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BREEDING BEHAVIOR OF THE HOODED VULTURE (*NECROSYRTES MONACHUS*) IN THE SUDANO-SAHELIAN AREA (GARANGO, BURKINA FASO)

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ABSTRACT.—Knowledge of Hooded Vulture (Necrosyrtes monachus) breeding behavior is important for monitoring purposes and to understand factors that may impact their breeding rates. In this study, we describe the breeding behavior of 65 Hooded Vulture pairs during two breeding seasons (2013/2014 and 2014/2015) in the Sudano-Sahelian area, Garango, in central-eastern Burkina Faso. The main behavioral patterns examined were aerial displays, copulation, nest building, incubation, nestling-rearing, and nest attendance. Hooded Vultures appeared highly selective with regard to nesting tree selection (91% of the 65 nests were in one of three species: Parkia biglobosa, Faidherbia albida, and Tamarindus indica). The breeding period of 65 pairs of Hooded Vultures spanned approximately 8 mo from egg-laying to fledging of the young. The constructed nests included a variety of human-made waste (plastic, paper, paperboard, and rags). Incubation lasted 48.1 \pm 2.0 (SD) d for 18 hatched eggs. Juveniles continued receiving food from their parents on the nesting site for at least 38 d after fledging, and stayed with their parents for >5 mo postfledging. Aerial displays were frequently performed by Hooded Vultures in pairs (two adults) or in threes (two adults with juvenile) and those observed early in the breeding season were considered to be courtship displays. Both sexes contributed to nest building and incubation tasks, and nestlings were relatively well attended by parents at all times of the day during the first weeks. Hooded Vultures produced 0.70 fledged young per nest where eggs were laid, or 0.57 fledged young per territorial pair. Hooded Vultures have a relatively healthy reproductive rate, but remain threatened primarily by direct human persecution. Local protection of Hooded Vultures in this area should be strengthened by public awareness campaigns to safeguard the population's long-term persistence.

KEY WORDS: Hooded Vulture; Necrosyrtes monachus; breeding behavior; breeding phenology; Burkina Faso; nesting; reproductive rate; West Africa.

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COMPORTAMIENTO REPRODUCTOR DE *NECROSYRTES MONACHUS* EN EL ÁREA SUDANO-SAHELIANA (GARANGO, BURKINA FASO)

RESUMEN.—Conocer el comportamiento reproductor de Necrosyrtes monachus es importante para fines de seguimiento y para comprender los factores que pueden afectar sus tasas reproductivas. En este estudio, describimos el comportamiento reproductor de 65 parejas de N. monachus durante dos temporadas de cría (2013/2014 y 2014/2015) en el área sudano-saheliana, Garango, centro-este de Burkina Faso. Los principales patrones de comportamiento examinados fueron las exhibiciones aéreas, la cópula, la construcción del nido, la incubación, la crianza de los polluelos y la asistencia al nido. Los individuos de N. monachus parecieron ser muy selectivos con respecto a la selección de árboles para anidar (91% de los 65 nidos estaban en una de las siguientes especies: Parkia biglobosa, Faidherbia albida y Tamarindus indica). El período reproductor de las 65 parejas abarcó aproximadamente 8 meses, desde la puesta de huevos hasta el emplumamiento de las crías. Los nidos construidos incluyeron una variedad de desechos antropogénicos (plástico, papel, cartón y trapos). La incubación duró 48.1 ± 2.0 (DE) d para 18 huevos eclosionados. Los juveniles continuaron recibiendo comida de sus progenitores en el sitio de anidación durante al menos 38 días después del salto del nido y permanecieron con sus progenitores durante >5 meses después de dicho salto. N. monachus realizó con frecuencia exhibiciones aéreas en parejas (dos adultos) o en tríos (dos adultos con un juvenil) y aquellas observadas al comienzo de la estación reproductiva fueron consideradas como exhibiciones de cortejo. Ambos sexos contribuyeron a las tareas de construcción e incubación del nido, y los polluelos estuvieron relativamente bien atendidos por sus progenitores en todo momento del día durante las primeras semanas. N. monachus produjo 0.70 pollos por nido donde se pusieron huevos, o 0.57 pollos por pareja territorial. N. monachus tiene una tasa reproductiva relativamente saludable, pero sigue amenazado principalmente por la persecución humana directa. La protección local de N. monachus en esta área debería ser fortalecida mediante campañas de concienciación pública para salvaguardar la persistencia a largo plazo de esta población.

[Traducción del equipo editorial]

INTRODUCTION

The Hooded Vulture (Necrosyrtes monachus) is the most common vulture among the seven West African species (Thiollay 2007). It is a tree-nesting raptor with a widespread distribution, resident throughout and endemic to sub-Saharan Africa (Mundy et al. 1992, Botha et al. 2017). In West, Central, and northeastern Africa, it is often associated with human settlements, but it is also found in open grassland, forest edge, wooded savannah, semidesert, and along coasts (Mundy et al. 1992, Ferguson-Lees and Christie 2001, Thiollay 2007, Jallow et al. 2016, Mullié et al. 2017, Henriques et al. 2018). In West African urban areas, this species congregates at slaughterhouse disposal sites and rubbish dumps, and usually nests in large trees near human settlements (Balança et al. 2007, Ogada and Buij 2011).

Although the estimated global population is almost 200,000 individuals (Ogada and Buij 2011), Hooded Vultures have rapidly declined throughout much of their West African range (Thiollay 2006, Ogada et al. 2015, Mullié et al. 2017, Nosazeogie et al. 2018). Empirical studies and models have estimated the median annual rate of decline for this species at 3.3% in this region (Ogada et al. 2015). At present the species is classified as critically endangered (BirdLife International 2022). Previous studies have attempted to assess the main drivers of the catastrophic decline in populations of this formerly abundant African vulture. The well-known threats to Hooded Vultures in West Africa include anthropogenic factors such as unintentional and intentional poisoning, and harvesting for belief-based use and consumption (Buij et al. 2016, Ogada et al. 2016, Botha et al. 2017, Daboné et al. 2022). Additional threats suspected to affect Hooded Vultures in this region include habitat degradation, electrocutions on unsafe powerlines, motor vehicle collisions, and decreasing food availability (Ogada and Buij 2011, Ogada et al. 2015, Daboné et al. 2022).

Despite the species' abundance, few published studies have described the Hooded Vulture's breeding behavior. Here, we describe the breeding behavior of Hooded Vultures during two breeding seasons (2013/2014 and 2014/2015) in the Sudano-Sahelian area in central-eastern Burkina Faso.

METHODS

Study Area. We studied Hooded Vultures in Garango rural township $(0^{\circ}33'W, 11^{\circ}48'N)$, in the province of Boulgou, 180 km southeast of Ouagadougou (the capital of Burkina Faso) and 20 km

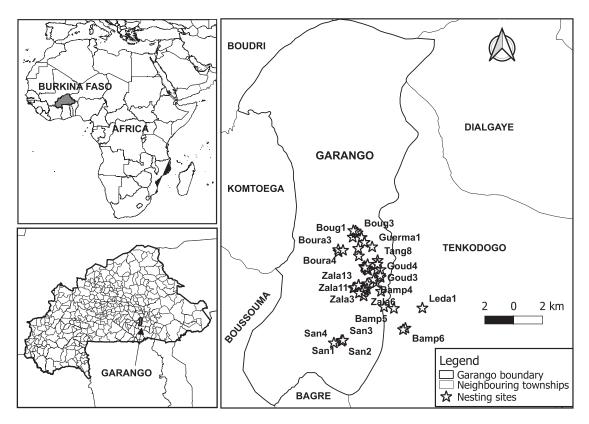


Figure 1. Study area and approximate locations of surveyed nests in Garango, Burkina Faso. The actual nest locations are not provided to protect nest sites from poaching and other disturbance. In most areas of high nest density, not all nest names appear on the map.

from Boulgou's capital, Tenkodogo. Garango is traversed by National Road 17 (Fig. 1). We choose this study area because the region supports many relatively easily accessible nests, not far apart, in various habitats, including towns, villages, and small patches of savanna forest outside of towns or villages.

Garango consists of a city center surrounded by many small agglomerations of houses (up to 10 km from the center). Houses in the center 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 in the outlying areas typically nest in large trees, either in small patches of forest outside of town, or in single trees in agricultural fields. In the city centers, nests are often only 5–10 m from houses (Daboné et al. 2016, 2019).

Garango is located in the Sudano-Sahelian climate zone, which has an annual rainfall between 600 and 900 mm, mostly from June to October (Ibrahim et al. 2014). Air temperature averages 20-30°C with extremes between 18 and 39°C (Dipama 2010). This area belongs to the North Sudanese phytogeographical zone, where savannas have been transformed into agricultural landscapes and the remaining savanna tree species are dominated by Adansonia digitata, Faidherbia albida, Lannea microcarpa, Parkia biglobosa, Tamarindus indica, and Vitellaria paradoxa, which grow naturally and are preserved by the farmers (Boussim 2010). The relief of Garango is moderate and it has the highest hill of the province (420 m). Garango's 2019 population was estimated at 91,158 inhabitants, mainly of the Bisa, Mossi, and Fulani ethnic groups (Institut National de la Statistique et de la Démographie 2019). Small-scale agriculture and livestock farming are the primary economic activities.

Nest Searches and Observation Schedules. We studied Hooded Vultures during two breeding seasons, 2013–2014 and 2014–2015. The Hooded

Vulture's breeding period in West Africa extends from October to April (Balança et al. 2007, Daboné et al. 2016). Thus, each year we began fieldwork as early as 1 September when Hooded Vultures perform conspicuous courtship displays in the breeding area and ended on 16 May, after fledging of the last juvenile.

We searched for Hooded Vulture nests by walking slowly in areas of the township and village where we had seen nests previously (Daboné et al. 2019). We searched for nests using binoculars or a spotting scope. We used the birds' territorial behaviors, such as circling with a mate, or collecting nesting materials, as an indication of the potential presence of a nest. To find nests, we solicited the help of local people, including secondary school students age 16-19 yr old. The students participated in the study as part of their ecology course, with the permission of their teachers and parents, and they were instructed to look for Hooded Vulture nests near their homes. During the two breeding seasons, the villagers and students led us to 22 Hooded Vulture nests. An additional 43 nests were subsequently found in the same area, totalling 65 Hooded Vulture occupied nests (Fig. 1).

Breeding Terminology. Hooded Vultures show fidelity to nest sites (Mundy et al. 1992, Daboné et al. 2016) and this increases the likelihood of seeing birds engaged in territorial behaviors such as nestbuilding, nest maintenance and repair, and nest defense. If mated birds or at least one adult were detected at least once at the nesting site (nesting territory) during the pre-laying season, or if there was fresh excreta and plant material (sticks, leaves) on the nest, indicating recent refurbishment, then we regarded these as occupied nests and the mated birds as a territorial pair (Krüger et al. 2014). A breeding attempt (or active nest) was defined as any nest where at least one egg was laid and the pair was defined as a breeding pair (sensu Fernández et al. 1998, Steenhof and Newton 2007). A successful nest was one where at least one nestling survived until fledging. Where a nest was seen but no bird and no evidence of recent use were seen, the nest was recorded as an unoccupied nest. In this study, productivity was defined as the number of nestlings fledged (here coinciding with the number of successful nests, as each pair laid only one egg) divided by the number of occupied nests. Breeding success was the number of nestlings fledged (coinciding with the number of successful nests) divided by the number of breeding attempts (or active nests). Hatching success was defined as the proportion of eggs hatched per number laid and fledging success as the proportion of nestlings fledged per egg hatched. Nesting rate was defined as the percentage of occupied nests where at least one egg was laid (Cheylan 1981, Steenhof and Newton 2007).

Assessment of Breeding Phenology (20 nests, 2013–2014). During the first breeding season, we surveyed 20 occupied nests (nests where there are signs of reproduction, such as copulation/courtship behaviors, a refurbished nest, two adults, etc., but eggs may or may not have been laid). Of these 20, eggs were laid in 19. We visited the 19 active Hooded Vulture nests a total of 294 times, with 8-20 visits per nest (mean = 16) between 0600–1800 H. These visits occurred from 8 October 2013 to 15 May 2014 and we assessed the nest status during each breeding phase (nest building, egg-laying, incubation, hatching, and nestling-rearing). Intervals between visits differed across breeding phases. Intervals were longer (7-14 d) during courtship/territory occupancy, early incubation, and early nestling-rearing periods, and shorter (2-3 d) during the presumed egg-laying period, late incubation, and late nestlingrearing periods. To minimize disturbance, we observed nests from the ground with a spotting scope (Kowa TSN-601, 60 mm) and binoculars (Nikon Prostaff 3S 10×42). During the laying and late incubation periods, when the presence of an egg or a newly hatched nestling was suspected, we climbed the tree (at 13 nests), or we used a mirror mounted on a stick to inspect the nest contents (at six inaccessible nests). Dates such as laying date, the start date of incubation, hatching date and fledging date were estimated as the midpoint between two consecutive visits when the new stages were noted (Xirouchakis 2010). Nest visits stopped once a nest had failed. For successful nests, two additional visits were made after fledging, one in July 2014 and another in September 2014, to assess the nestlings' dependence on their parents and post-fledging nest attendance.

Breeding Behavior (2014–2015). To document breeding behavior in a robust way, we monitored a large number of nests (n=52) using relatively brief visits. We then also closely monitored a selection of four nests (focal sampling; Martin and Bateson 1990, Xirouchakis and Mylonas 2007).

Large-scale monitoring of nest sites (52 nests). Based on the phenology results of 2013–2014, we set a new survey schedule for the 2014–2015 breeding season,

			PHASE OF THE BREEDING CYCLE	NG CYCLE		
	NEST OCCUPA	NEST OCCUPANCY AND COURTSHIP				
SURVEY DETAILS	BY TERRIT	itorial Pairs	EGG-LAVING	EGG HATCHING	YOUNG FLEDGING	GING
Survey date 7–10 Breeding phase Nest o	7–10 Oct 2014 Nest occupancy	7–10 Nov 2014 Late nest occupancy and egg-laying	26–28 Dec 2014 Egg-laying and replacement egg-laying if first egg was lost	29 Jan–1 Feb 2015 Egg hatching and late egg-laying	30 Apr–3 May 2015 16–20 May Nestling fledging Late nestlin fledging	16–20 May Late nestling fledging

Table 1. Survey schedule for large-scale nest monitoring of Hooded Vulture nests, Burkina Faso (52 nests, 2014–2015). One visit per nest was made during each of the

six listed breeding phases

in which 56 Hooded Vulture nests were monitored. We visited 52 of the 56 nests 247 times in total (4-5 visits per nest) for a total of 48 hr of observation over 24 field days, from 1 October 2014 to 20 May 2015. Visits lasted 10-20 min and were scheduled as: one or two visits from October to November to check territorial occupancy, one visit in late December to check for egg-laying, one in early February to check for egg hatching, one in late April to check for fledging and another one in mid-May for late fledging (Table 1). We assessed whether eggs had hatched based on the position and behavior of the adult: an adult standing over the nestling (the head and the body except the legs were visible from the ground) indicated that the egg had hatched. An adult hunched on the nest (only its head and/or its tail were seen from the ground) indicated that the bird was still incubating. During visits within the presumed fledging period, we recorded that the young had fledged when it was seen flying away or flying to a nearby tree and perching there, or when the nest was empty and the fledgling was seen perched in nearby tree.

In addition, early in the breeding season (September–October), we used a distant location (400–600 m from the nests) to observe five nests that were being built, on three successive days, for 5 hr in the morning (from 0600 to 1100 H) and 3 hr in the evening (from 1500 to 1800 H), to observe courtship, copulation, and nest building behavior.

Focal nest site monitoring (four nests). We conducted focal monitoring at four nests in 2014-2015 (Bamp1, Bamp2, Tang3, and Zala6) to document nest attendance, nestling-rearing, and food provisioning to the nestlings. We chose these four nests because they were relatively easy to access and were close together, only 100-200 m from houses in Garango rural township. The four focal nests were intensively monitored for 74 hr of observation spread over 47 field days. Each of the four nests was also directly monitored every 2-3 d by climbing the nest tree during the pre-laying, late incubation, and early nestling-rearing periods. To minimize any disturbance and possible impacts on reproductive output, at these relatively regular and frequent visits, we did not make a detailed study of the eggs and nestlings (no measurements were taken). Nevertheless, we paid particular attention to the nestling development and their feathers. Each visit lasted only 15-30 min. Near the middle of the nestling-rearing period (1 mo after hatching), climbing visits ceased, to prevent premature fledging of the nestlings.

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VARIABLE	DESCRIPTION OF NEST MEASUREMENT					
Nest height (m)	Height of nest above the ground; measured with a measuring tape during nest access.					
Nest tree species	Species of tree harboring the Hooded Vulture nest; reference: Arbonnier (2002).					
External nest depth (cm)	Exterior depth of the built-up nest; measured as the distance from the top rim of the nest sides to the bottom of the nest's exterior (i.e., the part in contact with the fork of the tree on which the nest is built; measured with a measuring tape during nest access.					
Internal nest depth (cm)	Interior depth of the built-up nest; measured as the distance from the top rim of the nest sides to the base of the interior nest cup where egg was placed; measured with a measuring tape during nest access.					
Tree height (m)	Height of the nest tree above ground level; measured with a measuring tape (during nest access) up to the nest location and estimated from nest location to the top of the tree.					
Distance to nearest- neighbor nest (m)	Linear distance between the Hooded Vulture nest and the nearest neighbor; measured with GPS.					

Table 2. Nest and nesting tree characteristics at 65 Hooded Vulture nests in the Garango area (2013–2015).

Pre-laying behaviors: occupancy, displays, copulations. While searching for nesting sites before egg-laying began, we observed vultures' territorial behaviors, such as when pairs flew close together, one above the other, and when birds flew in parallel, side by side, forming loops in the shape of a chain. We described these flights as Hooded Vultures' aerial displays. Occasionally these aerial displays were also seen when we were monitoring nest sites during the breeding season. Because monitoring these aerial displays was not the focus of our study, but rather a tool used to detect new Hooded Vulture nest locations, we did not measure the time birds spent performing aerial displays.

To examine Hooded Vulture nest building and copulation, we made observations occasionally while searching for territorial pairs during the pre-laying period and also during the distant observations (400-600 m from the nests) of the five sites where nests were being built. When observing nest building behavior, we also noted the material used and the distance from the nests where these materials were acquired if possible (Xirouchakis and Mylonas 2007). Copulations were regarded as successful when cloacal contact was recorded (González-Solís and Becker 2002). In addition, we measured several nest parameters including nest height, external and internal nest depth, nest tree height, nest tree species, and distance to nearest-neighbor nest (Table 2).

We recorded all Hooded Vulture aggressive interactions taking place in the nesting site or in the surrounding areas. We defined Hooded Vulture nest defense as any behavior consisting of an aerial chase ending when the intruder was expelled from the vicinity of the nest.

Incubation – nestling-rearing. At the four focal nesting sites, we examined the following activities: (1) incubation pattern, by direct observation; (2) food provisioning to the nestlings, by examining the prey remains in the nest when climbing the trees; and as nestlings aged and became feathered, by direct observation from the ground with a spotting scope and binoculars; and (3) nestling-rearing, by observing parental care and nestling development throughout their growth. Because Hooded Vultures were not individually recognizable, we were unable to assess the relative contributions of the sexes to parental care.

Assessment of Reproductive Rate. We calculated five measures of reproductive rate: productivity (only in 2014/2015), breeding success, hatching success, fledging success, and nesting rate (only in 2014/2015).

For nests that failed, we tried to assess the cause of nest failure. Because of the low rate of natural predation presumed in this highly anthropized area, we examined only 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/or nest materials seen on the ground. We also recorded the testimonies of people living in the vicinity of nesting sites who had witnessed others climb the nest tree.

Data Analysis. We provide descriptive statistics for breeding phenology, reproductive rate, and causes of reproductive failure. To help fill data gaps for this little known critically endangered raptor, we also report qualitative descriptions of behaviors includ-

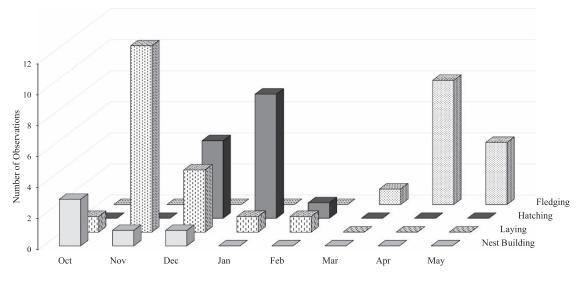


Figure 2. Breeding phenology assessed from 20 Hooded Vulture nests in the Garango area (2013–2014).

ing (1) aerial (courtship) displays, (2) territoriality, (3) copulation, (4) nest building, (5) incubation and nest attendance, and (6) food provisioning to the nestlings.

RESULTS

Breeding Phenology. The total breeding period of Hooded Vultures spanned approximately 8 mo, starting from laying eggs in late October and early November, and ending in mid-May when the last young birds fledged. Nest-building behavior started early in October and the last nest-building was observed in January. Copulations were observed on four occasions, three during the pre-laying period from October to November and once during the nestling-rearing period on 5 March 2014. The first laying date was 30 October 2013 and the latest 2 February 2014 (Fig. 2) but most eggs were laid from November to December (84%; n = 19). Of 64 clutches observed in 2013-2015, all (100%) were of single eggs. We were able to obtain good estimates of the Hooded Vulture's incubation period from 18 nests. Incubation averaged 48.1 ± 2.0 (SD) d (range = 45-52 d). Hatching dates ranged from 14 December 2013 to 9 February 2014. We were further able to obtain fairly accurate fledging dates for 17 nestlings. Apparent first flights of the young were recorded as early as 27 March and as late as 9 May. The average nestling age on apparent first flight was ranged from 110.5 \pm 6.7 (SD) d (n = 17; range = 101-121 d). The two post-fledging visits to nest sites

in July and September 2014 revealed that fledglings apparently remained with their parents for a relatively long period, well over 6 mo after fledging, and regularly returned to their nest or the vicinity. Indeed, although nestlings successfully fledged on 23 and 30 April 2014 at Bamp1 and Zala8, respectively, they were observed together with their parents at the breeding sites on 15 July and then later on 4 September, respectively, 83 and 127 d after fledging, at about 6–8 mo of age. Another young successfully fledged on 9 May and was seen with its parents on 8 October 2014 in the nest tree, 152 d after fledging, at about 8–9 mo of age.

Reproductive Rate and Causes of Breeding Failures. Breeding territories were fairly evenly distributed throughout the Garango city center and the surrounding small agglomerations of houses and agricultural fields, within a radius of approximately 4-5 km. Territories outside this main cluster were located in the surrounding Garango rural township up to 10 km from the center. We monitored 20 occupied nests in 2013-2014 and monitored 11 of those again in 2014-2015 along with 45 nests that were newly discovered in 2014-2015, for a total of 76 occupied "nest-years" (territorial pairs) over the two breeding seasons. Of these 76 territorial pairs, 64 laid eggs, and 45 raised young successfully (Table 3). In the 2013/ 2014 breeding season, given that we focused our survey only on 20 occupied nests, we were unable to obtain accurate counts of overall number of territo-

			BREEDING SUCCESS						
			(YOUNG PER	PRODUCTIVITY					
	TERRITORIAI	BREEDING	HATCHED	WITH	NESTING	HATCHING	FLEDGING	BREEDING	(YOUNG PER
Season	PAIRS	ATTEMPTS	EGGS	FLEDGLINGS	RATE	SUCCESS	SUCCESS	ATTEMPT)	Occupied Nest)
2013/2014	ND	19	14	13	ND	0.74	0.93	0.68	ND
2014/2015	56	45	37	32	0.80	0.82	0.86	0.71	0.57
Total	ND	64	51	45	ND	0.80	0.88	0.70	ND

Table 3. Breeding performance of Hooded Vultures in the Garango area in 2013–2015. ND = not determined.

rial pairs in the study area and consequently nesting rate and productivity were not determined. In the 2014/2015 breeding season, of the 56 territorial pairs monitored, no eggs were laid by 19 pairs (20%)and consequently, the overall productivity (0.57 young per territorial pair) was lower than breeding success (0.71 young per breeding attempt). The proportion of young fledged per egg hatched (0.88)was higher than the proportion of eggs hatched per number laid (0.80; Table 3). Nineteen breeding attempts (30%) failed and 45 (70%) were successful. Of the 19 breeding failures, thirteen (69%) were caused by direct human persecution, i.e., the removal of the egg or whole nests for belief-based use, and four (21%) by indirect human activities, such as the farmers cutting or pruning nest trees for firewood, or for feeding livestock. One nest (5%) had a dead adult bird on it, and one (5%) was destroyed, probably by wind.

Breeding Behavior. Aerial displays, territorial behaviors, and pre-laying behaviors. We observed Hooded Vultures in aerial displays throughout the breeding season. Two individuals often flew side by side, circling or soaring over the territory and near the nest site, primarily between 1000-1600 H. Aerial displays during the early breeding season (from September to October; n = 68) were particularly conspicuous. Birds were seen together, in pairs (two adults; n = 46) or in threes (two adults with juvenile; n = 22) flying together one above the other, flying closely next to each other, or flying in parallel side by side forming loops. Their feet were often outstretched and wings spread out. The upper individual flew slightly behind the lower one, often so close that they were nearly touching each other. We could not confirm that these birds were breeding pairs because birds were not individually recognizable. However, given that these aerial displays were seen prior to and during the vultures' egg-laying period and given that the two birds flying together were away from any others, we concluded that these displays signified courtship.

We occasionally observed intraspecific territorial defense attacks (n=5), particularly in the very dense territories (30-50 m between nearest-neighbor nests). One of these occurred during incubation and four during the nestling-rearing period. On these occasions, we observed an intruder Hooded Vulture attempting to perch on the nesting tree of another breeding pair, after which it was immediately driven out with an aerial chase by one of the nesting pair until it was expelled from the vicinity of the nest. During these territorial defense attacks, the vultures hissed loudly and screamed conspicuously. Hooded Vultures build large stick nests typically in a sturdy crotch of a large tree. Nests may be reused many times and repaired each breeding season. We observed vultures building, repairing, and adding material to their nests during the courtship and incubation phases (n = 34). The material included dry branches and sticks of about 1 cm in diameter collected from the vicinity of the nest tree at distances ranging from a few meters to up to 500 m from the nests and transported with the feet or in the bill. Breeding pairs also lined the interior of their nest with a variety of human-made waste such as pieces of plastic, paper, paperboard, rags, and other rubbish as well as dry or fresh grass and leaves. Both sexes were observed contributing to nest building activities. Hooded Vultures in our study area nested only in trees, particularly the evergreen species Parkia biglobosa (71%). Characteristics of the 65 Hooded Vulture occupied nests during the two breeding seasons varied substantially (Table 4).

We observed copulations on four occasions, including once during the nestling-rearing periods. Copulation lasted about 30 sec; the male stood on the female's back, spread its wings widely, lifted its wings up and emitted distinctive hoarse sounds together with high-pitched whistles. Cloacal contact was observed and ejaculation was presumed for each

5-35 333.8 \pm 272.4 30-1115

seasons.											
		Tree Height (m)		NEST HEIGHT (m)		External Depth (cm)		INTERNAL DEPTH (cm)		DISTANCE TO NEAREST- NEIGHBOR NEST (m)	
Period	n	$Mean \pm SD$	RANGE	$Mean \pm SD$	RANGE	$Mean \pm SD$	RANGE	$Mean \pm SD$	RANGE	Mean \pm SD	RANGE
										205.6 ± 184.7 390.7 ± 287	

 21 ± 8.3

Table 4. Characteristics of 65 Hooded Vulture nests in the Garango area during the 2013–2014 and 2014–2015 breeding seasons.

copulation attempt. Copulation was accompanied by strange and remarkable hissing and screaming emitted by one or both partners. We were unable to ascertain which sex of the two birds emitted this shrill whistling.

 13 ± 3.6

6 - 25

65 14.8 \pm 3.4 10-28

Incubation and nestling-rearing. During the incubation period, an adult incubated almost continuously, except when turning the eggs, rearranging the nest lining, or switching incubation duties. Rarely, both parents incubated the egg together (n = 4 such observations out of 91 visits during the incubation period); when this occurred, the mates were positioned close together and covered all the interior space of the nest. Of 19 pairs whose breeding attemps failed during 2013–2015, we know of only one that laid a replacement clutch. This renesting attempt took place 2 wk after failure and resulted in a second failure after egg-laying, as the nest tree (*Faidherbia albida*) was pruned by farmers for feeding livestock.

During the first 4 wk of its life, the nestling was constantly attended by one of the parents. As the nestling developed, parental attendance decreased. At the age of 1–2 mo, the nestling was left unattended for up to 1 hr at a time. After the age of 3 mo, the nestling was often left alone in the nest throughout the morning and midday, until the parents returned from foraging.

Food deliveries to the nest (observed during focal observations) were accompanied by low hisses, probably given by the nestling to beg for food. The nestling received food in its beak from the adults, although sometimes the adult regurgitated the food onto the nest and the nestlings picked it up from there. Such regurgitated food consisted of pieces of skin, bones, pieces of meat, or fresh coagulated blood clots likely obtained from foraging in an abattoir or at discarded domestic animal carcasses.

By the age of 3 mo, the nestling was almost fully feathered and resembled the adults but differed by having a pale crown, black facial whiskers, and a chestnut-brown nape; some traces of dark brown feathers remained on the face and around the eyes.

7-60 17.9 \pm 9.3

In several cases nearly grown nestlings (8–12 wk old) moved to nearby branches. On four occasions, we observed flights that appeared to be the nestling's first flight or certainly an early flight. On these flights the young did not go far from the nest. We noticed that the young continued receiving food from their parents on the nesting site for at least 38 d after fledging (observed on two occasions on 30 April and 9 May at their nesting trees, after they fledged on 27 March and 3 April, respectively).

DISCUSSION

Breeding Phenology. In our study area in Garango rural township, Boulgou province, Burkina Faso, the breeding period of Hooded Vultures spanned about 8 mo, starting with egg-laying in October and ending with fledging in May, coinciding with the dry season. In general, all breeding dates and the length of the nesting season were consistent with those reported for Hooded Vultures in East and West Africa (Mundy et al. 1992, Balança et al. 2007). Similarly, in the southern tropical zone from Tanzania to South Africa almost all egg-laying (excluding replacement clutches) occurs at the start of the dry season in May to August, with a peak in June and July (Tarboton and Allan 1984, Mundy et al. 1992, Tarboton 2001). In our study area, the incubation period in Hooded Vultures coincides with the months of the year with relatively low temperatures, from November to December, as in other vulture species (Mundy et al. 1992, Weesie and Belemsobgo 1997, Balança et al. 2007, Daboné et al. 2016). Incubation for our study birds averaged 48.1 ± 2.0 d, midway between that reported in Kenay (46 d) and that recorded in Nigeria (50-51 d; Mundy et al. 1992). Incubation in the coolest months of the year was reported elsewhere for other vultures (Margalida and Bertran 2000), which suggests that fledging would take place in the periods offering the highest chance of

Total

juvenile survival, a strategy that is common among raptors (Newton 1979).

Reproductive Rates and Cause of Breeding Failures. Because Hooded Vultures usually lay one egg, productivity and breeding success are relatively low (\leq 1). Urban Hooded Vulture populations in Sokoto, Nigeria, have an average productivity of 0.33 young per territorial breeding pair and breeding success of around 0.41 young per nest with egg[s]; Mundy et al. 1992). Compared to these results, Hooded Vultures breeding in Garango (with an overall productivity of 0.57 and a breeding success of 0.70) have a rather healthy reproductive rate, perhaps because of the species' local protection, a lower disturbance rate (Daboné et al. 2019) in this less-urbanized area, and/or high food availability (Xirouchakis 2010).

Breeding failure during this study was attributed to anthropogenic activities (89%, n = 19), primarily by direct human persecution (61%) consisting of the harvesting of the eggs, nestlings, or nest materials, most likely for belief-based use, and also by indirect human activities (21%) such as cutting/pruning of nest trees by farmers for firewood, or for feeding livestock. Eggs, vultures, and nest materials are often harvested for belief-based use or for food in West and South African countries, and this harvest often targets Hooded Vultures (Bamford et al. 2009, Saidu and Buij 2013, Buij et al. 2016, Craig et al. 2018). During our fieldwork and interviews in the main fetish market of Ouagadougou in 2019, we recorded more than 45 Hooded Vulture eggs and many pieces of Hooded Vulture nesting materials packed in bags for sale, evidently for belief-based use (C. Daboné unpubl. data). Similarly, human disturbance of vulture breeding was reported in Saudi Arabia where shepherds cut and pruned nesting trees for building materials or for feeding livestock (Shobrak 2011). There is a need for public awareness campaigns to highlight the negative effects of egg, nestling, and nest material harvesting, and to discourage disturbance at Hooded Vulture breeding sites. Such campaigns would improve the species' breeding output and safeguard its long-term survival in this area.

Breeding Behavior. *Territorial behavior.* Breeding territories were fairly densely distributed within a 4–5 km radius throughout Garango city center and the surrounding outlying houses and agricultural fields, which indicates the very low level of territoriality in this species (Mundy et al. 1992). Our study confirms the concentration of Hooded Vulture breeding

territories around human settlements, where there may be greater food availability, as reported for human-commensal scavengers in India (Kumar et al. 2018). In our study, Hooded Vulture breeding territories were close to human habitations (54% of nest trees were located within 100 m of houses), despite the greater potential for human disturbance and persecution at these sites. This might be partly explained by the species' local protection in Garango from poachers and tree cutters (Daboné et al. 2016, 2019). We also cannot exclude the possibility that the scarcity of adequate nesting trees has forced birds into agricultural fields and closer to houses where tall trees of economic, agronomic, and medicinal interest have been safeguarded.

A fairly large number (19.6% of 56) of nonbreeding territorial pairs (territorial pairs that did not lay eggs) were recorded during the 2014–2015 breeding season. This situation is not uncommon among vultures (Mundy et al. 1992, Wynne-Edwards 1995), and according to Mundy et al. (1992), about 20% of Hooded Vulture pairs may not breed in a given breeding season. Considering the prolonged breeding cycle (approximately 8 mo) and the time (5–6 mo) that the juvenile may stay with its parents, a yearly reproductive cycle for each breeding pair seems unlikely. In addition, in years with food shortages, many territorial pairs may not lay eggs (Gehlbach and Roberts 1997, Martínez-Abraín et al. 2002, Donázar et al. 2009).

Aerial displays. Aerial displays early in the breeding period likely are courtship, as in South Africa (Murn 2019). These in-flight behaviors described here and also in South Africa (Murn 2019) are not easily explained in terms of aggressive and/or territorial behavior because the birds involved appeared not to make territorial defense attacks and we observed no pursuit by any of the birds. These presumed nuptial flights performed by Hooded Vultures were similar to those recorded for Griffon Vultures (*Gyps fulvus*; Xirouchakis and Mylonas 2007) and other *Gyps* vultures (Ruby et al. 2018). The fact that juvenile birds sometimes took part in these flights suggests a complex social structure of Hooded Vulture groups.

The five intraspecific territorial defense attacks we observed occurred only where territories were close together and invariably, the intruder attempting to encroach on the territory was immediately driven out with an aerial chase by one of the nesting pair.

Nest building. Hooded Vultures build large and open nests exclusively in large trees, like most of the vultures nesting in West Africa (Mundy et al. 1992).

Several tall tree species were used but three were most commonly used (Parkia biglobosa, Faidherbia albida, and Tamarindus indica made up 91% of nesting trees). These species are included in the 10 dominant species in the phytogeographical zone (Nikiema et al 2001, Boussim 2010); all are 10-20 m tall and could potentially hold Hooded Vulture nests. Furthermore, throughout the Garango area and around human settlements, many other tall tree species such as Azadirachta indica, Manguifira indica, Balanites aegyptiaca, Lannea microcarpa, and Vitellaria paradoxa are common. This suggests that Hooded Vultures may be selective in choosing nesting trees in the Garango area. Similarly, in South Africa, Hooded Vultures apparently preferred some species for nest trees such as Diospyros mespiliformis (Roche 2006, Monadjem et al. 2016). Nests may be reused for years (Mundy et al. 1992, Daboné et al. 2016) if not destroyed by the winds of the subsequent rainy seasons, and if the trees sheltering these nests are not cut or pruned by farmers for firewood, or for feeding livestock (Daboné et al. 2019).

Hooded Vulture nests are made of strong, small sticks, green leaves and grasses, and also a variety of human-made waste. This reflects the adaptation of this species to living around human settlements, similar to the Black Kite (Milvus migrans), a commensal raptor species that uses human-made waste and objects for nest decoration (Sergio et al. 2011). Hooded Vultures in our study continuously lined their nests with green leaves, even during the incubation and nestling-rearing phases. The hypotheses suggesting explanations for this behavior, which is common in vultures and other raptors (Wimberger 1984, Xirouchakis and Mylonas 2007), have been discussed elsewhere (Newton 1979, Wimberger 1984, Clark and Mason 1988, Clark 1991) and were beyond the scope of our descriptive study

Copulation. We observed Hooded Vulture copulation at nest sites, which was where we made all our focal observations. As in other vulture species, copulation by Hooded Vultures is conspicuous and distinctive; the male emits a hoarse call as he grips the female's ruff while balancing on her back (Mundy 1982). Copulations thoughout the breeding period likely reinforce the pair bond (Mundy 1992). In other vultures, extra-pair copulations are frequent, with subsequent elevated risks of paternity loss (Birkhead et al. 1987, Møller 1987). Because birds were not marked in our study, we could not investigate extra-pair copulations. *Incubation and nestling-rearing.* Biparental incubation is common in vultures (Margalida and Bertran 2000, Xirouchakis and Mylonas 2007, Ruby et al. 2018) as noted for Hooded Vultures in this study. However, we were unable to determine the relative contributions of the sexes.

As in other raptors, the young nestling was attended almost continuously by at least one parent, which brooded/shaded, fed, and protected the nestling from predators (Margalida and Bertran 2000). As reported for other vulture species, the young are fed with the regurgitated food stored in the crop (Xirouchakis and Mylonas 2007, Kushwaha and Kanaujia 2009). The reduction in time spent attending the nestling was most pronounced from the age of 3 mo and older. At this age, nestlings are already relatively large and nearly fully feathered, with attendant high food requirements; the amount of prey brought to the nest increases and consequently so too does the time dedicated to searching for food (Margalida and Bertran 2000). The absence of the parent during the final stages of the nestling period (approximately age 3 mo) may be explained by the increased aggression that the young shows toward its parents, as it becomes excited and seizes food violently, causing adults to be reluctant to enter the nest (Bustamante and Hiraldo 1990, Hubert et al. 1995).

CONCLUSIONS

Hooded Vultures' reproductive output in Garango indicates a comparatively healthy population, likely due to the species' local protection. Hooded Vulture adults provide a high level of care for the egg and nestling, necessitating biparental care. However, direct human persecution (harvesting of the eggs, nestlings, and nesting materials) and indirect human activities (cutting and pruning of nest trees) threaten the birds and cause nesting failures. Furthermore, in this study area the Hooded Vulture primarily nests in only three tree species; given the increasing rate of deforestation in this area (Ariori and Ozer 2005, Zwarts et al. 2009), there may be nest-site limitations for this species, which is regarded as a loosely colonial breeder. In addition, the decrease in the availability of preferred habitats on the periphery of human settlements because of an increasing human population and associated developments (e.g., extension and intensification of agriculture, urbanization, and traffic; Thiollay 2006) could impact the Hooded Vulture's nesting success in this region. Urgent requirements for the

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cution and indirect disturbance of nesting vultures.

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