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ORIGINAL ARTICLE

The effects of weather, group size and type of nest on the timing of egg-laying in the Southern Ground-hornbill *Bucorvus leadbeateri*

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Abstract
The timing of breeding in birds has important consequences if food availability varies seasonally. Optimal timing of the most energetically demanding stages of breeding to coincide with peaks in food availability can increase breeding success. Early breeding may be challenging for females producing eggs, but generally birds initiating egg-laying early in the breeding season are more likely to succeed. Initiating egg-laying later may be less costly to females, but raising offspring after the peak in food availability becomes challenging. Balancing these costs and benefits is important for the cooperative breeding Southern Ground-hornbill *Bucorvus leadbeateri* (hereafter 'Ground-hornbill'), which typically produces only a single clutch of two eggs and fledges a single chick per breeding season. A previous study found that Ground-hornbill groups that lay early in the breeding season are more likely to fledge a chick than later-breeding groups. We investigated factors associated with the timing of breeding such as group size, the type of nest used, rainfall and temperature in a study site supplemented with nest boxes. Ground-hornbills laid eggs from 9 September to 14 November and the average number of days between the first and the last laying date in a season was 48 ± 32 days (range 10–101 days). Larger groups, particularly those using natural nests compared to those using nest boxes, laid later than smaller groups. Egg-laying was delayed under hot, dry spring conditions and laying dates were earlier following above-average spring rainfall.

Keywords Rainfall · Temperature · Early breeding · Breeding success

Zusammenfassung
Die Einflüsse von Wetter, Gruppengröße und Nesttyp auf den Zeitpunkt der Eiablage beim Kaffernhornraben Bucorvus leadbeateri

Wann Vögel brüten, ist wichtig, wenn die Nahrungsverfügbarkeit im Verlauf der Brutsaison schwankt. Die energieaufwendigsten Brutstadien mit der höchsten Nahrungsverfügbarkeit zu synchronisieren, kann den Bruterfolg erhöhen. Eine frühe Brut kann für die eierlegenden Weibchen eine Herausforderung bedeuten, doch generell sind Vögel, die früh in der Saison mit der Eiablage beginnen, mit höherer Wahrscheinlichkeit erfolgreich. Ein späterer Legebeginn kann für die Weibchen mit geringeren Kosten verbunden sein, aber die Küken erst aufzuziehen, wenn die Nahrungsverfügbarkeit bereits abnimmt, ist schwierig. Die richtige Kosten-Nutzen Balance zu finden, ist wichtig für den kooperativ brütenden Kaffernhornraben Bucorvus leadbeateri, welcher pro Brutsaison normalerweise nur ein einziges aus zwei Eiern bestehendes Gelege und ein flügges Küken produziert. Eine vorherige Studie fand, dass früh in der Brutsaison legende Kaffernhornraben-Gruppen mit höherer Wahrscheinlichkeit ein flügges Küken produzierten als später legende Gruppen. Wir haben mit dem Brutzeitpunkt assoziierte Faktoren wie Gruppengröße, Nesttyp, Regen und Temperatur in einem mit Nistkästen ausgestatteten Studiengebiet untersucht. Kaffernhornraben legten vom 9. September bis zum 14. November, und der durchschnittliche Unterschied zwischen erstem und letztem Legedatum betrug 48 ± 32 Tage (Variationsbreite 10-101 Tage). Größere Gruppen legten später als kleinere, besonders wenn sie in natürlichen Nisthöhlen und nicht in den Nistkästen brüteten. Die Eiablage war bei heißem, trockenem Frühlingswetter verzögert und erfolgte früher nach überdurchschnittlichen Frühlingsregenfällen.

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Introduction

Timing of breeding (laying date) has important consequences for the likelihood of a successful nesting attempt (Daan et al. 1989) and survival to breeding age of offspring (Perrins 1970). For many bird species, nests initiated in the first half of the breeding season are more likely to fledge a chick and have offspring that survive to the next season than breeding attempts initiated later in the breeding season (Perrins 1970; Daan et al. 1989; Verhulst and Nilsson 2008). Changes in environmental conditions due to climate change have affected the timing of breeding in many bird species, with mostly negative consequences (Dunn and Winkler 2010). However, most of the studies discussed by Dunn and Winkler (2010) were on passerines in the highly seasonal northern temperate zone, with fewer focused on the effects of environmental conditions on breeding phenology across a wider geographic scale.

In areas where food availability peaks predictably on a seasonal basis there are costs and benefits of both early and late breeding. Early breeders have a higher likelihood of success, possibly due to access to better forage (Saunders 1982), but producing eggs early can be costly (Perrins 1970; Williams and Rabenold 2005). In contrast, producing eggs later in the season may be less costly, but the risk of chicks hatching after the peak in food availability is greater (Perrins 1970). This has even been found in the tropics, where seasonality is limited (Poulin et al. 1992). The timing trade-offs are particularly important for species that produce only a single brood per season, where each nesting attempt represents the total seasonal reproductive investment (Svensson 1995). Given that the timing of breeding could mean the difference between a successful and a failed breeding season, there should be strong selection for birds to use environmental cues to select the most beneficial time to breed.

Timing of breeding in birds has been linked to triggers such as changes in photoperiod (Wikelski et al. 2000; Hau 2001; Trivedi et al. 2006), ambient temperature (Visser et al. 2009), rainfall (Zann et al. 1995; Lloyd 1999; Hau 2001; Saunders et al. 2013) and the combined effects of temperature and rainfall on food availability (Sinclair 1978; Perrins 1991; Eeva et al. 2000). Proximate and ultimate factors influencing the timing of breeding are well recognised for northern hemisphere, temperate bird species (Perrins 1970, 1991; Daan et al. 1989). For most species, these factors act in a hierarchy (Dunn and Winkler 2010), with photoperiod as the primary cue setting off the neuroendocrine cascade (Hau 2001), even in the tropics where there is less variation in day length between seasons (Hau 2001). Additional cues used to determine the timing of egg-laying are largely secondary to photoperiod, such as rainfall, temperature and food availability (Moreau 1950; Lloyd 1999).

In the southern hemisphere, temperature and precipitation play key roles in phenological changes (Chambers et al. 2013). In southern Africa, numerous factors have been suggested to control the timing of breeding, including day length, temperature, rainfall and its effect on food supply, as well as the occurrence of fires and regenerating vegetation (Moreau 1950; Brown and Brown 1984; Little and Crowe 1993; Lloyd 1999).

In addition to environmental cues, the type of nest used (Brazill-Boast et al. 2013) and female age and/or condition (Sydeman et al. 1991; McCleery et al. 2008; Low et al. 2015) can affect the timing of breeding. Among cooperative breeding species, the breeding group size or the number of helpers to provision nestlings can also influence the timing and success of breeding (Heinsohn 1992; Woxvold and Magrath 2005; Doerr and Doerr 2007). Different species-specific requirements for nesting under varying conditions likely provide the stimulus for and affect the timing of breeding (Thomson 1950).

Southern Ground-hornbills *Bucorvus leadbeateri* (hereafter 'Ground-hornbills') are the world's largest cooperative breeding bird and are a flagship species of the African savanna biome. Ground-hornbills occur in north-eastern South Africa, and the entire South African population is estimated to be 1290–2380 individuals, and declining (Taylor and Kemp 2015). They typically nest in natural tree cavities and readily occupy nest boxes (Wilson and Hockey 2013; Carstens et al. 2019). They have an expected life span of up to 50 years and reach maturity at 4–6 years (Kemp 1990). They live in groups of from two to 11 individuals comprising a breeding pair (alpha female and dominant male), non-breeding sub-adults (mostly male helpers) and immature individuals (Kemp 1990). Groups are territorial and occupy large home ranges (70–100 km^2) year-round (Wyness 2011; Kemp and Kemp 1980). They fledge on average only one chick every 2–9 years (Kemp 1990). Ground-hornbills feed on a wide array of prey including insects, snails, reptiles, amphibians, birds (including eggs and chicks) and small mammals (Kemp 2005). Young chicks in the nest are fed mostly on arthropods (Kemp 1976).

In South Africa, Ground-hornbills breed during the austral spring and summer (September–March) and typically only one breeding attempt is made each season (Kemp 2005). The nesting period lasts ~ 130 days, with 42 days for incubation and 87 days for the nestling period (Kemp and Kemp 1980). Breeding females generally lay two eggs 3–14 days apart, but only one chick (usually the first hatched) is raised to fledging. With time and energy focussed on a single breeding attempt per season, timing the onset of egg-laying to maximise the likelihood of success is crucial to achieve maximum fitness benefits. Timing of breeding by Ground-hornbills generally coincides with spring rains, and food availability is considered an important factor (Kemp and Kemp 1991). However, it remains to be tested what the effects of other climatic and social factors are. We investigated how group size, the type of nest used, temperature and rainfall affect the timing of the onset of breeding in an area supplemented with nest boxes.

Methods

This study took place in the Associated Private Nature Reserves (area 1800 km^2, centre 24.16°S, 31.18°E) in north-eastern South Africa. The study area has distinct wet (October–March) and dry (April–September) seasons with a mean annual rainfall of 501 ± 197 (113–905 mm). Altitude ranges from 300–500 m a.s.l. Daily mean minimum and maximum temperatures range seasonally between 10–20 °C in winter and 20–33 °C in summer. The geomorphology is undulating with rocky outcrops in the north and flat grassy plains in the south. The vegetation varies from open savanna to closed woodland (van der Waal 2010).

Ground-hornbills nested in both natural tree cavities and nest boxes in the study area. During the spring and summer of 2000–2015, thirty-one nest boxes and 13 natural tree cavity nests were checked every 7–10 days for signs of nesting activity. The frequency of nest visits was minimised to reduce potential predation risk induced by human presence, but was regarded as sufficiently frequent for the precision required to estimate the timing of egg-laying. Laying dates were not available for 2008 and 2009. A full, fresh lining of leaves (typically of mopane *Colophospermum mopane*) indicated that egg-laying was imminent. When one egg was found, the nest was re-visited after 5 days to check for the presence of a second egg. Laying date was estimated as the middle date between the day on which an egg was first discovered and the previous nest check. We are aware that using the middle date leaves room for error of up to ± 5, but precision of these data is not of concern, particularly when taking into account the variance in laying dates. Laying date was recorded as the number of days after 1 September (the start of spring) when the first egg was laid.

Daily temperatures were available for the town of Hoedspruit, 20 km west of the study site. Mean daily temperatures were the mid-point between the minimum and maximum. Rainfall was available from 14 rain gauges scattered throughout the study site. Rainfall estimates for each group's home range were taken from the nearest rain gauge, which were situated on average 5 ± 3 km (SD; range 1–11 km) from each nest. Group sizes were recorded annually during 1998–2015, except for 2008 and 2010, when group size was not recorded.

Statistical analyses

A linear mixed-effects model [package lme4 (Bates et al. 2015)] using laying date data for 23 groups during 2000–2015 ($n = 134$) was performed using the software programme R [version 3.03 (R Core Team 2014)]. Data exploration was carried out following the protocols described in Zuur and Ieno (2016). Laying day (continuous; the number of days after 1 September on which the first egg was laid) was modelled as a function of group size (discrete, sizes of groups ranged from 2–8 individuals), nest type (binary; natural tree cavity nest or artificial nest box), spring rainfall (millimetres; continuous, summed over September–November), winter rainfall (millimetres; continuous, summed over June–August), previous year's rainfall (millimetres; continuous, summed over July–June), spring temperature (degrees Celsius; continuous, mean daily temperature recorded during September–November), winter temperature (degrees Celsius; continuous, mean temperature recorded during June–August) and the number of hot spring days (discrete; the number of days in spring when the maximum daily temperature was above 30 °C). We included a random intercept for group identity (categorical). Three biologically relevant interactions were considered: group size × nest type, to investigate whether small or large groups occupying nest boxes lay earlier or later than groups of the same size using natural nests; spring rainfall × spring temperature, to investigate whether warm, wet springs affect the timing of egg-laying; and winter rainfall × winter temperatures, to investigate whether warm, wet winters affect egg-laying. All continuous variables in the models were standardised to zero mean and unit SD. Model fit was verified using plots of residuals against fitted values and residuals versus each explanatory variable used in the full model. A histogram of residuals confirmed a normal distribution. Variables were checked for collinearity by calculating variance inflation factors (VIF) in the car package (Fox and Weisberg 2011); all variables had a VIF < 3. A global model was created using all terms of interest, as well as the three biologically relevant interactions. A reduced model was created by removing each variable that had a *p*-value > 0.05; the estimates and *p*-values from this model are presented together with the values for the global model. Confidence intervals (CI 95%) for each parameter were obtained using Wald's approximation (Wald 1947). The marginal and conditional R^2-values for mixed-effect models (R^2_m and R^2_c, Nakagawa and Schielzeth 2013), were computed using piecewiseSEM to estimate the percentage variation in the model explained by fixed effects (R^2_m) and both random and fixed effects (R^2_c). We used a likelihood ratio test to determine if fixed effects collectively explained variation in laying dates. The presentation of variable effects from the model outside of the table focussed on the relationships where there is strong evidence of an effect (low *p*-values) and the magnitudes of the effects are not ecologically irrelevant. Averages are given ± 1 SD.

Results

Laying dates were recorded for 23 groups comprising, on average, 4 ± 1 individuals (range 2–8 individuals; *n* = 31 groups) during 2000–2015 (*n* = 134 group-years). Ground-hornbills displayed considerable variation in the timing of laying between seasons (Fig. 1). Mean laying date was 7 November, 66 ± 20 days after 1 September (range 8–134 days). Median laying date was 3 November. The average number of days between the first and the last nest to become active in a season was 48 ± 32 days (range 10–101 days; Fig. 1). Egg-laying started from as early as 9 September (in 2014) to as late as 14 November (in 2003). There was no change in the mean laying date over time ($r = 0.11$, $P = 0.18$). An average of 57 ± 18% (25–86%) of all known groups did not breed each year.

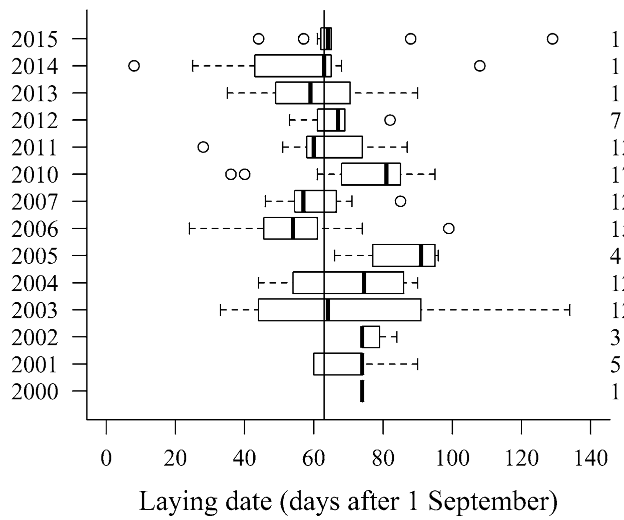

Fig. 1 Timing of egg-laying by Southern Ground-hornbill *Bucorvus leadbeateri* groups across 14 breeding seasons in north-eastern South Africa. Data for 2008–2009 not available. Vertical line at day 63 indicates the median laying date of 3 November. Sample sizes are given on the right

Of the 134 laying dates, 104 were recorded for nest boxes and 30 for natural tree cavity nests. Mean spring rainfall was 101 ± 54 mm (range 28–277 mm), mean winter rainfall was 73 ± 45 mm (range 0–173 mm) and mean rainfall over the previous year was 487 ± 147 mm (range 237–948 mm). The mean temperature during spring was 23 ± 0 °C (range 22–24 °C) and during winter 18 ± 1 °C (range 16–20 °C). On average, there were 43 ± 5 hot spring days each breeding season (range 34–51 days).

The timing of breeding in Ground-hornbills was associated with group size and its interaction with the type of nest used (Table 1). The impact of group size was 8.83 for groups using natural cavities, and 2.25 (8.83–6.58; 95% CI 2.20–15.33) for groups using nest boxes (Table 1). Nest boxes moderated the impact of group size ($P = 0.05$) on the timing of breeding: regardless of group size, laying dates of groups occupying nest boxes did not differ. However, when comparing groups of the same size, the type of nest used had an effect on the laying date. Groups of average size or larger using nest boxes laid earlier than groups of the same size that used natural nests (6 days earlier for groups of four individuals, and 21 days earlier for groups of six individuals). However, pairs using nest boxes laid 11 days later than pairs using natural nests.

Table 1 Linear mixed-effects models investigating how social and environmental variables influenced laying dates of Southern Ground-hornbills

Fixed terms	Full model				Reduced model			
	Est. (95% CIs)	SE	*t*-value	*p*-value	Est. (95% CIs)	SE	*t*-value	*p*-value
(Intercept)	69.09 (60.95, 77.25)	4.17	16.58	0.00	70.03 (62.37, 77.71)	3.89	18.03	0.00
Grp size	8.83 (1.53, 16.10)	3.87	2.28	0.02	8.60 (1.39, 15.82)	3.75	2.29	0.02
Nest.Nest box	− 6.58 (− 15.33, 2.20)	4.53	− 1.45	0.15	− 7.15 (− 15.70, 1.38)	4.36	− 1.64	0.10
$Rain_{spring}$	0.01 (− 0.06, 0.08)	0.04	0.21	0.83	0.0034 (− 0.06, 0.07)	0.03	0.10	0.92
T_{spring}	6.60 (− 4.20, 17.31)	5.70	1.16	0.25	8.20 (0.45, 16.13)	4.06	2.02	0.04
$Rain_{previous\ year}$	− 0.02 (− 0.04, 0.01)	0.01	− 1.25	0.21				
$Rain_{winter}$	0.03 (− 0.06, 0.12)	0.05	0.60	0.55				
T_{winter}	0.58 (− 4.90, 6.16)	2.92	0.20	0.84				
No. hot spring days	− 0.13 (− 1.15, 0.90)	0.54	− 0.24	0.81				
Grp size × Nest. Nest box	− 8.01 (− 15.73, − 0.36)	4.08	− 1.96	0.05	− 7.97 (− 15.69, − 0.36)	3.98	− 2.00	0.05
$Rain_{spring} \times T_{spring}$	− 0.16 (− 0.31, 0.0003)	0.08	− 1.97	0.05	− 0.14 (− 0.27, − 0.003)	0.07	− 2.01	0.04
$Rain_{winter} \times T_{winter}$	− 0.04 (− 0.11, 0.06)	0.05	− 0.83	0.41				

Data include laying dates for 23 breeding groups during 2000–2015 (*n* = 134 group-years). $R^2_m = 0.12$, $R^2_c = 0.18$ (see "Methods" for details)

Est. Estimate, *Grp*. group, *Nest*. nesting, *T* temperature

The effect of increasing average spring temperature on the timing of breeding varied under different rainfall scenarios (Table 1). Under average to relatively dry spring rainfall conditions, rising average spring temperatures delayed laying dates. However, during a relatively wet spring, laying dates advanced with rising spring temperatures. Specifically, at the average spring rainfall (101 mm), an increase in mean spring temperature of 1 °C delayed the average laying date by 7 days, and up to 15 days under relatively dry spring conditions (50 mm). However, in a breeding season that began with above-average spring rainfall (200 mm) laying dates were advanced by 9 days for every 1 °C increase in average spring temperature.

Group effects explained 7.2% of the variation in laying dates (random effects in the full model: group variance 26.92, SD 5.19; residual variance 344.73, SD 18.57). For every unit change in the number of hot spring days there was a 0.31 (1.15 to 0.90, $P = 0.81$) change in the average laying date. For every unit change in the total rainfall over the previous year, there was a 0.02 (0.04 to 0.01, $P = 0.21$) change in the average laying date.

Discussion

Studies from southern Africa suggest that day length, temperature, rainfall and its effect on food availability, as well as grass fires and resurgent green vegetation are factors affecting the timing of breeding in birds (Moreau 1950; Little and Crowe 1993; Lloyd 1999). In Australia, autumn rains act as a cue for the commencement of egg-laying in the endangered Carnaby's Cockatoo *Calyptorhynchus latirostris* (Saunders et al. 2013). For Ground-hornbills, timing of egg-laying in natural nests in the Kruger National Park, South Africa, was not affected by rainfall during the dry season or during the previous wet season (Kemp and Kemp 1991). Our results corroborated this finding, i.e. the timing of egg-laying was not explained by previous rainfall events, either during the dry season leading up to the breeding season or during the previous year. Rather, we found that both group size and its interaction with nest type, as well as spring weather conditions, affected the timing of breeding. Larger groups started egg-laying later, particularly groups using natural nests. In addition, the timing of breeding was delayed during dry, hot spring weather conditions.

The effects of group size and nest type used on the timing of breeding in Ground-hornbills are complex. Overall, group size had a greater effect on the timing of breeding for groups using natural nests than groups using nest boxes. In addition, timing of breeding differed among groups of the same size depending on nest type used. These differences in timing of breeding may be due to breeding experience (Sydeman et al. 1991) and the effect of learning on the timing of breeding (Grieco et al. 2002). It is reasonable to assume that many of the Ground-hornbill groups occupying territories with natural nests have more breeding experience than newly formed groups occupying territories with only a nest box available (Carstens et al. in press). The decline in breeding success as the breeding season progressed could be due to difficulties in finding food for the growing chick, as food supplies diminish towards the end of the breeding season (Kemp 1976). This is supported by failures in nests initiated late in the season occurring when chicks were older compared to the age of chicks when early nests failed (Carstens et al., in press). More experienced groups should therefore be better able to time the onset of breeding depending on social and environmental factors. However, this would be especially difficult for groups lacking helpers, where only the breeding pair provision the chick. Therefore, although raising chicks may be more difficult later in the season, larger groups appeared less constrained by later breeding.

Ground-hornbills delayed egg-laying during warmer springs, which is contrary to the general avian trend (shown in studies predominantly of north-temperate species) indicating that warmer spring temperatures typically promote earlier laying (Dunn 2004). Studies of the effect of temperature in the southern temperate region remain sparse. However, one such study supports the northern hemisphere trend in a southern hemisphere species, where warm temperatures advanced laying in the cooperative breeding Sociable Weaver *Philetairus socius* in the southwest African arid zone (Mares et al. 2017).

Egg-laying in Ground-hornbills may have been delayed by warmer temperatures due to food supply. In the savannas, hotter springs can limit food availability if higher temperatures cause the vegetation to dry out, resulting in a rapid decline in insect abundance (Koenig and Mumme 1987), especially in the phytophagous insect groups (Denlinger 1980) that form a large part of the Ground-hornbill nestling diet (Kemp 1976). This idea was supported by laying dates being particularly delayed under the combined conditions of warmer, drier springs. Any decline in, or low levels of, food availability experienced by Ground-hornbills, or low levels of food intake due to hot, dry conditions, might act as a cue to delay breeding due to the anticipation of harsher conditions in which to raise chicks than due to costs of egg production, which for Ground-hornbills are relatively small. The mean Ground-hornbill egg volume (95 ml for both the first egg and second egg; personal observations) and the mean clutch volume for two eggs (190 ml; personal observations) was less than a third of the value predicted by body mass (Watson et al. 2015). Indeed, some groups started egg-laying despite no prior spring rainfall, which might be expected to delay egg production if eggs are costly to produce.

Two findings support the importance of rainfall as a trigger for food availability, and hence the timing of breeding. First, a correlation between Ground-hornbill laying date and the start of the rainy season at various latitudes (0–32°S; Kemp 1976). Second, captive Ground-hornbills with stable food supplies lay out of season during the cold, dry winter months (Gunn and Meyer, personal communication). Declines in food availability towards the end of summer may place an unpredictable constraint on laying dates (Kemp 1976). The Ground-hornbill breeding cycle is relatively long (4 months), more than half of the 7-month breeding season (September–March). Therefore, unlike species that have a short breeding cycle relative to their breeding season and that can wait until various conditions are met before laying, or even have multiple broods if time and resources allow, Ground-hornbills are constrained by the length of their breeding cycle to produce a single brood and ensure that their chick fledges before the commencement of the dry season. If first breeding attempts fail, second attempts are rare (Carstens et al., in press), even if the failure occurs early in the breeding season. If attempted too late, a group with a chick that only fledges well into autumn would find it harder to provision the fledgling as feeding resources diminish into the dry season (Kemp 1976). Therefore, like north-temperate insectivorous species, food supply is an important consideration for Ground-hornbills in the southern sub-tropics.

Our investigation of differences in laying dates suggests that there is some group-specific effect on laying dates, based on the percentage of variation explained by group effects as a random variable. Data on alpha-female-specific characteristics might help us to understand which traits might influence the timing of breeding in Ground-hornbills, such as the breeding female's age and breeding experience (Sydeman et al. 1991; Saunders et al. 2016), and physical condition (Low et al. 2015), foraging ability or provisioning of the group (Goutte et al. 2010), or the need to avoid bad weather, such as storms, during incubation (Turner 1982).

Considering that north-eastern South Africa has experienced a cooling trend since 2000, with reduced precipitation (Cunningham et al. 2016), can Ground-hornbills track the cooling conditions by laying earlier or alternatively track the drier conditions by laying later? Furthermore, what might the long-term implications of this be when taking into consideration climate change and the potential mistiming between avian reproduction and peaks in food supplies (Both et al. 2004; Visser et al. 2009; Møller et al. 2010)? To answer these questions for Ground-hornbills, future research should attempt to assess seasonal food availability for this species.

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Compliance with ethical standards

Ethical approval All fieldwork was carried out in accordance with the ethical standards of the University of Cape Town (ethics protocol 2016/v2/PR).

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