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Impact of human activities on the reproduction of Hooded Vultures *Necrosyrtes monachus* in Burkina Faso

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During the last decades, the critically endangered Hooded Vulture *Necrosyrtes monachus* has strongly declined across its African range. Although direct persecution has been suggested as a major cause of this decline, little is known about the impact of humans on reproductive output in West Africa. We studied the impact of human activities on the reproductive output of Hooded Vultures in the Garango area of Burkina Faso. Twenty and 56 nesting attempts were monitored, respectively, during the breeding season in 2013/14 and 2014/15, to determine reproductive success and identify causes of nest failure. Annual breeding success varied between 0.68 and 0.71 chicks fledged per breeding pair per year and productivity was assessed at 0.57 chicks fledged per territorial pair in 2014/15. The main threats imposed by humans were poaching of eggs, chicks and collection of nest materials, leading to 20% (13 out of 64 breeding attempts) of nest failures over the two years. An additional important reason for nest failure was the pruning and (partial) cutting of nest trees. Despite this high level of human interference, we found that Hooded Vulture nest success increased with proximity to human settlements, probably because breeding vultures benefit from protection by people against persecution and disturbance.

Impact des activités anthropiques sur la reproduction du Vautour charognard *Necrosyrtes monachus* au Burkina Faso

Au cours des dernières décennies, le Vautour charognard *Necrosyrtes monachus* en danger critique d'extinction, a fortement décliné à travers son aire de répartition africaine. Bien que la persécution directe ait été suggérée comme une cause majeure de ce déclin, on en sait peu de l'impact de l'Homme sur la reproduction en Afrique de l'Ouest. Nous avons étudié l'impact des activités de l'Homme sur le succès de la reproduction des Vautours charognards dans la zone de Garango au Burkina Faso. Vingt et 56 tentatives de nidification ont été suivies respectivement au cours des saisons de reproduction 2013/14 et 2014/15 afin de déterminer le succès de la reproduction et les causes des échecs de ces tentatives. Le succès de reproduction annuel a varié entre 0.68–0.71 jeunes envolés par couple reproducteur par an et la productivité a été évaluée à 0.57 jeunes envolés par couple territorial en 2014/15. La principale menace provenant de l'activité de l'Homme est le braconnage des œufs, des jeunes et la récolte des matériaux de construction des nids, conduisant à 20% (13 sur 64 tentatives de nidification) d'échecs de reproduction en deux ans. Une autre raison importante des échecs de reproduction est l'élagage et la coupe (partielle) des arbres abritant les nids. Malgré ce niveau élevé de la pression d'origine anthropique, nous avons constaté que le succès de reproduction du Vautour charognard augmente avec la proximité des habitations humaines, probablement grâce à la protection de la part des populations contre les persécutions et les perturbations.

Keywords: Burkina Faso, conservation, Hooded Vulture, human impact, reproduction

Introduction

Worldwide, 14 of the 23 species of vultures are threatened with extinction, with the strongest recent declines reported in Asia and Africa (Ogada et al. 2012). Contrary to Asia, the African vulture crisis is characterised by a myriad of threats to vultures, which vary in importance across the continent. Similarly, the rates of decline differ between regions, with vulture populations in West Africa showing the largest average annual declines (Ogada et al. 2015), particularly outside protected areas (Thiollay 2006a). The two main threats to African vultures are believed to be poisoning and belief-based use (Ogada et al. 2015). Poisoning targets all post-fledgling age classes and is both intentional, such as when vultures are killed by elephant poachers who want to escape detection (Ogada et al. 2016), or unintentional, when vultures are collateral victims to poisoning aimed at large carnivores. Vultures are also killed for belief-based trade, especially in West Africa (Buij et al. 2016) and southern Africa (McKean et al. 2013), where vultures are sold in large numbers for

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their perceived value in treating a range of illnesses. Other widespread or increasing threats to African vultures include habitat loss and diminished carcass availability, and collisions with energy infrastructure (Ogada et al. 2015).

Of all African vultures, the Hooded Vulture *Necrosyrtes monachus* is the most closely associated with human habitations (Mundy et al. 1992). This close association with human settlements has been reported in the northern part of the distribution range, from Senegal east to Ethiopia (Ash and Atkins 2010; Buij et al. 2013a; Mullié et al. 2017), but is absent further south (Mundy et al. 1992; Ogada and Buij 2011). Possibly, the exploitation of human-dominated habitats has favoured the species' blossoming compared with other vulture species in West Africa (Anderson 1999), where it has historically been, and still is, among the most common raptors (Thiollay 1977; Buij et al. 2013b; Henriques et al. 2018). More recently, its proximity to human habitations in West Africa may also have made Hooded Vultures vulnerable to human exploitation, both as a source of food and for belief-based use (often referred to as 'traditional medicine'; Anderson 1999; Sodeinde and Soemu 1999; Adjakpa and Tchabi 2002; Buij et al. 2016).

In many parts of West Africa, such as in Dakar (Senegal) and Edo State (southern Nigeria), Hooded Vultures have dramatically declined (Mullié et al. 2017; Nosazeogie et al. 2018), although they remain among the commonest raptors in other areas (Buij et al. 2013b; Henriques et al. 2018). In Burkina Faso, Hooded Vultures declined by almost 77% on average between 1974 and 2004 (Thiollay 2006b). This decline occurred despite their protection by law and by local populations. Indeed, as also recorded in Namibia (Craig et al. 2018), Hooded Vultures are commonly recognised in central Burkina Faso as being sacred, stimulating protection from persecution and poaching by local communities (Daboné et al. 2016). The causes for such strong declines remain unknown, and particularly whether persecution affects post-fledging survival or reproductive rates, or both. This study aimed to examine the influence of humans on reproductive output of Hooded Vultures, by determining their reproductive success near human settlements during two breeding seasons (2013/14 and 2014/15) in central-eastern Burkina Faso. More specifically, we investigated whether proximity to humans positively influenced reproductive success, through apparent protection of nesting sites as reported previously for this area (Daboné et al. 2016), or whether this proximity to humans rather had a negative impact due to nesting site disturbance or other forms of persecution.

Methods

Study area

The study was conducted in Garango rural township (0°33′ W, 11°48′ N), which is located in the province of Boulgou, 180 km south-east of Ouagadougou (the capital of Burkina Faso) and 20 km from Boulgou's capital, Tenkodogo. Garango is traversed by National Route 17 (Figure 1). We choose this area to study Hooded Vultures because it supports many relatively easily accessible nests at varying distances from human habitations. Garango consists of a city centre surrounded by many small agglomerations of houses (up to 10 km from the centre). Houses in the centre of Garango are densely aggregated, whereas houses in the peripheral areas are more widely spaced and surrounded by agricultural fields with dispersed shrubs and trees. Hooded Vultures here often breed in large trees, in small patches of forest outside of town, single trees in agricultural fields and often only 5–10 m from houses in the city centre (Daboné et al. 2016).

Garango is located in the Sudano-Sahelian climate zone, which has an annual rainfall between 600 and 900 mm during 4–5 months (mostly from May to September). The temperatures are on average 20–30 °C with extremes between 18 and 39 °C (Dipama 2010). This area belongs to the North Sudanese phytogeographical zone, where savannas are agricultural landscapes dominated by *Adansonia digitata*, *Faidherbia albida*, *Lannea microcarpa*, *Parkia biglobosa*, *Tamarindus indica* and *Vitellaria paradoxa* (Boussim 2010). The relief of Garango is moderate and it has the highest hill of the province (420 m). Garango's population was estimated at 73 679 inhabitants in 2006, mainly composed of the Bisa, Mossi and Fulani ethnic groups (INSD/MEF 2008). Small-scale agriculture and livestock farming are the main economic activities.

Nest surveys

We searched for Hooded Vulture nests by walking slowly in areas of the township and village where we had seen nests previously. These walking surveys were conducted between 8:00 a.m. and 4:00 p.m. on foot using telescopes or binoculars to scan for distant Hooded Vulture's nests. We used territorial behaviour, such as circling pairs, or birds collecting nest materials as an indication of the potential presence of a Hooded Vulture's nest. We subsequently approached the birds to confirm the presence of an active nest and to take a GPS reading if we detected one. To rapidly track down a larger sample of nests we elicited the help of local populations including secondary school pupils between 16 and 19 years old. Advantages of this approach included the strengthening of youth education in terms of the ecological value of vultures, and a lower probability of missing out active nest sites. The pupils participated in the study as part of their ecology course with the permission of their teacher and parents, and were instructed to look for Hooded Vulture nests in the vicinity of their homes. During the two breeding seasons, the villagers and pupils led us to 22 Hooded Vulture nests. Subsequent nest monitoring was conducted discreetly by the same observer in order to avoid crowds and to minimize the effect of the monitoring activities on the reproductive success of the birds.

Breeding parameters

The Hooded Vulture's breeding period in central West Africa extends from October to April (Balança et al. 2007; Daboné et al. 2016), so we choose our monitoring period accordingly. In order to determine their reproductive output, during the first breeding season, 20 Hooded Vulture nests were visited from 8 October 2013 to 15 May 2014. During this first breeding season, nests were visited 294 times, with 8 to 20 visits per nest (on average 16), between 06:00 and 18:00 from the start of breeding until fledging. In order to minimise disturbance of breeding pairs, observations

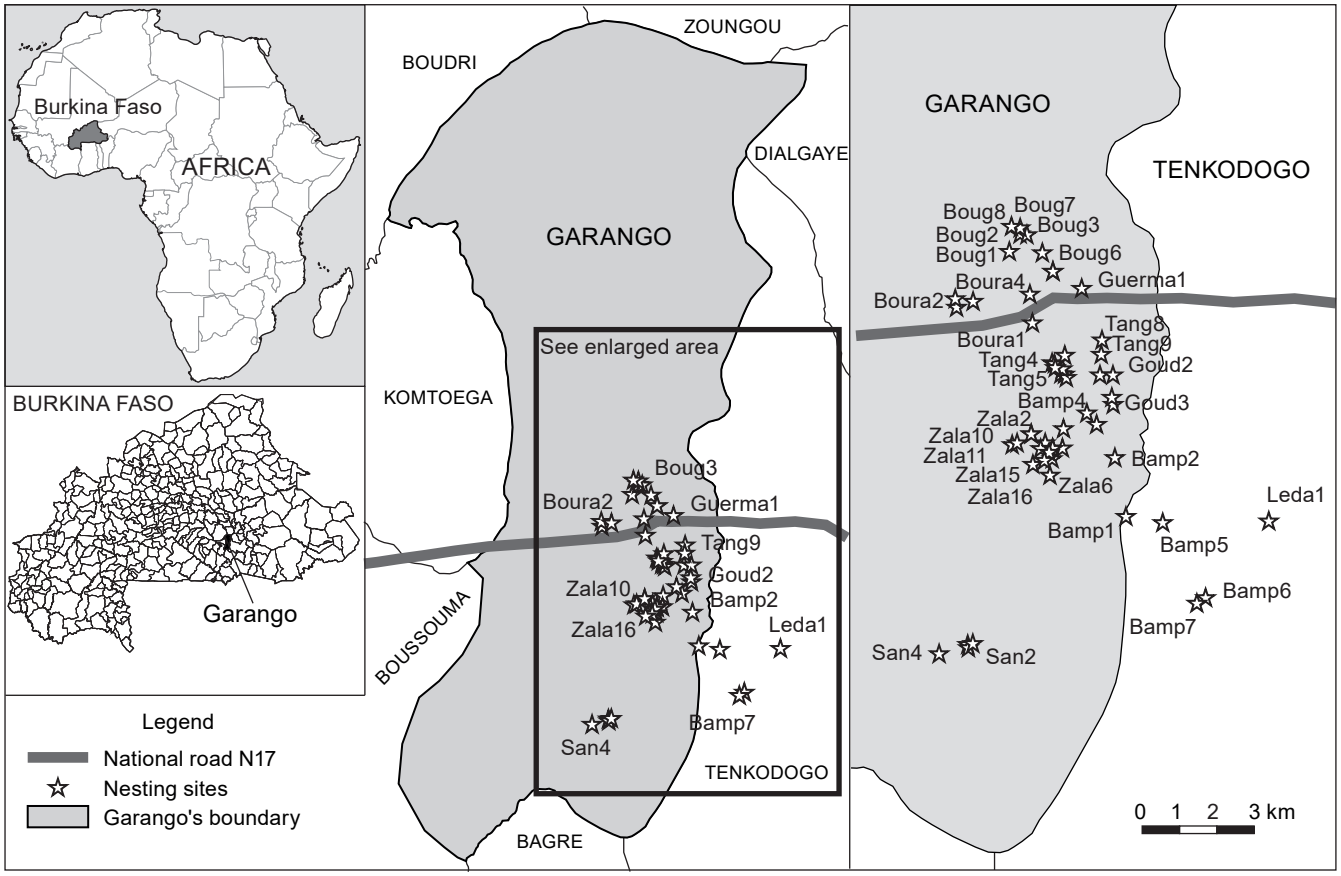

Figure 1: Study area and monitored nest locations. The coordinates are not given here to prevent this data being used for other purposes (poaching). In most areas of high nest density, not all nest names appear on the map

of the nest were made from the ground with the help of a telescope (Kowa TSN-601 60 mm Spotting Scope). When the presence of an egg or of a chick was suspected, the tree was climbed such that a mirror mounted on a stick could be used to inspect the nest contents. Two more visits to nest sites were made after fledging, one in July 2014 and another visit in September 2014. Nest visits stopped once a nest had failed.

During the second breeding season, 56 Hooded Vulture nests were monitored using the same methods, which included 45 newly discovered nest sites and 11 nests that were also studied during the first year. We cannot confirm that these 11 nests were used by the same breeding pairs because birds were not individually recognisable. Six nests from the first year were not in use in the second year, two nests had vanished from the tree and one nest tree was cut. The 56 nests in the second breeding season were visited 247 times from 1 October 2014 to 20 May 2015, on average 4 or 5 visits per nest. Mated birds detected repeatedly at the same nesting site (nesting territory) during the pre-laying season were designated as territorial pairs, whereas those that laid eggs were defined as breeding pairs (*sensu* Fernández et al. 1998). A nesting attempt was defined as any nest with adults attending and/or nest building; a breeding attempt was defined as those nesting attempts with at least one egg laid.

The following reproductive parameters were evaluated: productivity (the number of chicks fledged divided by the number of territorial pairs, in 2014/15), breeding success (the number of chicks fledged divided by the number of breeding pairs), hatching success (the proportion of eggs hatched per number laid) and fledging success (the proportion of chicks fledged per egg hatched). The nesting rate was determined by the percentage of territorial pairs that actually laid eggs (Cheylan 1981; Bildstein and Bird 2007). These parameters were compared between the two years of this study, and with the results from other studies.

We tried to assess the cause of nest failure during visits. Signs of human activity, such as cut branches, indicative of people climbing to the nest, the partial or complete removal of nest materials from the nest and left-over on the ground, as well as testimonies of people living in the vicinity of nesting sites and having witnessed others climb the nest tree, all helped us to determine the causes of nest failure.

Environmental and nest measurements

In order to determine the influence humans may have on the Hooded Vulture's reproduction, we recorded several types of human activities, including persecution, agricultural activities and livestock farming, within 25 m from the nest, as well as destruction of nest trees by pruning or cutting and rifle shooting. The proximity to roads and habitations

was noted. In addition, several nest characteristics were measured, during monitoring, including nest height and nest thickness. All measurements and observations were carried out by the first author during the two breeding seasons and are given in Table 1.

Data analysis

A total of 13 variables were considered to potentially influence reproductive success (Table 1). In an effort to limit the analysis to those variables that seemed most relevant from an ecological perspective, we pre-selected independent variables that were thought to be most relevant. We fitted a binomial logistic regression model in R 3.0.2 (R Development Core Team 2015) to the data on reproductive success to examine how nest height, distance to human habitation, distance to the nearest breeding pair, and number of trees over 10 m in height affected Hooded Vulture reproductive success (response variable: 0 = breeding attempt not successful, 1 = successful breeding attempt). We removed consecutive breeding attempts on nest sites used twice ($n = 6$) to avoid pseudo-replication. We used the Moran's *I* to check the presence of spatial autocorrelation in the data set (Fortin and Dale 2005), by ascertaining whether it was in fact likely to impact the planned analyses (Dormann et al. 2007). To calculate Moran's *I* (Moran's *I* standard deviate), we generated a matrix of inverse distance weights using the R package 'ape' in R 3.0.2. (R Development Core Team 2015). As the study locations were close together and far from the poles, for simplicity, we treated the latitude and longitude as values on a plane rather than on a sphere. We hypothesised that height of the nest tree would reduce the accessibility of the nest to potential nest predators (carnivores and humans), thus increasing the odds of a successful breeding attempt. Similarly, we expected nearby habitation and trees surrounding the nest to provide a level of protection, lowering detectability of the nest and therefore enhancing breeding success. The distance to the nearest breeding pair was thought to influence breeding success as a consequence of either agonistic interactions between breeding pairs or the benefits derived from social sharing of information by breeding neighbours (cf. Fernández-Bellon et al. 2016). We also included the year of nest attempt as a categorical variable in the model (for year 1 and 2). We explored all possible subsets of combinations of explanatory variables and examined the relative support for the role of these different variables in influencing reproductive success. We used the corrected Akaike information criterion (AIC_c) value to select the most parsimonious models (those that fit the data best with the fewest parameters; i.e. with the lowest AIC_c; Burnham and Anderson 2002) and the top four ΔAIC_c of models as the cut-off criterion for delineating a set of top models. We computed model-averaged parameters by averaging over all models in the set of top models. We used the dredge function in R (part of the package MuMIn 1.9.5.; Bartoń 2013) to implement a model-averaging approach for the top models to make robust parameter estimates and predictions (Johnson and Omland 2004) and estimated the relative importance of each variable, based on the sum of Akaike weights. We subsequently evaluated the effect of variables based on overlap of the 95% confidence intervals (following Burnham and Anderson 2002).

Results

Nest characteristics

Hooded Vulture nests were situated in trees from 10 to 28 m tall. The nests were predominantly built in *Parkia biglobosa* (71%), *Faidherbia albida* (12%) and *Tamarindus indica* (8%) with fewer nests in *Adansonia digitata*, *Ceiba pentandra*, *Terminalia mantaly* and *Ficus gnaphalocarpa* (Table 2). Nests were generally placed at heights ranging from 6 to 25 m above the ground. Based on our observations in Garango, the Hooded Vulture nests were rarely exposed to the sun (6% of nests were exposed and included those in deciduous trees, e.g. *Adansonia digitata*, *Ceiba pentandra* and *Terminalia mantaly)*. The mean distance between nests was 334 m, the mean nest depth was 21 cm and the mean nest thickness was 18 cm, but these measurements varied substantially between nests (Table 3).

Table 1: Environmental and nest measurements taken at each Hooded Vulture nest. Measurements were made by the first author

Variable	Description
Distance to human habitation	The distance (in m) between the Hooded Vulture nest and the nearest human's house, measured using a GPS
Distance to nearest neighbour	The distance (in m) between the Hooded Vulture nest and the closest neighbouring active Hooded Vulture nest
Distance to road	The distance (in m) of the base of the nest tree to the nearest (dirt) road
Location of the nest	Town, village or small patches of savanna's forest outside of town or village
Nest tree species	The species of tree harbouring the Hooded Vulture nest (using Arbonnier 2002)
Number of large trees	Number of large (>10 m) trees within a 25-m circle around the nest
Number of medium-sized trees	Number of medium-sized (6–10 m) trees within a 25-m circle around the nest
Number of small trees	Number of small (3–5 m) trees within a 25-m circle around the nest
Nest height	Height of the nest above the ground (in m) using measuring tape
Thickness of the nest	The thickness of the built-up nest, measured as the distance (in cm) between the rim of the nest and the fork of the tree on which the nest is built
Tree cover	Within a 25-m circle around the nest the summed projection of tree crowns on the ground in three categories: <33% tree cover; 33–66% tree cover; >66% tree cover
Tree height	The height of the nest tree above ground level (in m) using a measuring tape

Breeding parameters

A total of 20 and 56 nesting attempts were monitored respectively in 2013/14 and 2014/15. In total, 64 eggs (one egg per pair) were laid and 45 chicks successfully fledged (Table 4). The fledging success (0.88 fledglings per chick on average) was higher than the hatching success (0.80 chicks per egg on average), thus more losses were incurred before egg hatching than thereafter. In the 2014/15 breeding season overall productivity (0.57 chicks per breeding pair) was lower than breeding success (0.71 chicks per nests with eggs) and a high proportion of non-laying pairs was recorded (Table 4). In 2013/14, 16 of 19 eggs (84%) were laid between November and December with late egg-laying on two nests in January and February, in both instances on newly built nests. The latest recorded fledging date was 9 May 2014. In 2014/15, 41 of 45 eggs (91%) were laid before 8 December 2014. The latest fledgling left the nest on 20 May 2015. During visits to nest sites in July and September 2014, Hooded Vulture pairs and their young of the year (fledged since April 2014) were seen together, which suggests that fledglings remain with parent birds at least up to 5–6 months after fledging.

Table 2: Nest tree species used by Hooded Vultures in 76 breeding attempts in the 2013/14 and 2014/15 breeding seasons

Nesting trees	Number	Percentage
Parkia biglobosa	46	70.7
Faidherbia albida	8	12.3
Tamarindus indica	5	7.6
Ceiba pentandra	2	3.0
Ficus gnaphalocarpa	2	3.0
Adansonia digitata	1	1.5
Terminalia mantaly	1	1.5
Total	65	

Anthropogenic factors influencing reproductive success

Our models found most support for an influence of proximity to human habitation on Hooded Vulture reproductive success. All 11 plausible models included the influence of distance to human habitation, whereas nest height, number of large trees in the vicinity, distance to the nearest breeding neighbour, and year of reproduction were of less importance (Table 5). The model-averaged parameters of the top models (Table 5) strongly supported the hypothesis that Hooded Vulture reproduction declined with increasing distance from human habitation (Figure 2). The parameter estimates were comparable when a single nest located at 1 700 m from human habitation was excluded from the analysis. Based on Moran's *I*

Table 3: Characteristics of 65 different Hooded Vulture nests in the Garango area during the 2013/14 and 2014/15 breeding seasons

Season	*N*	Tree height (m)		Nest height (m)		Nest depth (cm)		Nest thickness (cm)		Nearest breeding neighbour (m)	
		Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD
2013/14	20	10–28	15.8 ± 5.0	8–25	13.1 ± 5.5	9–60	28 ± 7.7	10–30	22.0 ± 8.1	30–700	205.6 ± 184.7
2014/15	45	12–23	14.4 ± 2.3	6–17	11.5 ± 2.2	7–40	16 ± 4.1	5–35	14.2 ± 6.7	68–1 115	390.7 ± 287.0
Total	65	10–28	14.8 ± 3.4	6–25	13.0 ± 3.6	7–60	21 ± 8.3	5–35	17.9 ± 9.3	30–1 115	333.8 ± 272.4

Table 4: Reproductive performance of Hooded Vultures in Garango area in 2013–2015. Nesting rate is the percentage of territorial pairs that actually laid eggs; hatching success is the proportion of eggs hatched per number laid; fledging success is the proportion of chicks fledged per egg hatched; breeding success is the number of chicks fledged divided by the number of breeding pairs and productivity is the number of chicks fledged divided by the number of territorial pairs. ND = not determined

Season	Breeding attempts/ territorial pairs	Pairs with hatched eggs	Pairs with fledglings	Nesting rate	Hatching success	Fledging success	Breeding success	Productivity
2013/14	19/ND	14	13	ND	0.74	0.93	0.68	ND
2014/15	45/56	37	32	0.80	0.82	0.86	0.71	0.57
Total	64/ND	51	45	ND	0.80	0.88	0.70	ND

Table 5: Effects of variables assumed to influence Hooded Vulture reproductive output in Burkina Faso in two years between 2013–2015, with model-averaged parameter estimates for each variable in the 11 most strongly supported models, and the relative importance of explanatory variables (n = 58 breeding attempts)

Variable	Parameter estimate (95% CI)	Relative importance[1]
(Intercept)	1.997 (−0.219 to 4.213)	
Distance to human habitation	**−0.007 (−0.011 to −0.002)**	**1.00**
Year of attempt[2]	0.584 (−0.944 to 2.111)	0.27
Height of nest	0.081 (−0.171 to 0.335)	0.25
Number of large trees	−0.026 (−0.114 to 0.061)	0.24
Distance to nearest breeding neighbour	0.000 (−0.002 to 0.003)	0.21

[1] Calculated by summing Akaike weights across the top model set (Burnham and Anderson 2002). 95% confidence intervals of the estimate not overlapping zero are indicated in bold

[2] Reference year is 2013/14

assessment, no spatial autocorrelation was detected in the data set (Table 6).

Cause of breeding failures

Of the 64 breeding attempts during the two breeding seasons, 19 failures were noted (Table 7). The 19 failures can be categorised into the following categories: indirect human activities (nest trees [*Parkia biglobosa* and *Faidherbia albida*] were cut or pruned by farmers for firewood, or for feeding livestock: four cases), direct human persecution (removal of the egg or the entire nest including egg or young: 13 cases), and unknown or non-anthropogenic causes (once a dead adult Hooded Vulture was found at the nest, and one nest was most likely destroyed by the wind). Overall, 27% of 64 breeding attempts failed due to human activities. During field work, local people approached us on occasion to demand nest materials, such as sticks, and on two occasions we found people gathering nest materials. Ten out of the 13 cases of direct human persecutions occurred at nests further than 100 m from the closest habitation, whereas three cases occurred at 5–100 m from the nearest houses (Pearson χ^2 test = 5.56, df = 1, *p*-value = 0.012). This points to a possible protective influence of human habitations on nearby nesting sites.

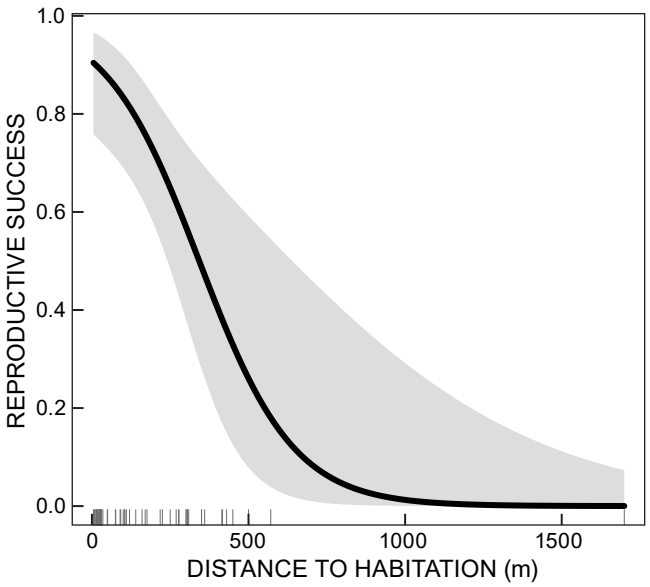

Figure 2: Plot of the modelled relationship between reproductive success of Hooded Vulture and the distance to human habitation as estimated by the top model. The black horizontal line represents the model-predicted value and the shaded areas indicate 95% confidence bands; the vertical ticks indicate the distance to habitation of individual nest records

Table 6: Spatial autocorrelation in the data set given as Moran's *I* (significance level $\alpha = 0.05$)

Variable	Moran's *I* ± SD	Sig.
Distance to human habitation	0.2073233 ± 0.0212766	ns
Year of attempt*	0.9917566 ± 0.08536268	ns
Height of nest	0.6051053 ± 0.08706677	ns
Number of large trees	0.1722465 ± 0.08839771	ns
Distance to nearest breeding neighbour	0.20791784 ± 0.09569098	ns

ns = not significant

Discussion

The results of our study suggest that human activities had an important impact on Hooded Vulture reproduction in the Garango area in Burkina Faso, with more than a quarter of 64 breeding attempts failing due to human activities, mostly during incubation. The main negative impact came from intentional human action directed at the nest or its contents (20% of breeding attempts), most likely related to harvesting for belief-based use. Previous studies already established that eggs, vultures and nest materials are often harvested for belief-based use in West and South African countries, or for food, and this often targets Hooded Vultures (Bamford et al. 2009; Saidu and Buij 2013; Buij et al. 2016; Craig et al. 2018). Although we have no firm evidence and rely mostly on hear-say in this regard, we believe that harvesting of Hooded Vultures could be explained by a progressive change in people's attitudes possibly stimulated by the decreasing availability of vultures and the increasing profitability of the regional vulture trade for belief-based use (Nikolaus 2011; Buij et al. 2016). During our fieldwork and interviews throughout Burkina Faso in 2015/16, we learnt of more than 10 cases of intentional poisoning of Hooded Vultures, mostly in the south-eastern part of the country. For example, more than 50 beheaded Hooded Vultures were found by agents of the national veterinary service at the abattoir of Bittou, a township ~80 km south of Garango in 2011 (Agence de l'Information du Burkina 2012). At least some of the poisoned vultures were to be exported to neighbouring countries; officers of the ministry of environment were

Table 7: Table documenting the fate of failed nests, highlighting some important threats to breeding Hooded Vultures in Burkina Faso

Fate	During incubation	During nestling phase	Percentage of failed nests of total breeding attempts
Cutting of the entire nest tree	1	1	3.1
Pruning of the nest tree	2	0	3.1
Removal of the nest (the entire nest is removed: nest materials with eggs or chicks)	4	5	14.1
Removal of eggs	4	0	6.3
Dead adult bird on the nest	1	0	1.6
Nest destruction (probably by the wind)	1	0	1.6
Total	13	6	29.7

reported to have arrested a Nigerian lady and two Burkinabe accomplices with more than 70 dead Hooded Vultures destined to be exported to Nigeria in 2011 (Nabaloum 2012).

The increased reproductive output of Hooded Vultures with decreasing distance to human settlements as reported by us here is perhaps surprising in light of the above. In general, the proximity of nest sites to human settlements may make nesting vultures vulnerable to human disturbance and persecution (Arroyo and Razin 2006; Zuberogoitia et al. 2008), reducing their suitable habitat to those areas far from centres of human activity (Bamford et al. 2009). However, Hooded Vultures appear to be much less sensitive to disturbance than other vulture species (Mundy et al. 1992). Any positive effects of humans might be due to suitable foraging conditions, such as greater food provisioning closer to human settlements as reported for human-commensal scavengers in India (Kumar et al. 2018). In the present case, the incidence of nest disturbance was higher further from habitation, suggesting that humans provide some degree of protection from poachers and tree cutters. Indeed, we previously found that people provide local protection to this species in the present study area (Daboné et al. 2016). According to elderly and fetish priests in the vicinity of our known nest sites, the Hooded Vulture is considered a sacred bird. These people claim that any persecution of Hooded Vultures can inflict misfortune to the culprit, his accomplices and their family (CD unpublished data). Similar to fetish traditions dictating the use of vulture body parts elsewhere in West Africa (Nikolaus 2006, 2011), Hooded Vulture behaviour in Burkina Faso is interpreted by fetish priests to predict future events. So rather than harvesting vultures for belief-based use, most people in Garango have traditionally been taught to protect this species, and any action aimed to kill or ill-treat Hooded Vultures, or harvest their eggs, is forbidden by tradition. For this reason, nesting trees are habitually preserved from pruning or cutting, particularly during the breeding period. These traditions might explain why most of the raided nests were out of sight of local people, at some distance from human habitation, as well as the predominant failure of the more remotely situated nests in the present study.

We found that nests failed not only due to harvesting of nest contents but also, unintentionally perhaps in most cases, due to the pruning and cutting of nest trees for firewood or livestock fodder. During the dry season, when Hooded Vultures breed, shepherds frequently use the green leaves of *Faidherbia albida* and *Tamarindus indica* to feed their livestock. Such tree pruning is often excessive, altering the shape of trees throughout the Sahelian and Sudan savannas of West Africa (Zwarts et al. 2009). We observed that after the pruning of nest trees, Hooded Vulture nests and their contents were often more exposed to the sun, which may have reduced the future suitability of such nest trees to breeding vultures. Given that in the Garango area trees are often pruned every year, the pruning and cutting of trees may contribute to a steady reduction of available nest sites.

Despite high levels of human disturbance and persecution, the fairly high fledging success (0.88 chicks fledged per egg hatched per year), also noted in Nigeria, in South Africa and in Zimbabwe (Mundy et al. 1992; Monadjem et al. 2016), indicates that nest losses after hatching are fairly low. The breeding success over the present two-year study period in Garango (0.68 and 0.71 chicks per nests with eggs) is also higher than that recorded in north-eastern South Africa in 2015 (0.23 chicks per nests with eggs; Thompson et al. 2016), but within the range of records elsewhere in that region in 2013/14 (0.44–0.89 chicks per nests with eggs; Monadjem et al. 2016). In Hwange National Park in Zimbabwe, breeding success estimated across multiple years was 0.54 chicks per nest with eggs (Hustler and Howells 1988). We suspect that the relatively high breeding success in the more agricultural Garango area may at least be partly due to the relative scarcity of a range of natural predators that may impact breeding success in some of the more uninhabited savannas of southern Africa (e.g. Chacma Baboon *Papio ursinus* and Martial Eagle *Polemaetus bellicosus*; Thompson et al. 2017).

Productivity by Hooded Vultures in the Garango area of Burkina Faso (0.57 chicks fledged per territorial pair per year) was higher than that reported in Nigeria around the town of Sokoto (0.34 chicks fledged per territorial pair per year; Mundy et al. 1992). This difference might be partly explained by the species' local protection in Garango, and a greater disturbance rate of nests in Nigeria, but this remains speculative. In general, a large number of non-laying pairs such as reported here (20% of 56 territorial pairs did not lay during the 2014/15 breeding season) is not uncommon in vultures (Mundy et al. 1992). A major factor influencing egg laying is food supply and, in poor food years, many territorial pairs may fail to lay eggs. Future longer-term monitoring of Hooded Vulture productivity in Garango may help to understand how its population responds to changing, probably largely anthropogenic food supplies.

Vultures provide a range of ecosystem services to humans, from the prevention of spread of disease through rapid carcass disposal (Buechley and Şekercioğlu 2016), to their considerable cultural and religious significance attached to their role of disposing of human bodies (Markandya et al. 2008), and for curing a range of illnesses or preventing misfortune (Nikolaus 2011; McKean et al. 2013). In addition, other services have recently been described, such as farmers making use of vultures to find dead livestock in the field (Santangeli et al. 2016; Craig et al. 2018). Of all African vultures, the ecosystem services provided by Hooded Vultures are possibly the greatest, because of their relatively large numbers, close association with human settlements from West to north-east Africa, and their largely anthropogenic diet in this region (Mundy et al. 1992). To date, such services remain unquantified. At the same time, the widespread harvesting of Hooded Vultures for belief-based use is likely to be unsustainable (Buij et al. 2016), negatively impacting their numbers and their potential for ecosystem service provision. On the other hand, we show here that cultural values attributed to Hooded Vultures may also contribute to their protection. Our results show that in the largely agricultural Garango area of central Burkina Faso, Hooded Vultures have a higher reproductive success closer to human habitations thanks to the protection provided by traditional customs and convictions, possibly aided by low natural predation

pressure. Unfortunately, this positive effect appears to be counteracted by the illicit harvesting particularly of eggs and nest materials from nests located at some distance from human habitation, most likely mainly for belief-based use.

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