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# 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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## ► To cite this version:

S. Zanvo, Philippe Gaubert, C.A.M.S. Djagoun, A.F. Azihou, B. Djossa, et al.. Assessing the spatiotemporal dynamics of endangered mammals through local ecological knowledge combined with direct evidence: the case of pangolins in Benin (West Africa). *Global Ecology and Conservation*, 2020, 23, art. e01085 [12 p.]. 10.1016/j.gecco.2020.e01085 . hal-02887960

**HAL Id: hal-02887960**

<https://hal.science/hal-02887960v1>

Submitted on 22 Aug 2022

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

3

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13

14 **Abstract**

15 Although pangolins are considered to be one of the most trafficked wild mammals in the world,  
16 their conservation status remains uncertain through most of their ranges, and notably in western  
17 Africa. Using local ecological knowledge in combination with direct occurrence evidence, we  
18 assessed the distribution and abundance of the white-bellied pangolin (*Phataginus tricuspis*)  
19 and the giant pangolin (*Smutsia gigantea*) in Benin over the last two decades (1998 - 2018). We  
20 organised focus groups with local hunters in 312 villages within sampling units of 25 km x 25  
21 km covering the whole country. Participatory maps of past and current geographic ranges of  
22 pangolins combined with direct evidence (96 collected scales) suggested that the white-bellied  
23 pangolin had a wide distribution and reached higher latitudes than previously known, whereas

24 the giant pangolin could be restricted to a single forest and has been absent from the northern  
25 part of the country over **at least** the last two decades. Local hunters perceived a significant  
26 decline of the white-bellied pangolin (range contraction = 31 % in 20 years) and almost  
27 unanimously an extirpation of the giant pangolin (93 %), the latter being restricted to the Alibori  
28 forest reserve (northern Benin). Protected areas were identified as the main potential occurrence  
29 zones for pangolins: 77 and 100 % of the potential geographic ranges of the white-bellied and  
30 the giant pangolins, respectively, overlapped partially or totally with the protected area network  
31 of Benin. Using a generalized linear model, we showed that the probability of reporting recent  
32 observations of the white-bellied pangolin was significantly higher for villages near protected  
33 areas and distant from main roads. The forests perceived as having sustainable populations of  
34 white-bellied pangolins were the Lama Forest reserve (southern Benin) and the complex  
35 comprising Monts Kouffé - Wari Maro - Ouémé supérieur (central Benin), a view that was  
36 supported by the great number of direct occurrence evidence collected in those areas. Overall,  
37 our study highlights an important geographic range contraction of the white-bellied pangolin  
38 and a possible entire extirpation of the giant pangolin over the last two decades in Benin.

39

40 **Key words:** geographic range, local ecological knowledge, pangolins, population decline, local  
41 extirpation, Benin

42

## 43 1. Introduction

44 Pangolins (Pholidota, Mammalia), or scaly anteaters, are one of the most trafficked wild  
45 mammals in the world (Challender and Waterman, 2017; Heinrich *et al.*, 2017). They are facing  
46 unprecedented levels of harvesting to supply local bushmeat market networks (Mambeya *et al.*,  
47 2018) and, more importantly, to feed the ever-increasing demand from the Chinese Traditional  
48 Medicine market (Challender *et al.*, 2015; Boakye *et al.*, 2016; Heinrich *et al.*, 2016; Mwale *et*  
49 *al.*, 2017; Ingram *et al.*, 2019). Because of a recent decline of the Asian pangolin populations,  
50 an illegal, international trade sourcing from Africa into Asia has emerged (Baker *et al.*, 2014;  
51 TRAFFIC/WWF-UK, 2018; Challender *et al.*, 2020), likely facilitated by the increasing  
52 economic ties between East Asia (China) and many African countries (Ingram *et al.*, 2019).  
53 These trafficking routes probably follow the same criminal networks as the ivory trade  
54 (TRAFFIC, 2019).

55 Globally, around 895,000 pangolins were trafficked since the early 19<sup>th</sup> century (Challender *et*  
56 *al.*, 2020) and the Gulf of Guinea is one of the main hub of the trade (Ingram *et al.*, 2019).  
57 Although recent investigations using CITES trade data (Challender *et al.*, 2015; Heinrich *et al.*,  
58 2016), bushmeat and traditional medicine market surveys (Boakye *et al.*, 2016; Ingram *et al.*,  
59 2018; Mambeya *et al.*, 2018; Ingram *et al.*, 2019) and DNA profiling of seized scales (Zhang  
60 *et al.*, 2015; Mwale *et al.*, 2017) have shed light on the extent of the pangolin trade in Africa,  
61 the ecology, distribution and population trends of the four species occurring across the continent  
62 remain poorly studied.

63 Understanding spatiotemporal changes in distribution and abundance, and their drivers is a  
64 prerequisite for implementing successful wildlife conservation actions (Parry and Peres, 2015).  
65 Such investigations have been carried out in part of the ranges for *Manis pentadactyla*, *M.*  
66 *crassicaudata*, and *M. javanica* in China and Bangladesh (Nash *et al.*, 2016; Trageser *et al.*,  
67 2017) and *Smutsia temminckii* in southern African (Pietersen *et al.*, 2016). Ingram *et al.* (2019)

68 highlighted the need of baseline ecological data for African pangolins in West Africa to inform  
69 policy makers and implement efficient conservation efforts. As such, investigating the  
70 spatiotemporal dynamics of African pangolins can help design effective conservation strategies  
71 at the country and continental scales.

72 Two species of pangolins are reported to occur in Benin: the white-bellied pangolin (*Phataginus*  
73 *tricuspis*) and the giant pangolin (*Smutsia gigantea*). The white-bellied pangolin is considered  
74 Endangered on both the IUCN Red List and the Red List for Benin, whereas the giant pangolin  
75 is considered Endangered on the IUCN Red List and Critically Endangered on the Red List for  
76 Benin. A certain number of discrepancies exist between the geographic range delineated for  
77 each species on the Red List for Benin (Akpona and Daouda, 2011) and the global IUCN Red  
78 List assessments (Pietersen *et al.*, 2019; Nixon *et al.*, 2019). Indeed, the IUCN Red List  
79 suggested the uncertain presence (i.e. possible extinction, no recent observations) of the giant  
80 pangolin in northern Benin (citing Akpona and Daouda, 2011) and a latitudinally limited  
81 (6°10'-10°0' N) distribution of the white-bellied pangolin, whereas the Red List for Benin  
82 showed a widespread distribution of both species in the national parks and forest reserves from  
83 southern to northern Benin.

84 In West Africa, pangolins are used for nutritional, medicinal and spiritual purposes, those  
85 having constituted drivers of population decline since the last three decades (Soewu *et al.*,  
86 2020). There is an urgent need to re-assess the distribution and population trends of the two  
87 species occurring in Benin, given the human-induced pressures that pangolins are facing, which  
88 combine agricultural activities and road infrastructure development (Mama *et al.*, 2013; Alohou  
89 *et al.*, 2017) and the local trade for bushmeat and traditional medicine (Codjia *et al.*, 2004;  
90 Akpona *et al.*, 2008; Djagoun and Gaubert, 2009; Djagoun *et al.*, 2012; S. Zanvo, unpublished  
91 data). In addition, the international trafficking network has probably reached pangolin  
92 populations in Benin, with 513 kg of pangolin scales recently seized at the international airport

93 of Cotonou (March 2018; Ingram *et al.*, 2019). So far, only one local-scale study has  
94 investigated the ecological aspect of the white-bellied pangolin in Benin (in the Lama forest  
95 reserve; Akpona *et al.*, 2008).

96 Large-scale (here, countrywide) assessments of species' distribution and population trends are  
97 especially challenging for nocturnal and elusive species such as pangolins (Thompson, 2004;  
98 Pillay *et al.*, 2011). The lack of country-scale and long term data in Benin hampers a literature-  
99 based analysis, which can provide an alternative to surveys in countries where there is a paucity  
100 of research (Mota-Vargas and Rojas-Soto, 2012). In this context, the use of local ecological  
101 knowledge (LEK) represents a cost-effective, reliable approach for monitoring past and current  
102 species distribution and population trends at large scales (Silvertown, 2009; Turvey *et al.*,  
103 2014). LEK has received growing interest in ecology over the last two decades (Brook *et al.*,  
104 2008; Bélisle *et al.*, 2018). This approach is especially appropriate in tropical regions where  
105 people depend mainly on natural resources (Pardo de Santayana and Macía, 2015) and where  
106 collection of biological data is scarce (Lima *et al.*, 2017; Martinez-Levasseur *et al.*, 2017), such  
107 as in Benin (Gaillard, 2010). LEK has been recommended for studying the distribution and  
108 population trends of cryptic and threatened species (Turvey *et al.*, 2014), and has been used to  
109 study the distribution and conservation status of pangolins in Asia (Nash *et al.*, 2016; Trageser  
110 *et al.*, 2017) and southern Africa (Pietersen *et al.*, 2016).

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

115

## 116 **2. Material and Methods**

## 117 2.1. Study area

118 The study was conducted from April 2018 to March 2019 in the Republic of Benin, at a  
119 countrywide scale. Benin is located between latitudes 6°10' - 12°25' N and longitudes 0°45' -  
120 3°55'E (Fig. 1). The country covers 114,673 km<sup>2</sup> with an estimated population of c. 10 M  
121 inhabitants (INSAE, 2013). Benin is subdivided into three ecological regions (White, 1983): 1)  
122 the Guineo-Congolian region located 6°10' - 7°15' N and characterized by bimodal rainfalls,  
123 2) the Sudano-Guinean region extending 7°15' - 9°45' N, and 3) the Sudanian region between  
124 9°45' - 12°25' N, both characterized by unimodal rainfalls. Benin shows a highly human-  
125 dominated landscape with mosaics of natural vegetation including savannah and forest patches  
126 (White, 1983). Natural vegetation represents 26 % of total land area with 23.3 % of protected  
127 areas patchily distributed across two national parks and 56 forest reserves (CENAGREF/PAPE,  
128 2013). Forests are classified into two groups according to the national forest legislation: forest  
129 reserves, protected and managed by public forest agents and community forests managed by  
130 local communities (CENAGREF/PAPE, 2013). White-bellied and giant pangolins have been  
131 reported to occur in most of the Beninese forest reserves and in some community forests  
132 (Akpona and Daouda, 2011). The white-bellied pangolin has been confirmed through scientific  
133 investigation exclusively in the Lama forest, southern Benin (Akpona *et al.*, 2008), whereas the  
134 giant pangolin was documented over three decades ago in the hunting zone of the Pendjari  
135 Biosphere Reserve, northern Benin (Sayer and Green, 1984).

## 136 2.2. Sampling design and data collection

137 Benin was subdivided into 228 grids of 25 km x 25 km using ArcMap 10.1 (ESRI Inc.) (Fig.  
138 1). At this grid size, 80 % of the sampling units included a core of natural or semi-natural  
139 vegetation (potential hunting zones) with human presence, essential for collecting LEK. Forty-  
140 six grids were not considered due to the absence of villages within their boundaries. In southern,  
141 central and a part of northern regions, grid-based surveys were conducted within 122 grids. [This](#)

142 [sampling approach was](#) not carried out for the remaining 48 grids in northern Benin and two  
143 incomplete grids (i.e. a small portion of grid cell without any potential habitat) in central Benin.  
144 We restricted our grid-based sampling efforts in northern Benin since we were able to gather  
145 grid level data for these areas from the Pendjari and W National Parks staff, in addition to  
146 professional hunters' associations (wildlife hunting management organizations, AVIGREF and  
147 professional hunter organizations from the departments of Borgou and Alibori, ACPBA) and  
148 former poachers. These structures (AVIGREF and ACPBA) are affiliated to the two National  
149 Parks (Pendjari and W respectively). [The two small portions of grid located in the central were](#)  
150 [covered by discussions in neighbouring grid cells.](#)

151 We gathered information on the past and current occurrence of pangolins on the basis of key-  
152 respondent surveys in villages surrounded by habitats potentially favourable to pangolins  
153 (forest, tree and shrub savannah, gallery forest, wetland, swamped forest and old plantation).  
154 Target villages were selected using the source origins of the pangolins found in 49 bushmeat  
155 and traditional medicine markets (S. Zanvo, unpublished data) and the potential habitats  
156 identified during meetings with stakeholder groups (and sometimes through informal  
157 interviews when we did not detain any prior information). At least one village per grid was  
158 sampled, except in the northern region where we were able to collect data for many grids from  
159 a reduced grid number. The sampling efforts varied from a grid to another according to the  
160 spatial extent of hunters' LEK, potential habitat diversity and size, and the presence of direct  
161 evidence. We used a focus group technique to collect data with different stakeholder groups  
162 (hunters, rangers and former poachers), except the wildlife-monitoring officers with whom we  
163 performed individual interviews before starting data collection in the Pendjari and W National  
164 Parks. [Focus group technique is a cost effective](#) approach that has been widely used for  
165 addressing biodiversity conservation issues, notably in surveys of local communities with a  
166 similar hunting background to ours (Nyumba *et al.*, 2018). Such an approach was relevant in



167 the Beninese context where local hunters are likely to avoid giving their opinion individually,  
168 fearing negative repercussions from forest management authorities (S. Zanvo, pers. obs. March  
169 2018). Moreover, hunting fraternities are known to exist across Benin, with memberships  
170 following well-defined internal rules to keep secrets and knowledge (Kougniazondé *et al.*,  
171 2014).

172 Focus groups participants were identified through informal interviews with villagers and  
173 mediated by local community leaders and/or gatekeepers (the authorities of particular divinities  
174 ‘Vodoun’ or a secret organizations in villages) whom assisted us during exchanges but not as  
175 respondents. Single focus groups (8 - 15 persons) were organized in 312 villages. Respondents  
176 selected to participate in the focus groups were local hunters, at least thirty years old generally,  
177 volunteers and having long-term (>10 years) residency in the area (Kotschwar Logan *et al.*,  
178 2015). However, in some villages, twenty years old hunters were also involved in the focus  
179 groups because they were strongly recommended as knowledgeable persons for recent  
180 observations of pangolins. They have just provided information on the frequency of  
181 observing/harvesting pangolins and potential habitats during the last five years. Snowball  
182 sampling approach (Berg, 2001) was used to collect additional, potential occurrence sites of  
183 pangolins with non-participants (i.e. people not included in the focus groups) who provided us  
184 direct evidence at the end of focus groups. A local translator was used in some villages,  
185 generally a student able to speak French in order to facilitate discussion with participants. All  
186 participants were guaranteed confidentiality and anonymity before starting discussion. Groups  
187 of participants were all composed of adult males, with at least one experienced hunter (over 50  
188 years old) able to give us accurate trends on species dynamics over the last two decades. We  
189 started surveys in southern Benin around two reference habitats close to our home institution:  
190 the forest reserves of Pahou (unknown absence/presence) and Lama (confirmed presence).

191 These first two ‘pilot’ focus groups allowed us to validate our protocol before the countrywide  
192 survey.

193 A colour poster and an identification guide comprising the four African pangolin species were  
194 used to guide the debate during the focus groups (Beaudreau *et al.*, 2011; Kotschwar Logan *et*  
195 *al.*, 2015). The poster comprised nine photographs of native mammals, with two photographs  
196 of pangolins, and three photographs of non-native mammals. The combination of native and  
197 non-native mammals on the poster was necessary to be sure that local hunters were able to  
198 genuinely identify pangolins, in order to avoid any social desirability bias (Krumpal *et al.*,  
199 2013). For each pangolin species, the identification guide showed the different parts (head,  
200 belly, tail and scales) of the animal in order to optimize identification by participants.  
201 Discussions were conducted following three steps: 1) identification of mammalian species by  
202 respondents on the poster; 2) identification of pangolin species occurring in the local  
203 environment (and based on the identification guide); 3) answer to a short questionnaire. During  
204 the focus groups, participants were asked to identify the mammals that occur in their local  
205 environment and give their local names. If pangolins were included in the list, participants were  
206 asked to spot the species they refer to among the four African species on the identification  
207 guide. When the species was accurately identified, participants were asked to give their  
208 perceptions on the abundance trends over the past 20 years (2018, 2013, 2008 and 1998), and  
209 to list the drivers of these trends and the potential occurrence sites within the grid extent. The  
210 proposed response options for characterizing the abundance trends were defined as follows:  
211 ‘missing’- probability of observing an individual at the target period is zero in the local  
212 environment; ‘scarce’- probability of observing an individual at the target period is near to zero  
213 in the local environment; ‘medium’ high probability of observing an individual every month in  
214 the hunting season for the target period; and ‘abundant’ high probability of observing many  
215 individuals every month in the hunting season at the target period in the local environment.

216 Questions on drivers and potential habitats were open. We delimited a period of two decades in  
217 order to avoid the bias related to the probable loss of LEK with time (Saynes-Vasquez *et al.*,  
218 2013; Aswani *et al.*, Sauer, 2018). The geographic coordinates of each village were recorded.  
219 For each step, the consensual decision of participants was recorded, except for questions about  
220 drivers of abundance trends and potential habitats where we recorded all responses.

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

### 232 2.3. Data analysis

233 In order to build the distribution maps of the white-bellied and giant pangolins, we considered  
234 the geographic coordinates of all the villages ( $N = 235$ ) where focus group participants  
235 successfully and in a consensual manner (100 % of participants when there is no direct  
236 evidence) agreed on a pangolin species presence, with or without collecting direct evidence  
237 (scales). Whenever the above conditions were not met, the species were considered absent from  
238 the village. As such, only the villages where respondents reported pangolins to be “scarce”,  
239 “medium” or “abundant” for a given time period were considered as valid occurrences. We  
240 used ArcMap 10.1 (ESRI Inc.) to generate superimposed layers (25 km x 25 km grids)

241 representing each period/species, where the grids containing villages reporting the presence of  
242 pangolins were considered as occupancy areas of the targeted species. Occupancy area is here  
243 defined as the probability that a grid was occupied at a given time period (over the past 20  
244 years) by a pangolin species (see Latif *et al.*, 2016). For each reported potential habitat with or  
245 without direct evidence collection, the total area was calculated using the recent shapefile in  
246 ArcMap 10.1 (ESRI Inc.). The management modality for each forest and its national  
247 classification were extracted from official documents (FAO, 2010; CENAGREF/PAPE, 2013;  
248 DGEFC, 2017).

249 In order to assess local people's perceptions about trends in the abundance of the white-bellied  
250 and giant pangolins over the last two decades and identify factors causing these trends, each  
251 focus group was considered as an independent observation. R version 3.5.1 (R Core  
252 development team) was used for all the statistical analyses. Local hunters' perceptions  
253 regarding pangolin abundance level (missing, scarce, medium and abundant) were plotted for  
254 each species using the cumulative barplot in the ggplot2 R package for four different periods  
255 (2018, 2013, 2008 and 1998). Differences among abundance levels across time periods were  
256 tested with the Pearson's  $\chi^2$  test for the white-bellied pangolin and the Fisher exact test for the  
257 giant pangolin due to low observation numbers. The drivers of pangolin declines as extracted  
258 from the respondents were classified into the six following categories, for which frequencies of  
259 citations were calculated: wood energy harvesting (deforestation), hunting, agriculture,  
260 transhumance (livestock), fire and urbanization.

261 In order to understand the landscape characteristics that may influence the current geographic  
262 distribution of the white-bellied pangolin, we computed in ArcMap the Euclidean distances  
263 from villages to the nearest (i) protected areas (*DistAP*), (ii) permanent watercourses  
264 (*DistWater*), and (iii) main roads (*DistRoad*). For all the villages considered ( $N = 235$ ), focus  
265 group participants were hunters with similar hunting background. So, we assume an equal

266 understanding of the white-bellied pangolin distribution in the local areas among villages. Only  
267 2018 was considered and presence/absence data were defined as described above, and were  
268 modelled with these landscape variables (*DistAP*, *DistWater* and *DistRoad*) using a generalized  
269 linear model. We did not model the current distribution of the giant pangolin because only two  
270 villages reported its presence in 2018, without any direct evidence of occurrence.

271

### 272 **3. Results**

273 Focus groups gathered 3,282 respondents (hunters, rangers and former poachers), 291 local  
274 community leaders, 21 gatekeepers. The average age per focus group varied between 33 and 52  
275 years old and all the participants were men. All the collected pangolin scales (96 samples)  
276 belonged to the white-bellied pangolin with 6, 38, 15 and 47 % harvested respectively in 2016,  
277 2017, 2018 and 2019 by local people.

#### 278 *3.1. Geographic range over the last two decades*

279 The geographic distribution of the two species of pangolins as extrapolated from the focus  
280 groups extended between 6°10' and 11°00' N, with the giant pangolin being restricted to 10°  
281 20'-11°00' N (Fig. 2a and b). Our investigations suggested that the white-bellied pangolin  
282 over the last two decades (from 1998 to 2018) underwent a 31 % (14,169 km<sup>2</sup>) contraction of  
283 its occupancy area while that of the giant pangolin was reduced by 93 % (15,955 km<sup>2</sup>) (Table1).

284 In total, c. 77 and 100 % of the occupancy areas (Table 1) of the white-bellied pangolin and the  
285 giant pangolin, respectively, were partially or totally included in protected areas in  
286 2018, against c. 60 % two decades ago (1998). Twelve forest reserves and two game ranches  
287 out of the 23 forest islands cited by local hunters are the current potential habitats of the white-  
288 bellied pangolin with only one out of 23 forests cited by local hunters for the giant pangolin  
289 (Table 2). These forest reserves and ranches are managed as wildlife reserves and for wood

290 energy harvesting (Table 2). Forest reserves and ranches (protected areas) supplied 76 % of the  
291 pangolin scales collected as direct evidence (66 % from wildlife reserves and 10 % from wood  
292 energy forests). The wildlife reserve complex constituted by Monts Kouffé, Wari-Marou and  
293 Ouémé supérieur in the central part of Benin provided 46 % of the scale samples and the Lama  
294 forest in southern Benin provided 13 %.

### 295 *3.2. Abundance trends according to respondents*

296 Respondents perceived a decline in the abundance level of the white-bellied pangolin in Benin  
297 (Fig. 3a), and their perceptions depended significantly on time periods ( $\chi^2=126.7, p < 0.001$ )  
298 over the last two decades. The species was seen as abundant for 37 % of the focus groups in  
299 1998, in comparison with 4 % in 2018. Inversely, its extirpation (missing) was mentioned in 33  
300 % of the focus groups in 1998 against 54 % in 2018. The extirpation of the giant pangolin was  
301 perceived almost unanimously over the last period of our study (2013-2018; Fig. 3b), and this  
302 perception was also related to time periods ( $p < 0.001$ ).

303 Respondents perceived wood energy harvesting (81.5 %), hunting (77.08 %) and agriculture  
304 (70.84 %) (Table 3) as the major drivers of the white-bellied pangolin's decline, and hunting  
305 (91.2 %) as mainly driving the extirpation of the giant pangolin.

### 306 *2.3. Drivers of geographic distribution of the white-bellied pangolin*

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

## 312 **4. Discussion**

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

318 Our approach combining LEK and direct evidence of occurrence (pangolin scales) yielded a  
319 reliable assessment of the current ranges of pangolins in Benin, and likely improved the  
320 accuracy of the current ranges delineated in global or national red lists that serve as references  
321 for the community involved in wildlife conservation (Akpona and Daouda, 2011; Nixon *et al.*,  
322 2019; Pietersen *et al.*, 2019). From the respondents and direct occurrence evidence collected in  
323 this study, it appears that the ranges of both the white-bellied and giant pangolins probably  
324 never occurred beyond a latitude of 11°00'N, at least within the last 20 years. The national  
325 parks occurring beyond that latitude are the Biosphere Reserve of Pendjari and the  
326 Transboundary Park W, where wildlife biomonitoring done in recent years (camera traps and  
327 wildlife census, 2012-2015) by park managers has failed to report any sightings of pangolins  
328 (S. Zanvo, pers. obs. December 2018). Unanimously, the oldest hunters, together with rangers  
329 and former poachers stated that the two species of pangolins had never occurred in the National  
330 Parks of Pendjari and W, and their surrounding areas, contradicting what was suggested in the  
331 Red List for Benin on the basis of vague assumptions without photographic evidence or voucher  
332 specimen (Akpona and Daouda, 2011). This contradiction is equally observed with the IUCN  
333 Red List (Nixon *et al.*, 2019), which listed the giant pangolin as “probably extant” in those two  
334 national Parks (citing Akpona and Daouda 2011; but the supposed record from Pendjari comes  
335 from Sayer and Green 1984). Although LEK may be subject to erosion through time (Saynes-  
336 Vasquez *et al.*, 2013; Aswani *et al.*, Sauer, 2018), we believe that the absence of the giant  
337 pangolins from those two national parks is plausible since such northern latitudes may represent

338 unfavourable climatic conditions for the species. Our study suggests that the giant pangolin  
339 was subject to a rapid decline and total extirpation from southern and central Benin,  
340 representing 93 % of range contraction in the last 20 years. In the last five years, the giant  
341 pangolin was only mentioned by a focus group from the Alibori forest reserve, showing a very  
342 restricted potential range in Benin (10°20' - 11°00' N; c. 259,000 km<sup>2</sup>). No direct occurrence  
343 evidence (scales) from giant pangolin was retained by villagers confirming the rarity of the  
344 species in the country as reported in other parts of its range (Bräutigam *et al.*, 1994), but is at  
345 odds with the relatively widespread occurrence of the species in Benin suggested by Akpona  
346 and Douada (2011).

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

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



363 in the abundance of the two pangolin species over the last two decades in Benin, as perceived  
364 by local hunters. For the giant pangolin, 100 % of the focus groups declared the species either  
365 rare (15 %) or missing (85 %) ten years ago, with the species being reported as missing in 2018  
366 by 98 % of the groups. Such perceptions are consistent with general population trends for the  
367 species, again supporting the view that the giant pangolin is generally rare and declining  
368 throughout its range (Nixon *et al.*, 2019). In Benin, traders from traditional medicine markets  
369 also confirmed this trend (S. Zanvo, unpublished data). A decrease in abundance was also  
370 perceived in the white-bellied pangolin over the last two decades, the species being declared  
371 abundant in 1998 by 37 % of the focal groups but only by 4 % in 2018. Although the species is  
372 considered the most common African pangolin (Pagès, 1975; Angelici *et al.*, 1999; Gaubert,  
373 2011), it is believed to be declining in Ghana and Guinea, and to near extinction in Rwanda  
374 (Pietersen *et al.* 2019). Soewu and Ayodele (2009) also reported that 92 % of the traditional  
375 practitioners in the nearby Ogun State, Nigeria, stated that the abundance of white-bellied  
376 pangolin was continuously decreasing. Although a previous study from the Lama Forest  
377 Reserve in southern Benin reported a density of 0.84 individuals per km<sup>2</sup> (Akpona *et al.*, 2008),  
378 our study suggests that such relatively high density estimates may not be common or reflective  
379 of the current situation in the country. Khwaja *et al.* (2019) suggested that degraded habitats  
380 could lead to a greater detection probability of the white-bellied pangolin, amplifying its time  
381 of activity on exposed parcels. So, in the current context of highly degraded forests in Benin,  
382 the general decline perceived by local communities over the last two decades could be  
383 considered as a genuine representation of the population trends in pangolins.

384 Nixon *et al.* (2019) associated the decline of the giant pangolin to habitat alteration and  
385 unsustainable exploitation for bushmeat and traditional medicine, feeding both local and  
386 international markets (Djagoun *et al.*, 2012; Heinrich *et al.*, 2016; Ingram *et al.*, 2019). Its large  
387 size, low reproductive rate and terrestrial habits make it particularly vulnerable to

388 overexploitation (Kingdon *et al.*, 2013). In Benin, the major cause for the species' depletion  
389 was identified as hunting by c. 91 % of the focus groups, followed to a lesser extent by habitat  
390 alteration (45 - 60 %), in agreement with Akpona and Douada, (2011). Because the species is  
391 restricted to forested habitats (Gaubert, 2011), deforestation and agricultural activities might  
392 have played a significant role in its local extinction and range fragmentation in Benin. Despite  
393 almost one year of survey at the country scale, no direct occurrence evidence (scales) of giant  
394 pangolin could be collected (whereas 96 items were collected for the white-bellied pangolin).  
395 We posit that the giant pangolin, which was already considered rare in Benin 20 years ago, is  
396 now at best restrained to the forest reserve of Alibori and is facing high extinction risk,  
397 especially since its former presence in southern and central forest reserves did not prevent from  
398 its rapid extirpation. Field investigations using camera trapping (Khwaja *et al.*, 2019; Morin *et*  
399 *al.*, 2020) are urgently needed to confirm the existence and status of the remaining populations  
400 and to investigate their habitat use in order to propose concrete solutions for the conservation  
401 of the giant pangolin in Benin.

402 Pietersen *et al.* (2019) linked the decline of the white-bellied pangolin across its range to habitat  
403 alteration, wood plantation and unsustainable hunting. In Benin, the major causes of decline  
404 were identified as deforestation (81 %), agriculture (70 %) and hunting (77 %). Although the  
405 species predominantly occurs in moist tropical lowland forests, it can also be found in dense  
406 woodlands and secondary growth forests such as abandoned oil palm or even teak plantations  
407 (Sodeinde and Adedipe, 1994; Angelici *et al.*, 1999; Akpona *et al.*, 2008; Gaubert, 2011), thus  
408 suggesting a certain level of adaptability to human-induced habitat transformation. However,  
409 severe fragmentation of forested habitats by intense agriculture activities, growing urbanization  
410 and forest exploitation for wood energy (FAO, 2010; Alohou *et al.*, 2017) are likely to  
411 significantly reduce the coverage of suitable habitats for the white-bellied pangolin in Benin.  
412 The species is subject to intense exploitation across its range for bushmeat and traditional

413 medicine, and is the most represented pangolin species in bushmeat markets (Djagoun and  
414 Gaubert, 2009; Djagoun *et al.*, 2012). The important quantity of direct occurrence evidence (96  
415 samples of scales) collected during our survey showed that hunters stored pangolin scales in  
416 their houses either as trophies or for uses in traditional medicine (Akpona *et al.*, 2008; Djagoun  
417 *et al.*, 2012), and possibly for supplying traditional medicine markets.

418 The expanding scale of the illegal international trade towards Asia (Challender and Hywood,  
419 2012; Xu *et al.*, 2016) is likely contributing to the depletion of white-bellied pangolin  
420 populations. In Benin, international trafficking has been confirmed by a recent seizure of 513  
421 kg of pangolin scales at the airport of Cotonou (Ingram *et al.*, 2019). This potentially highlights  
422 an extension of the western African pangolin trafficking network towards Asia, which was so  
423 far preeminent in Sierra Leone, Ivory Coast, Ghana, and Nigeria (Xu *et al.*, 2016). Our study  
424 suggested that the white-bellied pangolin in Benin mostly occurred far from the road network  
425 and near or within protected areas, emphasizing avoidance of the most disturbed human-  
426 dominated landscapes by road networks (Shanley and Pyare, 2011) and the crucial role played  
427 by protected areas for the survival of the species. The road networks would have facilitated  
428 defaunation from impacted areas due to the good access to pangolin's habitats for hunting  
429 activities. However, the high percentage (76 %) of scales collected from protected areas is a  
430 token of the ongoing poaching pressure within those reserves. Besides, the classification  
431 objective into wood energy production of almost half of the forest reserves where the species  
432 was reported to occur (Table 4) may prove rapidly unsuitable relative to the ecological  
433 requirements of the species, which involve large trees for sheltering.

434 In the current context, conservation actions should be urgently engaged to design a sound  
435 species-conservation and land-management plan in Benin. The classification of the main  
436 reserves potentially housing pangolins to limit anthropogenic disturbance –especially  
437 deforestation– should be encouraged. An upstream regulation of local bushmeat and traditional

438 medicine markets should also be implemented, in order to limit local trafficking (Djagoun and  
439 Gaubert, 2009; Djagoun *et al.*, 2012). Because the Lama forest reserve in southern Benin and  
440 the complex Monts Kouffé - Wari Maro - Ouémé supérieur in central Benin are the two sole  
441 forest relics that have been identified as housing large populations of white-bellied pangolins,  
442 those two areas, together with the Alibori forest reserve as the last potential stronghold for the  
443 giant pangolin, should be urgently investigated.

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

450

#### 451 **Declaration of competing interest**

452 All authors declare there are no conflicts of interest.

453

#### 454 **Acknowledgments**

455 This study was approved by Public Forest Service through a research authorization and received  
456 the prior consent from local authorities in each district. We thank these different authorities  
457 without whom this study should not be possible. We are grateful to all the participants for  
458 generously giving their time to complete this survey. Léopold Woto played a significant role in  
459 data collection. [We thank reviewers for their useful inputs on the early version of the](#)  
460 [manuscript.](#)

461

462 **Role of the funding source**

463 This research received financial support from the program Jeune Equipe Associée à l'IRD  
464 (RADAR-BE) for data collection and analysis. SZ is supported by a PhD grant "ARTS-IRD".

465

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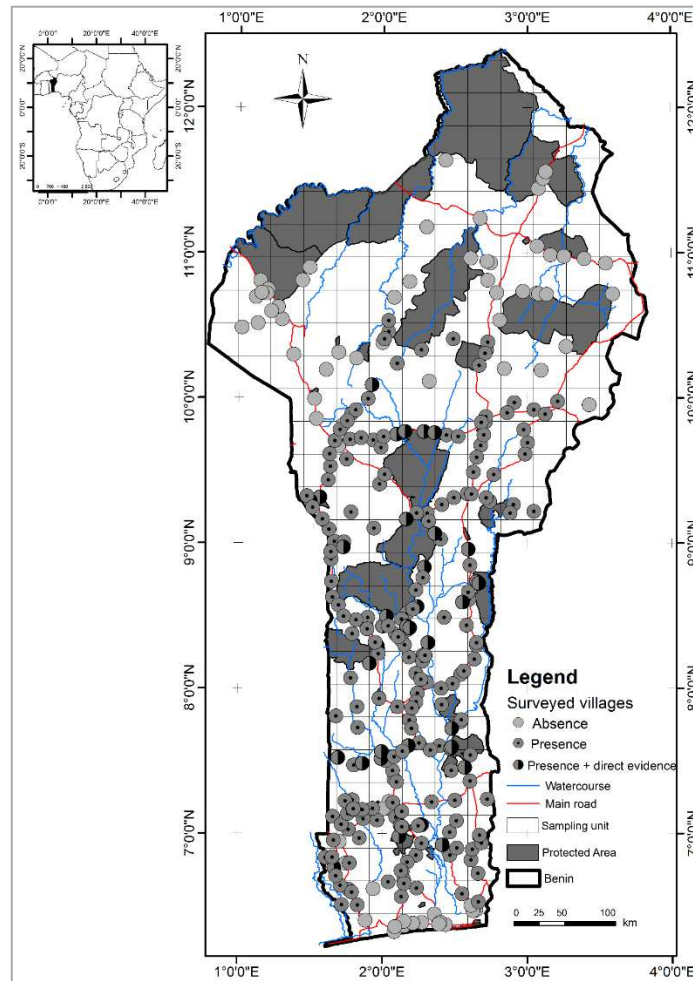
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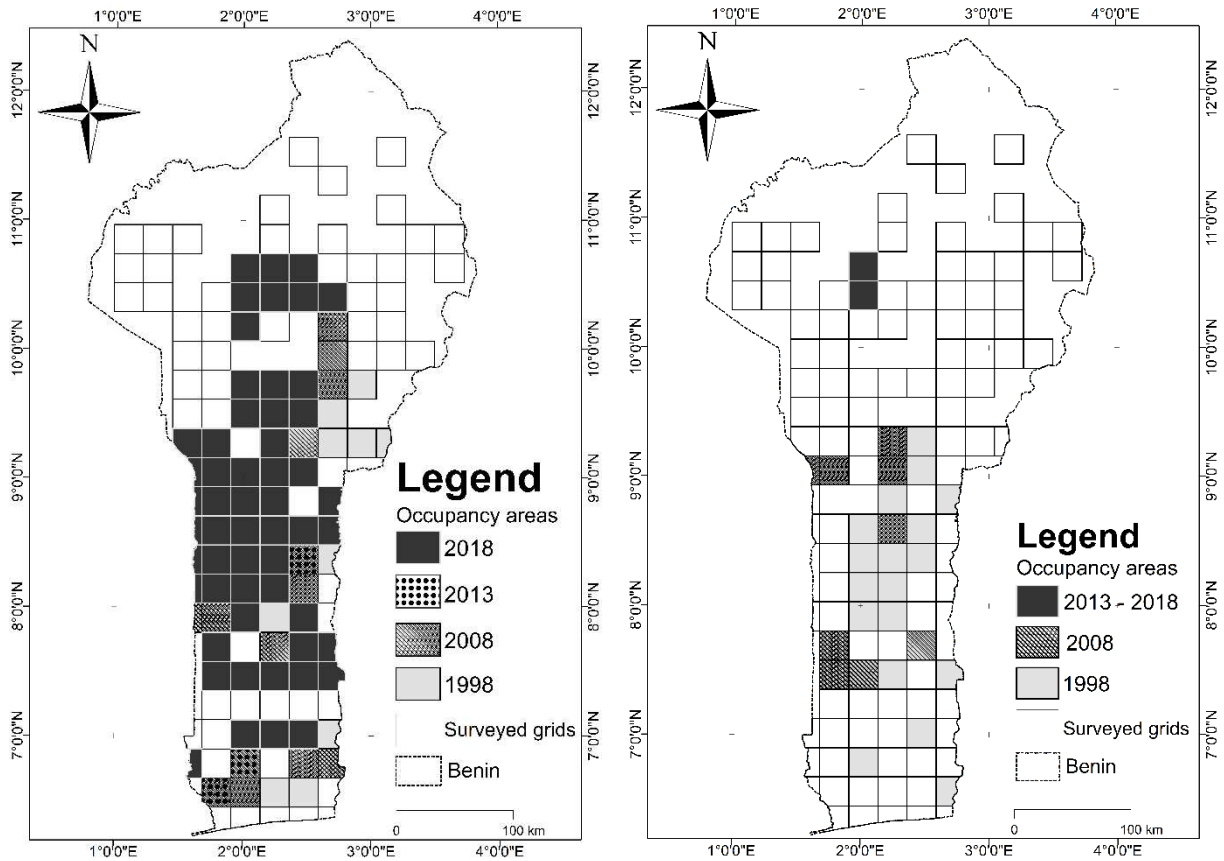
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656 **Fig. 1.** Location of the 312 villages in which the focus groups were held with local hunters from April 2018 to  
 657 March 2019 in combination with direct evidence collection. Grids (sample units) are 25 x 25 km. ‘Absence’:  
 658 villages in which focus group participants mentioned the absence of pangolins; ‘Presence’: villages in which focus  
 659 group participants mentioned the presence of pangolins without providing direct evidence (scales); ‘Presence +  
 660 direct evidence’: villages in which focus group participants supported their statement with direct evidence (scales).

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(a)

(b)

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664 **Fig. 2.** Geographical range dynamics of (a) the white-bellied pangolin and (b) the giant pangolin in Benin from  
 665 1998 to 2018. Each grid cell represents an occupancy area for one or several time period(s) by overlaying sampled  
 666 units (grids) and responses of focus groups. During this period, no new colonization and recolonization events  
 667 have been mentioned by participants. Thus, the time of occupancy of a grid cell implies that the species has been  
 668 present since 1998.

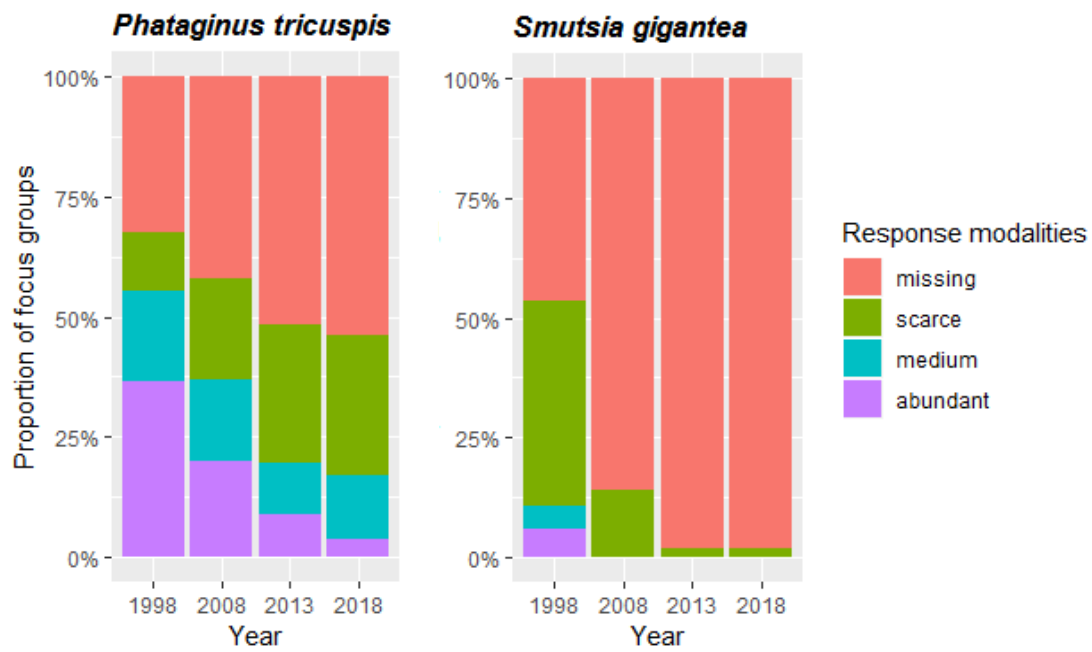
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(a)

(b)

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676 **Fig. 3.** Focus group representations of abundance trends of pangolins in Benin over the last two decades (1998-  
677 2018).

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688 **Table 1**

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

691

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

694 **Table 2**

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

Forest/Habitat	Management modality	Classification objective	Total area (km <sup>2</sup> )	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
Gnanhouzoun*	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-Maró*	Forest reserve	Wildlife reserve	117615.512	7
Gallery forests*	NA	Soil and water protection	NA	8

697 (\* ) white-bellied pangolin (\*\* ) white-bellied and giant pangolins

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700 **Table 3**

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

Threats	Frequency of citations (%)	
	<i>P. tricuspis</i>	<i>S. gigantea</i>
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	-

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704 **Table 4**

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

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Variables (m)	Estimate	<i>p</i> -value
<i>DistAP</i>	-0.0001	0.0000 ***
<i>DistRoad</i>	0.0001	0.0000 ***
<i>DistWater</i>	-0.000031	0.1419

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