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An ethogram for the nesting and breeding behaviour of the Hooded Vulture *Necrosyrtes monachus*

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Most vulture species worldwide are in decline and of conservation concern. Despite the growing attention to vultures, relatively few studies have focused on their breeding behaviour. Understanding all aspects of a species' behaviour and its behavioural needs could help to inform conservation efforts. Behavioural studies can be enhanced with the use of an ethogram that clearly defines and describes distinct behaviours. We present the first ethogram detailing the nesting and breeding behaviours of the Critically Endangered Hooded Vulture *Necrosyrtes monachus*, compiled from over 400 000 nest camera photographs and from hours of direct personal observations at nests in north-eastern South Africa. We describe 28 behaviours that Hooded Vultures exhibited in and around their nests, and these fell into five discrete categories: Movement, Resting, Body Care, Social, and Nesting. We also present 34 camera trap images depicting behaviours from within each category, and discuss the uses and limitations of behaviour-recording technologies. Many of these behavioural elements may be common across vulture species, and so this ethogram may be a useful starting point for other researchers studying vultures globally.

Un éthogramme pour le comportement de nidification et de reproduction du Vautour charognard *Necrosyrtes monachus*

La plupart des espèces de vautours dans le monde sont en déclin et font l'objet de préoccupations en matière de conservation. Malgré l'attention croissante portée aux vautours, relativement peu d'études ont porté sur leur comportement de reproduction. La compréhension de tous les aspects du comportement d'une espèce et de ses besoins comportementaux pourrait contribuer à éclairer les efforts de conservation. Les études comportementales peuvent être améliorées par l'utilisation d'un éthogramme qui définit et décrit clairement des comportements distincts. Les auteurs présentent le premier éthogramme détaillant les comportements de nidification et de reproduction du vautour charognard *Necrosyrtes monachus*, une espèce en danger critique d'extinction. Cet éthogramme a été compilé à partir de plus de 400 000 photographies prises par des caméras de nidification et d'heures d'observation personnelle directe des nids. Nous décrivons 28 comportements que les vautours charognards manifestent à l'intérieur et autour de leurs nids, et ceux-ci se répartissent en cinq catégories distinctes: Mouvement, repos, soins corporels, social et nidification. Nous présentons également 34 images de pièges à caméra illustrant des comportements de chaque catégorie et discutons des utilisations et des limites des technologies d'enregistrement des comportements. Bon nombre de ces éléments comportementaux peuvent être communs à toutes les espèces de vautours, et cet éthogramme peut donc constituer un point de départ utile pour d'autres chercheurs étudiant les vautours à l'échelle mondiale.

Keywords: behaviour monitoring, camera trap, Critically Endangered species, direct observation, ethology, South Africa

Introduction

Vulture populations in Africa are in rapid decline as a result of various factors, including poisoning, habitat loss and degradation, collisions and electrocutions on linear infrastructure, and the illegal killing of vultures for the traditional medicine trade or for bushmeat (Ogada and Buij 2011; Angelov et al. 2013; Phipps et al. 2013; Rushworth and Krüger 2014; Buij et al. 2016; Santangeli et al. 2016; Daboné et al. 2019; Gore et al. 2020; Mashele et al. 2021a). Of the 10 vulture species commonly found in Africa, six are classed as globally Critically Endangered or Endangered (Thompson et al. 2021; IUCN 2022). This African vulture crisis is of particular importance to conservationists, because as obligate scavengers vultures are one of the most functionally important groups of animals on the planet owing to the irreplaceable ecosystem services they provide (Ogada et al. 2016). Vultures play a central role in nutrient cycling and carcass removal, and they likely limit the spread of pathogenic microorganisms (Ogada et al. 2012a; Moleón et al. 2014; Pfeiffer et al. 2015; Plaza et al. 2020).

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The Hooded Vulture *Necrosyrtes monachus* is one of Africa's most widespread vulture species, with an estimated population size of 197 000 individuals (IUCN 2022). However, it is classified as Critically Endangered because of an estimated average population decline of 83% over three generations (Ogada et al. 2016). While anthropogenic factors affecting vulture populations are well-known, less is known about aspects of their life history, and specifically the factors affecting their reproduction in the wild (Bamford et al. 2009; Plaza and Lambertucci 2020; Pfeiffer et al. 2017). An improved understanding of vultures' breeding biology could benefit conservation efforts (Reading et al. 2005; Carrete et al. 2006; Margalida et al. 2008; Zuberogoitia et al. 2008). For example, knowledge of the timing of breeding, the preferred nesting tree species, and how disturbance affects vulture breeding success (Robertson 1984; Margalida et al. 2011) could help guide whether (and when) recreational activities are allowed within vulture nesting habitat, whether nesting tree species or nesting habitats are protected (Thompson and Blackmore, 2020), and whether housing or other developments are permitted in vulture nesting habitat. The relative lack of knowledge on the breeding behaviour of most vulture species is thus an area in urgent need of attention.

In ethological studies, researchers attempt to explain behaviour in functional, causal and evolutionary terms (Ficken and Ficken 1966). The initial step in ethological studies is to describe and classify an animal's behaviours: to produce an ethogram. Ethograms provide a template for recording and understanding behaviour with clear behavioural descriptions and classifications. They can be used to standardise data collection across studies while ensuring objectivity and uniformity of methods (Nerlekar et al. 2014; Smith and Wassmer 2016).

The compilation of an ethogram may be time-consuming and can require weeks of fieldwork to obtain large enough data sets, depending of the ease with which the target species may be viewed. Camera traps offer a quicker and less-invasive method for obtaining images from which to record behavioural data (Carney and Sydeman 1999; Thompson et al. 2017a). The only published ethograms we could find relate to vultures' classified feeding behaviours in wild Griffon Vultures *Gyps fulvus* (Alvarez et al. 1976; Bosè and Sarrazin 2007) and to displays of territorial defence and dominance in captive Palm-nut Vultures *Gypohierax angolensis* (Schlee and Iorgulescu 2003). Kruuk (1967) and Londei (2010) also described the feeding and fighting behaviours of wild vultures in Africa. Other studies mentioned ethograms but did not provide the ethograms themselves (Hartt et al. 1994; Rolando et al. 1998).

Unlike other tree-nesting vultures, which usually nest on top of canopies, the Hooded Vulture generally nests within the canopy of densely foliated trees, which makes direct observation of its behaviour while the birds are in and near the nest challenging (Roche 2006; Monadjem et al. 2016). The recent use of strategically positioned camera traps in nesting trees has made it possible to gather large quantities of photographic data at nests previously considered visually inaccessible (Thompson et al. 2017a,b; Le Corre et al. 2020). The advantages of using camera traps to collect data include:

- continous operation, day and night, in all weather conditions;
- greatly reduced disturbance to nesting birds at a critical point in their life-cycle;
- no incidence of observer fatigue; and
- removal of the Hawthorne effect, whereby the presence of researchers may influence the behaviour of unhabituated wild birds (Bolgan et al. 2016).

Here, we used images from camera traps at Hooded Vulture nests in north-eastern South Africa to describe and characterise their breeding behaviour and to compile an ethogram, which will be useful for standardising the collection of behavioural data from both direct observations and images from camera traps.

Methods

As part of a study on the use of Hooded Vulture nests by other species throughout the year (Thompson et al. 2017a), we installed a single camera trap (Ltl Acorn® model 6210MC or Bushnell NatureView HD) at each of 11 Hooded Vulture nests along the Olifants, Mohlatse and Crocodile rivers within Limpopo and Mpumalanga provinces of north-eastern South Africa (Figure 1). The 11 Hooded Vulture nests in this study were all located in the sub-canopy, positioned either against the tree trunk (9 nests) or at a prominent branch fork (2 nests) of jackal-berry *Diospyros mespiliformis*, matumi *Breonadia salicina* or sycamore fig *Ficus sycomorus*, at a mean (± standard deviation) height of 11.2 ± 1.8 m (n = 8), as measured with a laser rangefinder (Nikon Forestry Pro) (Table 1). Trees were accessed using a rope and harness (Thompson et al. 2017a), and all camera traps were secured to branches using cable ties and/or adjustable straps. The camera trap faced the nest bowl, at a distance of 40 cm to 3 m from the nest, with each photograph capturing as much of the nest and adjacent branches as possible.

We used instantaneous focal sampling, with camera traps set to take a photograph every 5 min, day and night. Batteries and SD cards were changed monthly (just before they were fully drained) to avoid battery exhaustion and thus to maximise data capture, while causing as little disturbance to the nesting birds as possible. If egg-laying was imminent (typically during June: Steyn 1982; Roche 2006) or if the chick was very small (in August: Thompson et al. 2017a), then camera trap maintenance was delayed to reduce disturbance to breeding birds during sensitive stages of their breeding. Our data collection started in August 2015 and ended in March 2018; however, because of delays in some camera traps being serviced (batteries changed), there are some gaps in our data collection, where some nest cameras did not capture any photographs for some months (Thompson et al. 2017a).

We supplemented these camera trap data with behavioural data recorded from direct field observations (by LJT and FKF) at three Hooded Vulture nests where camera traps could not be placed because the nests were inaccessible (either right on top of the tree or on a thatched roof). We observed these three nests for one or two days each, from as far away as possible (50–200 m), and recorded

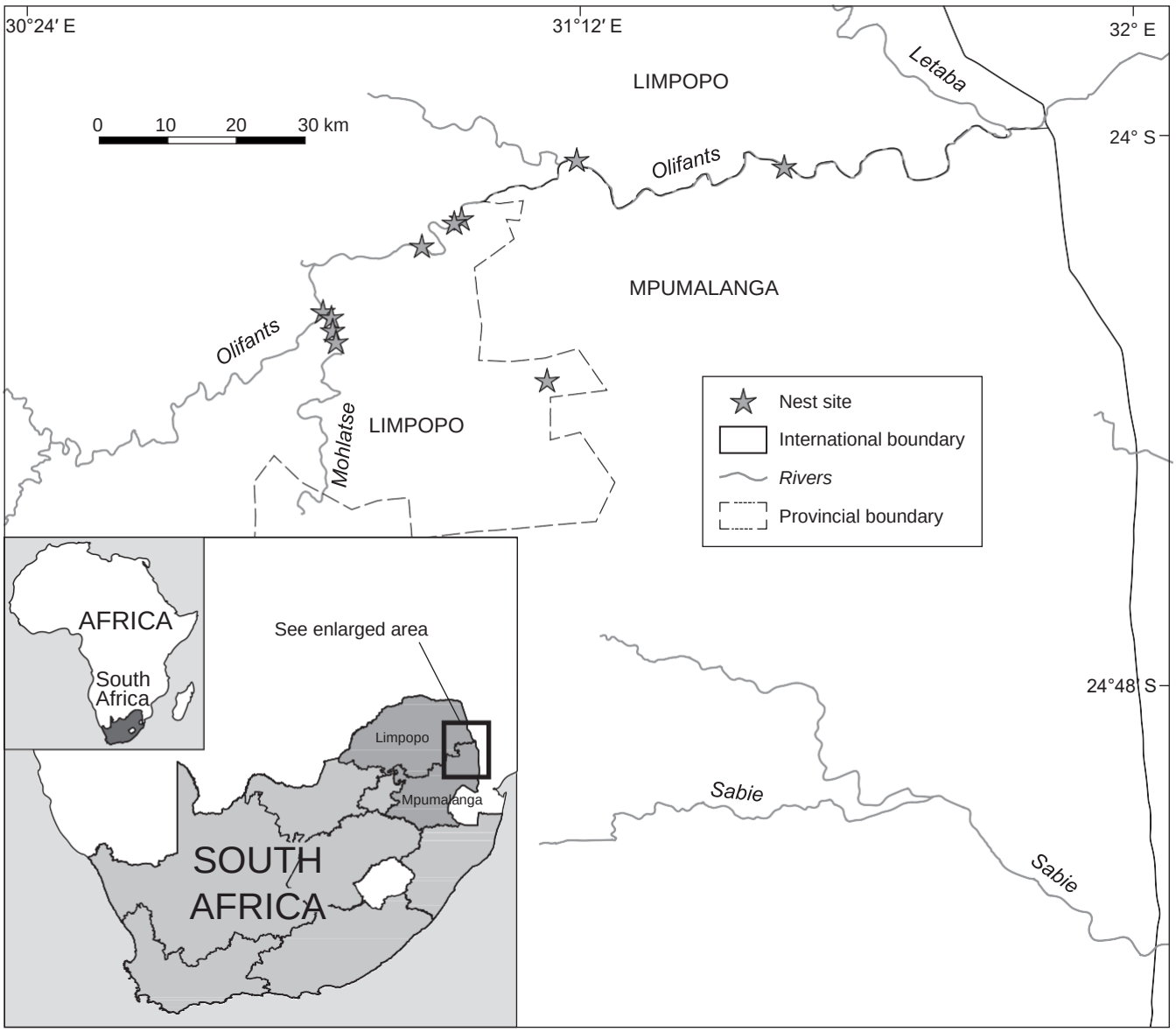

Figure 1: Maps showing (a) the location of South Africa, (b) the provincial boundaries of South Africa, and (c) the location of the Olifants and Mohlatse rivers in Limpopo and Mpumalanga provinces

behavioural data every 5 min, from sunrise until sunset, for 12 h each day, totalling 48 h of behavioural observations.

For ease of recording and analysing data, we used an alphanumeric notation system following Walter (1983). We then described and characterised the observed vulture breeding behaviours.

Results

A total of 416 967 camera trap photographs were taken at the 11 monitored nests, from August 2015 to March 2018 (Thompson et al. 2017a) (Table 1). The ethogram (Table 2) combines results of the camera trap data captured at 11 Hooded Vulture nests (22 adults and 5 chicks), plus four days of sunrise to sunset direct behavioural observations, as well as the authors' knowledge of bird behaviour. We identified at least 28 behaviours that Hooded Vultures exhibit in and around their nest, and classified the behaviours into five discrete categories: Movement, Resting, Body Care, Social, and Nesting (following Walter 1983; Nerlekar et al. 2014) (Table 2; Figures 2–7). All movement behaviours were associated with the motion of the bird (Table 2; Figure 2). Resting behaviours were stationary moments without purposeful activity (Table 2; Figure 3). Body Care activities were maintenance behaviours that ensured the continuing functioning of the body to a healthy standard (Table 2; Figures 4 and 5). Social behaviours were those directed at a conspecific or a potential nest usurper (Table 2; Figure 6). Nesting activities were the behaviours surrounding the maintenance of the nest area and those directed towards an egg or nestling (Table 2; Figure 7).

Discussion

Here, we present the first ethogram for the nesting behaviour of the Hooded Vulture. It is our intention that this ethogram, in which we have defined and described 28 behaviours, will be a useful tool for researchers when they are categorising the breeding behaviours of wild vultures, whether observed in person or remotely using camera trapping or other surveillance technology (Margalida et al. 2010). For example, the thermoregulatory behaviour seen in Hooded Vulture chicks was similar to that seen in Lappet-faced vulture *Trogos tracheliotus* chicks (Shobrak 2001), indicating that at least some nesting behaviours may be similar across vulture species.

The main difficulty when recording behaviours, either remotely or in person, is ensuring a full-body view of the subject; if this is not possible, it can be difficult to discern into which category the behaviour falls. For example, if the bird is lying low in the nest bowl and the head is out of view, it could be either awake and resting, or it could be sleeping, depending on whether its eyes are open or closed (unilateral and bilateral eyelid closure indicate unihemispheric and bihemispheric sleep, respectively: Rattenborg et al. 2001, 2005). Thus, we included an 'Obscured' category for occasions like this, where the obstruction of certain body parts means that a decision cannot be made with the available information. When camera trap photographs are used, a snapshot of behaviour could be ambiguous, with the added complication of the time delay between photographs. This is a limitation of using camera trap photographs rather than continual video recordings, as the researcher is unable to know what occurred in the time between the photographs. For example, if a vulture is seen leaving the nest, it may be doing so to change over with its partner during incubation or in response to a threat from a potential predator in the nest tree, such as by a Chacma Baboon *Papio ursinus* (Thompson et al. 2017a). Sometimes, one can gather additional information by looking at the sequence of photographs before and after an unclear picture; however, determining behaviour in this way necessitates an assumption, which becomes less reliable as the interval between successive photographs increases.

The importance of supplementing behavioural data gleaned from camera trap photographs with data from direct observation is evident from the fact that we did not see either defecation or the regurgitation of a pellet in the photographs, yet we observed both (though infrequently) during our direct observations of Hooded Vultures. This is most likely because defecation is over very quickly, and therefore unlikely to be recorded often on camera trap photographs, particularly when there is a 5-min interval between photographs such as we had. With regards to regurgitation of a pellet, this seems to be a rarer behaviour (it has also been documented in the Turkey Vulture *Cathartes aura*: Paterson 1984), which we have observed only once, and not at a nest. Therefore, we have not included regurgitation of a pellet in our ethogram for Hooded Vulture breeding behaviour, although it can be included at a later stage if it is observed at the nest. We have, however, included defecation in our ethogram because we have observed a Hooded Vulture nestling stand up in the nest and then walk backwards until it was standing on the edge of the nest bowl, where it leaned forward and then defecated so that the excreta was projected out of the nest.

The above-mentioned limitations of our sampling method emanated from a compromise between the photograph quality (file size), frequency with which photographs were taken, and how often cameras needed to be serviced (have the batteries and SD card changed), with the associated disturbance to the breeding birds (Altmann, 1974). To improve the likelihood of capturing brief or rare behaviours at a nest, one could use solar-powered camera traps (with higher-capacity memory cards, set with a shorter interval between photographs) or video recordings. To avoid needing to replace batteries every day or two, the video camera would need to have a cable connected to an electrical power supply, but this could only be done where vulture nests are located very close to human dwellings.

Table 1: Summary data for 11 Hooded Vulture nests in north-eastern South Africa, monitored using camera traps. No. of images = total number of camera trap photographs recorded at each nest; Tree species denotes the common name of the nesting tree in which the camera trap was placed; Subcanopy? = whether or not the nest was positioned within the canopy (rather than on top); Positioned against trunk? = whether or not the nest was placed against the tree trunk. We only recorded tree and nest heights for eight of the nests

Nest	Nest code	No. of images	Tree species	Subcanopy?	Positioned against trunk?	Tree height (m)	Nest height (m)
1	HVn001	27 901	Jackalberry	Yes	Yes	16.1	10.0
2	HVn004	89 419	Sycamore fig	Yes	No (on forked sidebranch)	15.2	9.1
3	HVn005	84 065	Jackalberry	Yes	Yes	15.7	10.4
4	HVn024	75 906	Jackalberry	Yes	Yes	19.7	12.6
5	HVn038	5 395	Jackalberry	Yes	Yes		
6	HVn048	27 455	Jackalberry	Yes	No (high up, in smaller fork)	17.0	15.0
7	HVn052	60 346	Jackalberry	Yes	Yes	13.0	11.0
8	HVn060	10 780	Matumi	Yes	Yes		
9	HVn063	8 969	Matumi	Yes	Yes	15.3	11.1
10	HVn065	21 786	Jackalberry	Yes	Yes	13.9	10.2
11	HVn064	4 945	Jackalberry	Yes	Yes		
Total		416 967			Mean ± standard deviation (*n*):	15.7 ± 2.0 (8)	11.2 ± 1.8 (8)

Table 2: Ethogram of recorded behaviours that Hooded Vultures exhibited in and around their nests. The five behaviour categories used in this study are in bold (following Walter 1983; Nerlekar et al. 2014), plus the category 'Obscured' used when the full-body view of the subject was not dicernable

Behaviour	Description
M. Movement	
M1. Hopping/walking	Locomotion via movement of legs; part of the photograph may be blurred, indicating motion.
M2. Entering nest	Bird arrives via flight and lands on the edge of nest or nearby branch. Camera trap image may be blurred, indicating motion. Bird is usually facing towards nest with the body leaning forward.
M3. Leaving nest	Bird flies out of the nest from the edge of the nest or a nearby branch. Camera trap image may be blurred, indicating motion; the bird is usually facing away from the nest.
M4. Other	Action not clear because of blurred image, but falls within the movement category.
R. Resting	
R1. Perched	Standing stationary on nest, with wings folded close to the body, both eyes are open.
R1.1. Branch	On branch, not in or on nest.
R2. Sitting up in the nest	Body upright at an angle of 45–90° from the base of the nest, wings by side of the body.
R3. Lying down	Breast is in contact with the base of the nest, body is horizontal. Bird is alert with head up and eyes open. There is no egg in the nest at this time.
R4. Sleeping	
R4.1. Front sleep	Can be perched or lying down in nest, motionless, with head held out in front of body, and one or both eyes closed.
R4.2. Back sleep	Can be perched or lying down in nest, motionless, with bill tucked under the scapular feathers.
B. Body care	
B1. Preening	Using beak to clean and fix feathers.
B2. Thermoregulation	Wings held apart from the body while perched or laying down.
B2.1 Panting	Beak is slightly open to enable panting (evaporative water loss): can be done in combination with B2 or separately. Can be distinguished from yawning which lasts only a second or two, while panting lasts longer than that, however the two could be difficult to tell apart with camera trap images (unless consecutive images show the same behaviour, coupled with high temperatures).
B3. Defecation	Standing near the edge of the nest, facing into the nest bowl, with the head and breast leaning down, and the tail lifted up, with excreta possibly seen being expelled.
B4. Ear scratch	Foot lifted up to head.
B5. Stretching	One or both wings outstretched; can be combined with leg stretched out.
B6. Anti-predator behaviour	Adult flies out of nest either because of researcher presence or other perceived threat in the tree or on the ground. Preceding or subsequent photographs (especially those showing predators) lead the observer to conclude that predator avoidance is what is happening here, rather than M3.
B6.1. Chick: Death-feigning	Chick lies down, motionless (other than occasional eye movements), with body and head horizontal to the base of the nest and with beak open and tongue visible, in what may be 'death-feigning' or 'thanatosis', as described in cathartid vultures by Vogel (1950) and Spina and Silveira (2019).
S. Social	
S1. Allopreening	Bird uses beak to preen the feathers of another bird.
S2. Mounting/treading	Male stands on female's back (Cheng and Burns 1988); may precede copulation.
S3. Begging	Chick lies with belly on the base of the nest, body in horizontal position, with head held very low down while looking up at adult. Alternatively, chick may sit in upright position, mouth wide open, towards adult.
S4. Receives food	Beaks of adult and chick are in very close contact and open. Chick is ingesting food from adult.
S5. Provides food	Beaks of adult and chick are in very close contact and open. Adult regurgitates food for chick.
S6. Nest defence	Hooded Vulture is seen on the nest, during the breeding season, with a bird of a different species, where the latter could conceivably use the same stick nest for breeding. There may or may not be physical contact between the Hooded Vulture and the other bird, and the facial skin of the adult vulture may flush pink (e.g. Thompson et al. 2019).
N. Nesting	
N1. Building/repairing nest	New (green) leaves or branches are brought to the nest or else the nesting material is moved around using the beak.
N2. Incubation	Lying on egg, body is horizontal with belly in contact with base of nest, obscuring view of the egg.
N3. Turning egg	Face held low into nest cup with bill touching the egg.
N4. Hatching	A small hole (pipping) or cracks can be seen on the egg, or chick can be seen surrounded by egg shell.
N5. Brooding	Close frontal body contact to facilitate transfer of heat to chick. When chick is less than approximately 2 weeks old, brooding will take the form of laying on chick, as described in N2. This can occur simultaneously with R4.1 and R4.2, but presence of chick must be known for this to be the case.
N6. Shading	Adult shading the chick either with its body, by standing over or with an upright body (perched position) or with both wings outstretched. Adult and chick will be in close proximity or in body contact.
O. Obscured	
O1. Not in view	Not in view: all or part of body not visible.
O2. Unclear photograph	Behavioural category cannot be determined because photograph is blurred due to movement, or the lighting is too bright or too dim.
O3. Face not in view	Used to denote when we are unable to determine whether a bird is sleeping or not, because we cannot see both of the bird's eyes.

Figure 2: Examples of Hooded Vulture movement behaviours at the nests monitored in this study: (a) walking (M1); (b) entering the nest (M2)—note how the body is leaning forward; and (c) leaving the nest (M3). See Table 2 for the description of each behaviour

Figure 3: Examples of Hooded Vulture resting behaviours at the nests monitored in this study: (a, b) perched (R1); (c) chick sitting up in the nest (R2); (d) adult lying down (R3); (e, f) sleeping: front sleep (R4.1) and back sleep (R4.2). See Table 2 for the description of each behaviour

Figure 4: Examples of Hooded Vulture Body Care behaviours at the nests monitored in this study: (a–d) preening behaviour (B1); (e, f) thermoregulation sitting up (B2); (g) thermoregulation lying down (B2); (h) thermoregulation by evaporative cooling through panting (B2.1), which can be determined through direct observation, although by observing this in a photograph we can only record it as 'bill open' (B2.1); and (i) chick death-feigning (B6.1). See Table 2 for the description of each behaviour

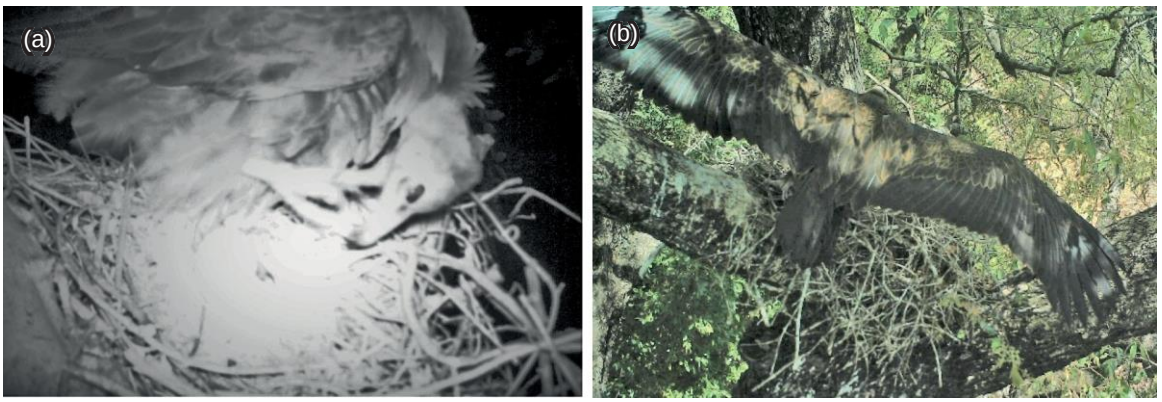

Figure 5: Examples of Hooded Vulture scratching and stretching Body Care behaviours at the nests: (a) ear scratch (B4) and (b) stretching, here with both wings outstretched (B5). See Table 2 for the description of each behaviour

Figure 6: Examples of Hooded Vulture social behaviours at the nests monitored in this study: (a, b) allopreening (S1); (c, d) mounting/treading (S2); and (e) provisioning, with the chick (bottom of photograph) receiving food (S4) and the adult (top of photograph) providing food (S5). See Table 2 for the description of each behaviour

Figure 7: Examples of Hooded Vulture nesting behaviours at the nests monitored in this study: (a, b) building/repairing the nest (N1); (c) incubation (N2); (d) turning the egg (N3); (e) pipping (N4); (f, g) hatching (N4); (h) brooding (N5); and (i) adult shading the chick (N6), with the chick thermoregulating (B2). See Table 2 for the description of each behaviour

For visually inaccessible, cryptic or easily disturbed species, recording technologies are preferred over direct observation (Zuberogoitia et al. 2008). Currently, camera traps are one of the most affordable, easily accessible and easy to use technologies available to researchers. While camera traps can record images continually, day and night, without introducing bias and without affecting the behaviour of the target species, they do have limitations when it comes to analysing data from the images they collect, as mentioned above (Leoni et al. 2020).

To fully understand breeding behaviours, it is important to distinguish between the individuals in a breeding pair. Hooded Vultures are a sexually monomorphic species but can sometimes be differentiated by their facial feathers (Figure 8). If a photograph shows the pair copulating, and if the two individuals have distinguishing features so they can be identified, then both individuals of a pair can be identified and sexed.

We present this ethogram as a tool or guide to assist in making behavioural studies of breeding vultures more comparable between studies and species, by promoting the use of standardised behavioural descriptions. We acknowledge that there is more than one way to record behavioural data for ethological studies; however, we encourage the use of this ethogram (for behavioural studies on breeding Hooded Vultures) to reduce the time required to analyse camera trap photographs to create behavioural definitions, and thereby to ensure that the time spent classifying behaviours is used as efficiently as possible. The next step is for this ethogram to be used to assist in determining the proportion of time for which these various breeding behaviours are observed, at the nests of vultures, and particularly those of Hooded Vultures.

In addition to increasing our understanding of vulture species, behavioural studies on vultures can also yield useful information for conservation marketing, whereby social-marketing strategies are applied to conservation issues with the aim of influencing people's behaviour to benefit biodiversity conservation (Ryan et al. 2020). For example, numerous studies have highlighted the ecological importance of vultures (Ogada et al. 2012b; Hill et al. 2018; Van den Heever et al. 2021), their cultural value (Craig et al. 2018; Boakye et al. 2019; Mashele et al. 2021b) and the economic worth of the ecosystem services vultures provide (Becker et al. 2005; Markandya et al. 2008; Grilli et al. 2019). However, little attention has been paid to the behavioural repertoire of vultures, such as the 'exceptional' copulatory behaviour of certain vulture species (Donázar et al. 1994), the parental care displayed by adult vultures (Maphalala and Monadjem 2017), and how vultures may defend their nest sites against competitors (Thompson et al. 2019). Understanding more about these behavioural aspects could help people better relate to vultures, increase their public appeal, and thereby aid in conservation marketing, and ultimately conservation efforts, for this often maligned group of birds (Mashele et al. 2021b).

Competing interests — The authors declare they have no conflicts of interest to disclose.

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Figure 8: Examples of differing feather growth on the faces of a pair of adult Hooded Vultures at the same nest

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