective into wood energy production of almost half of the forest reserves where the species was reported to occur (Table 4) may prove rapidly unsuitable relative to the ecological requirements of the species, which involve large trees for sheltering.

In the current context, conservation actions should be urgently engaged to design a sound species-conservation and land-management plan in Benin. The classification of the main reserves potentially housing pangolins to limit anthropogenic disturbance −especially deforestation− should be encouraged. An upstream regulation of local bushmeat and traditional medicine markets should also be implemented, in order to limit local trafficking (Djagoun and Gaubert, 2009; Djagoun et al., 2012). Because the Lama forest reserve in southern Benin and the complex Monts Kouffé - Wari Maro - Ouémé supérieur in central Benin are the two sole forest relics that have been identified as housing large populations of white-bellied pangolins, those two areas, together with the Alibori forest reserve as the last potential stronghold for the giant pangolin, should be urgently investigated.

Our study cross-validating LEK data with direct evidence constitutes a useful reference framework for future field-based investigations on pangolin populations in Benin and the establishment of a national strategy for pangolin conservation. Despite the reliability of our methodological approach, further field surveys based on newly validated methods (Khwaja et al., 2019) will be essential to confirm occurrences, population status and population trends of pangolins in Benin.

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Declaration of competing interest

All authors declare there are no conflicts of interest.

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