

Double-brooding in Southern Yellow-billed Hornbills *Tockus leucomelas*

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Double-brooding is an avian breeding strategy where birds produce at least two successful nests in a single season. Double-brooding is seen most frequently in small passerines for which the breeding season is lengthy enough that they can easily fit in multiple nesting attempts. Such a pattern of breeding is therefore less common among large birds with long incubation periods and slow offspring development. In the case of hornbills (Family Bucerotidae), double-brooding would be unexpected for not only these reasons, but also due to the fact that the females of nearly all hornbill species exhibit a synchronous moult of flight feathers immediately following clutch completion. Double-brooding would thus require not only an exceptionally long breeding season, but also that females undergo two very costly flight feather moults in a single season. Here we describe the double-brooding of 10 individual female Southern Yellow-billed Hornbills (*Tockus leucomelas*) in a single Namibian population during the 2019/2020 breeding season. Because the breeding cycle of Yellow-billed Hornbills lasts three months, double brooding requires that conditions remain appropriate for breeding for more than half the year, a stringent requirement in a relatively arid country. Our analysis demonstrates that double-brooding is not a response to either small spring brood sizes or the disappearance of fledglings and appears not to be limited to females of above-average mass. Rather, we found that double-brooding is most common among females who initiated their spring nest early and appears to be associated with wetter-than-average years.

Double couvaison chez le Calao leucomèle *Tockus leucomelas*

La double couvaison est une stratégie de reproduction des oiseaux qui consiste à produire au moins deux nids réussis en une seule saison. La double couvaison se rencontre le plus souvent chez les petits passereaux dont la saison de reproduction est suffisamment longue pour qu'ils puissent facilement s'adapter à plusieurs tentatives de nidification. Un tel mode de reproduction est donc moins fréquent chez les grands oiseaux avec de longues périodes d'incubation et un développement lent de la progéniture. Dans le cas des calaos (famille des Bucerotidae), une double couvaison serait inattendue pour ces raisons, mais aussi parce que les femelles de presque toutes les espèces de calaos présentent une mue synchrone des plumes de vol immédiatement après la fin de la ponte. La double couvaison nécessiterait donc non seulement une saison de reproduction exceptionnellement longue, mais aussi que les femelles subissent deux mues très coûteuses des plumes de vol en une seule saison. Nous décrivons ici la double couvaison de 10 individus femelles de calao leucomèle (*Tockus leucomelas*) dans une seule population namibienne pendant la saison de reproduction 2019/2020. Comme le cycle de reproduction de *T. leucomelas* dure trois mois, la double couvaison exige que les conditions restent appropriées pour la reproduction pendant plus de la moitié de l'année - une exigence rigoureuse dans un pays relativement aride. Notre analyse démontre que la double couvaison n'est pas une réponse à la petite taille des couvées printanières ni à la disparition des oisillons et ne semble pas se limiter aux femelles de masse supérieure à la moyenne. Nous avons plutôt constaté que la double couvée est plus fréquente chez les femelles qui ont commencé leur nid de printemps tôt et semble être associée à des années plus humides que la moyenne.

Keywords: breeding cycle, molt, Namibia, two nests, wet season

Introduction

Double-brooding (aka Facultative Multiple Breeding *sensu*; Verhulst et al. 1997; Verhulst 1998) is an avian breeding strategy where some birds within a population produce at least two successful nests in a single season (Geupel and Desante 1990; Fargallo et al. 1996; Bennet and Owens 2002; Jamieson 2011; Jacobs et al. 2013; Carro et al.

2014; Hoffmann et al. 2015). Double-brooding is seen most frequently in small passerines that suffer high rates of both annual mortality and nest predation and for which the breeding season is lengthy enough that they can fit in multiple nesting attempts (Lack 1954; Verhulst et al. 1997; Verhulst 1998; Bennett and Owens 2002; Carro et al.

2014). Such a pattern of breeding is therefore less common among large, long-lived birds with lengthy incubation periods and slow offspring development (Newton 1979), but see Curtis et al. (2005) and Beziers and Roulin (2015). In the case of hornbills (Family Bucerotidae), double-brooding is unexpected for multiple reasons. Not only are these large-bodied birds with extremely slow chick development (Kemp 1995), but the unusual nesting habit of nearly all members of this Family involves the female sealing herself inside a nest cavity (Kemp 1995) and undergoing a synchronous moult of her flight feathers immediately following clutch completion (Kemp 1995; Stanback et al. 2018). She then spends the remainder of the incubation period and a large part of the lengthy chick-rearing period regrowing flight feathers (Kemp 1995; Mills et al. 2005; Stanback et al. 2018). Given that moult is considered to be one of the more expensive components of the annual cycle of birds (Newton 2009; Kjellen 2015), completing two flight feather moults back-to-back would not only be extremely expensive, it also runs counter to the temporal biology of avian moult (Humphrey and Parkes 1959; Newton 2009; Kjellen 2015). Indeed, the only species known to undergo two moults per year are small passerines that live in abrasive vegetation that causes significant feather wear (Newton 2009; Kjellen 2015). Such species include the Willow Warbler *Phylloscopus trochilus* (Underhill et al. 1992), Bobolink *Dolichonyx oryzivorus* (Renfrew et al. 2011) and Marsh Wren *Cistothorus palustris* (Kroodsma and Verner 2020).

Additionally, because the breeding cycle of most hornbills is unusually lengthy (typically at least three months) (Kemp 1995; Mills et al. 2005; Stanback et al. 2018), double-brooding would require that conditions remain appropriate for breeding for more than half the year. Although most hornbills live and breed in the tropics (Kemp 1995), low latitude is no guarantor of a lengthy breeding season. Many tropical regions are quite seasonal, with breeding typically occurring only at particularly favourable times. In southern Africa, breeding for most birds corresponds to the wet (summer) season (Maclean 1970, 1974; Immelmann 1973; Lloyd 1999; Dean et al. 2009; Brown et al. 2014); conditions typically do not remain ideal for breeding for long periods of time. In summary, given the length of the hornbill breeding cycle, the incorporation of the female's annual flight feather moult into the nesting cycle, the costs imposed on the male during breeding, and the typically narrow time-frame available for breeding in southern Africa, it is perhaps not surprising that African hornbills typically breed only once per year.

Despite its improbability, there have been anecdotal accounts of female hornbills double-brooding. For example, in north-central Namibia, MTS observed several Southern Yellow-billed Hornbill *Tockus leucomelas* chicks fledge from a nest box in early February 2017. On 18 February MTS observed a female copulating with a male and also pecking at the remaining nest plug material on the nest box from which the chicks had recently fledged. On 24 February, the female entered the box and produced a clutch of eggs and eventually a brood of young. Although we did not have access to the contents of this nest and were unable to determine with complete confidence that

this was the same female and male, the presence of fledglings from the first nest suggests it was.

Other observers have been able to more clearly demonstrate double-brooding in an African hornbill. Brown et al. (2014) observed a ringed African Grey Hornbill *Lophoceros nasutus* that fledged chicks from a nest box in late 2013 and found her in a new (and ultimately successful) nest in the same nest box in early 2014 at a site near Windhoek, Namibia. H. Bohme (pers. comm.) observed double-brooding by a ringed Southern Yellow-billed Hornbill at the same site in the 2019/2020 breeding season. Both the 2013/2014 and the 2019/2020 breeding seasons were characterised by above-average rainfall.

Here we report on double-brooding by a total of 10 female Southern Yellow-billed Hornbills during the 2019/2020 breeding season in north-central Namibia and investigate some of the possible reasons that these, but not other monitored females, engaged in this behaviour. In particular, we examine the roles of female quality, rainfall, and the timing of nesting.

Materials and methods

The Southern Yellow-billed Hornbill (Family Bucerotidae) is a common hornbill of the southern African bush. This species readily uses nest boxes at our study site in north-central Namibia, an area characterised as Thornbush Scrubland (Mendelsohn et al. 2010). Over the past four years MTS has installed approximately 200 nest boxes along service roads on a 7 000 ha farm managed by the Cheetah Conservation Fund (CCF) (20°29'14" S, 17°02'03" E). The study site is located between the city of Otjiwarongo and the Waterberg Plateau National Park. The nest boxes vary substantially: some are made of plastic, some are made of wood planks (Brown et al. 2014), some are made of plywood (Stanback 2020); some are erected vertically, some horizontally. All box types are found in all parts of the study area. In all four years of the study, Yellow-billed Hornbills nested in each type of nest box; there was no noticeable difference in the timing of nests in each type of nest box. Because of the small stature of the vast majority of trees in the area, boxes are installed approximately 1.5 m off the ground. All boxes have entrance holes with a diameter of 60 mm, large enough to be used not only by Yellow-billed Hornbills, but also by the substantially larger Monteiro's hornbills *T. monteiri*. We monitored nest boxes approximately every three days.

Although we lack direct measurements of food availability for hornbills, other work in southern Africa has demonstrated that annual spring/summer rainfall has a profound effect on resource availability and subsequent breeding by birds (Maclean 1970, 1974; Immelmann 1973; Lloyd 1999; Dean et al. 2009; Brown et al. 2014). Although the degree to which hornbill breeding is limited by nest sites vs resources is beyond the scope of this paper, we can address how rainfall over the past several years has affected the breeding of hornbills in our nest boxes, which are provided in excess.

We have observed three species of hornbills breeding in the nest boxes at CCF: the Yellow-billed Hornbill, the Monteiro's Hornbill and the Damara Hornbill *T. damarensis*.

The Yellow-billed Hornbill is thought to have a bimodal breeding season, with the first peak of nest initiations occurring before or during the ‘small rains’ in October/November, with a second peak in January/February, following the ‘big rains’ (Brown et al. 2014). However, the extent to which this second peak of breeding is the result of double-brooding is unclear. Both Monteiro’s and Damara Hornbills generally wait until after substantive rains (in December and January) have resulted in considerable plant growth. For all hornbill species, we ringed unringed females (and read rings on ringed females) as soon as they had undergone their post-oviposition moult (Stanback et al. 2018). In some cases, we were able to read rings prior to the completion of egg-laying. We weighed and measured all females immediately after their post-oviposition moult and periodically throughout the chick-rearing stage (with a final set of measurements within three days of their departure from the nest).

We measured precipitation at the study site using two independent methods. CCF has monitored multiple rain gauges for years. However, because of some irregularities in the collection of these data, we also sought an alternative method for quantifying rain at the study site. CHIRPS (Climate Hazards Group InfraRed Precipitation with Station data) was created in collaboration with scientists at the USGS Earth Resources Observation and Science (EROS) Center to produce rainfall maps, especially in areas where surface data is sparse (Funk et al. 2015). CHIRPS evaluate satellite cloud data to estimate rainfall. We present 25 years of CHIRPS rainfall data and 25 years of CCF rain gauge data (Table 1).

Results

In late 2019, more than 50 pairs of Yellow-billed Hornbills bred in nest boxes at the CCF study site. Because some of these spring nest females and/or boxes were unavailable for summer/second nests (because of predation of the first nest and damage to the nest box after the fledging of the first brood), we restricted our analysis to those 43 females for whom a second nest in the same box was a possibility. Of these 43, 10 females had actually double-brooded. Nine of these re-entered the same nest box from which they fledged their first brood; one female moved from her original box to a new box installed approximately 200 m away (installation occurred while the chicks were still in the first nest). In fact, of the 11 Yellow-billed Hornbill nests initiated after 1 January 2020, 10 were by double-brooding females. The 11th was either a very late-nesting female, a female re-nesting after nest failure in a natural cavity, or a double-brooding female whose first nest was in a natural cavity (the nest box she used was installed in January 2020).

For the 10 females known to have laid a second clutch, the latest date that the last chick emerged from the first nest was 15 February 2020. If we assume that the timing of the emergence of the last chick represents some sort of limit on the lateness that a female would be willing to enter a cavity for another nest attempt, we can assign 15 February 2020 as the date beyond which a second nest is particularly unlikely. Of the 43 females we considered in this analysis, 23 had their last chick emerge after 15 February 2020 and 20 had their last chick on or before 15 February 2020.

Table 1: Annual estimated CCF rainfall (breeding season): CHIRPS and rain gauge (1995–2020) 2020). SEM = Standard Error of the Mean

Years	Spring rain (mm) CHIRPS	Total rain (mm) CHIRPS	Number of CCF rain gauges	Mean CCF rainfall (mm)	CCF rainfall SEM
1995–1996	27.7	255.7	6	272	21.3
1996–1997	33.9	547.9	7	482	41.1
1997–1998	51.9	370.1	7	147	11.3
1998–1999	32.6	344.9	7	216	24.5
1999–2000	58.7	717.7	10	824	23.7
2000–2001	24.3	486.3	10	411	15.4
2001–2002	40.0	425.3	10	242	16.9
2002–2003	48.8	370.9	10	139	8.9
2003–2004	44.4	473.6	10	265	16.2
2004–2005	82.1	461.6	10	432	20.2
2005–2006	26.7	694.7	10	393	36.6
2006–2007	74.2	344.7	8	395	51.3
2007–2008	26.3	461.0	8	411	28.4
2008–2009	74.9	633.6	7	523	35.2
2009–2010	40.9	448.7	8	449	52.6
2010–2011	85.1	796.9	9	838	57.6
2011–2012	46.6	728.7	8	321	68.9
2012–2013	46.4	321.0	4	142	23.7
2013–2014	56.1	698.6	4	501	44.2
2014–2015	53.4	327.6	3	346	81.7
2015–2016	16.3	330.2	9	99	48.5
2016–2017	81.9	657.6	9	600	85.2
2017–2018	47.1	421.1	9	171	24.0
2018–2019	23.4	212.7	9	135	14.1
2019–2020	27.9	483.1	9	709	120.4

Double-brooding could be considered a form of re-nesting, if the number of young produced in the first nest was substantially lower than that of non-double-brooding females nesting at a similar time in the breeding season. The mean number of fledglings produced in the first/spring nest of the 10 females who double-brooded was 2.1; the mean number produced by the 10 early-nesting females who did not double-brood was 2.5. This difference was not significant ($t = 1.124$, $df = 18$, $p = 0.276$), suggesting that females that double-brood are not doing so to compensate for low reproductive success in their spring nest.

If double-brooding was an option open only to those females in superior condition, we would expect the mass (prior to their departure from the nest) of the 10 females that went on to double-brood to be greater than the pre-departure mass of the 10 early-nesting females that did not double-brood. However, we found no difference ($t = 0.862$, $df = 18$, $p = 0.399$) in the mass of these two groups of females: the mean pre-departure mass of double-brooding females was 213.4 ± 15.2 g, the mean for those that did not double-brood was 207.8 ± 13.8 g.

Although we lack historical reproductive data, we can examine rainfall data for CCF in order to gauge the overall quality of recent breeding seasons. According to Table 1, annual rainfall in this part of Namibia has been highly variable in recent decades. CCF rain gauge data indicate that 2019/2020 was unusually wet (708 mm), with only two other breeding seasons in the past 25 years having higher rainfall. However, according to the CHIRPS data (483 mm), seven of the past 25 years were wetter. Although the 2019/2020 breeding season was wetter than the CHIRPS 39-year mean (467.5 mm), it was certainly not the wettest in recent memory, suggesting that double-brooding is dependent on above-average, but not exceptional, rainfall. Because of the late arrival of MTS in the 2016/2017 breeding season, (in mid-January), it is unclear how many of the numerous 'summer' (initiated after 1 January) Yellow-billed Hornbill nests (Table 2) were the result of double-brooding that year. It is possible that most or all were simply late-nesting hornbill pairs. However, given the wet spring conditions in late 2016, it seems at least as likely that most of the early 2017 nests were the result of double-brooding. In other words, it seems unlikely that such a large number of females would delay breeding until January during the wettest spring in half a decade (Table 2).

Unlike the wet spring of 2016, spring rainfall in 2019 (27.85 mm) was below the 39-year CHIRPS average of 49.58 mm (Table 1), suggesting that double-brooding decisions may be determined by summer rather than spring conditions. In contrast, the breeding seasons of 2017/2018 and 2018/2019 were characterised by both below-average rainfall and a complete lack of summer nesting by Yellow-billed Hornbills. Moreover, the success of Yellow-billed Hornbill nests in the springs of 2017 and 2018 was considerably lower than that of those in the spring of 2019 (MTS unpubl. data), again suggesting the dependence of hornbill breeding success on rainfall.

Finally, during the past four years, both Monteiro's and Damara Hornbills bred successfully only in the two wetter years, whereas there were zero nest attempts by either

species during the drier intervening years (although both species were present and guarding nest boxes, at least early in the season). Given that Monteiro's and Damara Hornbills appear to breed at our site in only the years when Yellow-billed Hornbills initiate nests after 1 January, we suggest that double-brooding by Yellow-billed Hornbills may be no less common than any breeding by Monteiro's and Damara Hornbills in this part of their breeding range.

However, if double-brooding was strictly a matter of high rainfall, one would expect more female *T. leucomelas* to be able to take advantage of the unusual breeding conditions of summer 2020. Yet of more than 43 Yellow-billed Hornbill females, only 11 initiated nests after 1 January 2020, indicating that not all females are able to capitalise equally on the resource abundance produced by above-average rainfall. We propose that time is the primary factor determining which females are able to take advantage of wet summers.

As mentioned earlier, for the 10 females that double-brooded, the latest date that the last chick emerged from the first nest was 15 February 2020. The earliest emergence date for a last chick from a 2019 spring nest was 28 January 2020, resulting in an 18-day span over which 20 females decided to double-brood (10 females) or not (10 females). In the first half of this 18-day span, nine females chose to double-brood whereas four did not. In the second 9-day period, only one female double-brooded, whereas six females did not. Despite these small sample sizes, this difference approached significance (Fisher Exact $p = 0.057$), suggesting that double-brooding is constrained, at least in part, by time. A simple comparison of the departure date of the last chick for these 20 early-breeding females demonstrates even more convincingly that time is a critical factor. The mean departure date for the last chick of the 10 double-brooding females was 2 February 2020, whereas the mean departure date for the last chick of females that did not double-brood was 8 February 2020. This difference was significant ($t = 2.407$, $DF = 18$, $p = 0.027$).

Discussion

Here we describe double-brooding in 10 female Yellow-billed Hornbills at a single site in Namibia. Although we determined that the majority of Yellow-billed Hornbill pairs did not engage in double-brooding, the fact that a relatively large number did suggests that double-brooding is part of the reproductive repertoire for this species in this part of their breeding range.

If double-brooding provides females with a means of boosting their annual reproductive success following a poor performance in their first breeding attempt, one would predict that females whose first nests failed would be more likely to re-nest. However, neither of the two Yellow-billed Hornbill females departing their nest box with zero offspring inside re-nested. Nor does it appear that double-brooding is a consequence of the death of offspring immediately after fledging: although we did not monitor families to assess juvenile survivorship, we did observe juveniles from the first nest accompanying the breeding male at two boxes where the female had re-entered the nest box.

Table 2: CCF hornbill breeding activity and breeding season rainfall (2016–2020)

Breeding season	Spring rainfall (mm) CHIRPS	Total rainfall (mm) CHIRPS	Total rainfall (mm) rain gauge	<i>T. leucomelas</i> nests initiated after 1 January	<i>T. monteiri</i> nests	<i>T. damarensis</i> nests
2016–2017	81.8	657.6	600	22	32	17
2017–2018	47.1	421.1	171	0	0	0
2018–2019	23.4	212.7	135	0	0	0
2019–2020	27.9	483.1	709	11	36	14

Both of the afore-mentioned predictions arise from the theory that energy not expended on current reproduction can be shifted to subsequent reproductive efforts (Stearns 1992; Saino et al. 1999). Thus, an additional prediction one might make is that females with smaller spring broods would be more likely to exhibit double-brooding. However, contrary to these expectations, we found no difference in the number of young fledging from the spring nests of females that did and did not engage in double-brooding (controlling for nest date). Of course, despite the ubiquity of trade-offs in life history theory (Stearns 1992), researchers frequently fail to find a negative relationship between current and future reproductive investment. Beziers and Roulin (2015) found no evidence that Barn Owls *Tyto alba*, use double-brooding to compensate for poor reproductive performance in the first brood. Double-brooding female Eurasian hoopoes *Upupa epops* actually had higher survivorship than did females who did not double-brood (Hoffmann et al. 2015). Eldegard and Sonnerud (2009) found a positive relationship between the brood size of the first nest and the likelihood of a second nest in Tengmalm's owls *Aegolius funereus*.

These results suggest, perhaps unsurprisingly, that success begets success; that it is the highest quality females mated to the highest quality males on the highest quality territories that are most likely to double-brood (Geupel and DeSante 1990, Jacobs et al. 2013, Hoffmann et al. 2015, Beziers and Roulin 2015, Johns et al. 2017). Following this line of thinking, we should expect to find the nutritional condition of double-brooding female Yellow-billed Hornbills to exceed that of females with similarly timed first nests that opted not to double-brood. However, when we compared the pre-departure mass of early-nesting female Yellow-billed Hornbills that did and did not go on to double-brood, we found no difference. Although higher female body condition is sometimes associated with double-brooding, this is not always the case (Ogden and Stutchbury 1996, Nagy and Holmes 2005).

Regardless of the role that individual differences may play, most workers agree that, at least for larger species, double-brooding tends to occur under conditions of unusual resource abundance (Marks and Perkins 1999, Moore and Morris 2005, Nagy and Holmes 2005, Eldegard and Sonnerud 2009, Husby et al. 2009, Carro et al. 2014). In semiarid subtropical areas, rainfall is the key proximate determinant of avian breeding via its direct link to food availability (Marchant 1960, Immelmann 1973, Boag and Grant 1984). This is certainly true in southern Africa, where variation in the amount and timing of rain benefits species capable of breeding opportunistically (Immelmann 1973, Maclean 1970, Maclean

1974, Lloyd 1999, Dean et al. 2009).

Because the seasonality of the southern African climate is defined more by precipitation than by temperature, the narrow window of opportunity for breeding in many Namibian birds can be enlarged substantially by additional rain. To quantify this property, Wyndham (1986) introduced the concept of Equally Good Months (EGMs). These are months where there are breeding records equal to or above the average number of breeding records per month for the species. For example, in most years, the month of May in north-central Namibia is too dry and inhospitable for breeding by birds. However, in years when rains are especially heavy and/or late, the food remains plentiful despite the shortening days, making May an 'equally good month' for chick rearing as March. Both southern Africa and Australia tend to have large EGM values (Wyndham 1986, Yom-Tov 1987), suggesting that birds are capable of taking advantage of unpredictable rains. Indeed, several diurnal Namibian raptors are known to engage in double-brooding in wet years, including the Rock Kestrel *Falco rupicolus* (JMM, unpubl. data), Black-winged Kite *Elanus caeruleus* (Mendelsohn 1983, 1989), and Pale Chanting Goshawk *Melierax canorous* (Malan et al. 1997).

Although we present rainfall data going back decades, we lack the hornbill reproductive data to fully understand the relationship between rainfall and double-brooding by Yellow-billed Hornbills. At our study site, two of the past four years have been substantially wetter than average, whereas two have been substantially drier than average (Table 2). Because MTS did not arrive at the study site until mid-January of 2017, we are unable to determine with certainty whether the summer nests of Yellow-billed Hornbills in 2017 were second nests or simply late first nests. However, we are inclined to categorise these summer nests as likely second nests: it seems unlikely that a large number of Yellow-billed Hornbills would delay the onset of breeding until summer 2017 when the rains of spring 2016 were so unusually heavy.

Of course, if double-brooding by Yellow-billed Hornbills was strictly a matter of high rainfall, one might expect all females to be able to take advantage of exceptional breeding conditions. Yet of 43 Yellow-billed Hornbill females known to have initiated a nest in the spring of 2019, only 10 initiated a second nest, indicating that not all females are able to capitalise equally on the resource abundance produced by above-average rainfall. Our results suggest that above-average rainfall (particularly summer rainfall) is a necessary but not sufficient explanation for double-brooding by Yellow-billed Hornbills. The EGM theory (Wyndham 1986) hints at one missing ingredient: time.

Double-brooding can occur only if there is sufficient time in the breeding season for two back-to-back nests. In a variety of taxa, it is the most early-breeding individuals that are most likely to engage in double-brooding (Stouffer 1991; Verboven and Verhulst 1996; Martin-Vivaldi et al. 1999; Verboven et al. 2001; Brinkhof et al. 2002; Parejo and Danchin 2006; O'Brien and Dawson 2012; Bulluck et al. 2013; Hoffmann et al. 2015; Beziers and Roulin 2015).

We find similar results with Yellow-billed Hornbills: only females that initiate breeding early in the Namibian spring go on to have second nests in those unusually productive summers. The 10 females we documented as double-brooders initiated their first nest significantly earlier in the spring than did the 33 females that did not double-brood. Given that the breeding cycle of Yellow-billed Hornbills is extremely lengthy (>3 months), it is somewhat surprising that the difference of a few days appears to have such a strong influence on double-brooding decisions. However, an anecdotal observation provides additional support for this view. In early February 2020, one female apparently re-entered her nest box on the same day that her penultimate chick emerged from it (before the youngest chick could reseal the nest entrance). This female began laying her second clutch soon after the fledging of the last chick. This action on the part of the female probably advanced the First Egg Date of her second nest by only a few days, but this benefit was presumably great enough to warrant this highly unusual behaviour.

Although resource availability and time are presumably the primary determinants of double-brooding in Yellow-billed Hornbills, other factors undoubtedly influence the decision of females to attempt a second brood. As mentioned earlier, two females that failed to produce any fledglings from their first (spring) nest did not re-enter their boxes for a second (summer) nest. It seems likely that selection may favour individuals that sever ties with nest sites and/or mates that participated in such spectacular breeding failure (Choudhury 1995). More intriguing were the few females that successfully fledged young from their first nest and did so earlier in the season than some female that did go on to double-brood. It is possible that age, breeding experience, and/or territory quality can increase the likelihood of double-brooding, as has been shown in multiple other avian species (Geupel and Desante 1990; Verhulst and Hut 1996; Bulluck et al. 2013; Jacobs et al. 2013; Carro et al. 2014; Hoffmann et al. 2015). Unfortunately, the above female hornbills were ringed for the first time during their spring nest, therefore we know nothing of their age or breeding experience. In fact, we were not even able to confirm the presence of these females on their territory following the fledging of their spring chicks; it is possible that they failed to re-nest because they were dead (or that they re-nested elsewhere).

The fact that we observed 10 female Yellow-billed Hornbills double-brooding at a single site in a single year suggests that this behaviour is a periodic feature of the Yellow-billed Hornbill life history repertoire. Of course, this is not to say that double-brooding is an annual occurrence. Although the 2019/2020 breeding season at our study site in Namibia was both wet and successful (Table 2), the two prior breeding seasons were characterised by

dry conditions, zero nests by either Monteiro's or Damara Hornbills (Table 2), and very poor reproductive performance by the Yellow-billed Hornbills that chose to initiate spring nests (MTS, unpubl. data). Indeed, it is possible that the motivation for females to double-brood in the summer of 2019/2020 was increased, as a result of their poor breeding outcomes during the previous two years.

In summary, Yellow-billed Hornbills appear to engage in double-brooding under a limited set of conditions. Double-brooding appears to occur only during years (particularly summers) with above-average rainfall and among females that initiated their spring nest relatively early. The role that age and/or experience plays in spring nest initiation date (as well as in double-brooding in general) remains unknown, at least in our population. Moreover, it seems likely that the infrequency of double-brooding in the Bucerotidae is related to the unusual moult exhibited by females. Double-brooding in Yellow-billed Hornbills results in two moults of both remiges and rectrices, a presumably expensive undertaking for a large bird (Newton 2009). Finally, the possibility of double-brooding is presumably not open to all hornbills of southern Africa, high EGM values notwithstanding. In Namibia, only hornbill species that routinely initiate their nests well before the onset of heavy/summer rains have the option of double-brooding. At our study site, Yellow-billed Hornbills begin nesting as early as October, whereas Monteiro's and Damara Hornbills wait until the arrival of sustained and substantive rains in late December and early January to initiate their breeding. Although we have not observed African Grey Hornbills breeding at our current study site, they too are known for initiating breeding in the spring (Brown et al. 2014). Consequently, only Yellow-billed Hornbills and African Grey Hornbills presumably have the opportunity to double-brood in Namibia.

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References

- Bennett PM, Owens IP. 2002. Evolutionary ecology of birds – life histories, mating systems and extinction. Oxford: Oxford University Press.
- Beziers P, Roulin P. 2015. Double brooding and offspring desertion in the Barn Owl *Tyto alba*. *Journal of Avian Biology* 46: 1–10.
- Boag PT, Grant PR. 1984. Darwin's Finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecological Monographs* 54: 463–489. <https://doi.org/10.2307/1942596>.
- Brinkhof MWG, Cave AJ, Daan A, Perdeck AC. 2002. Timing of current reproduction directly affects future reproductive output in European Coots. *Evolution; International Journal of Organic Evolution* 56: 400–411. <https://doi.org/10.1111/j.0014-3820.2002.tb01349.x>.

- Brown C, Bohme H, Stanback M, Tarr J, Tarr P, Heinrich D. 2014. Results of year one of a new nesting box project near Windhoek. *Lanioturdus* 47: 2–13.
- Bulluck L, Huber S, Viverette C, Blem C. 2013. Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. *Ecology and Evolution* 3: 3298–3306. <https://doi.org/10.1002/ece3.673>.
- Carro ME, Mermoz ME, Fernández GJ. 2014. Factors affecting the probability of double brooding by Southern House Wrens. *Journal of Field Ornithology* 85: 227–236. <https://doi.org/10.1111/jof.12064>.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour* 50: 413–429. <https://doi.org/10.1006/anbe.1995.0256>.
- Curtis O, Malan G, Jenkins A, Myburgh N. 2005. Multiple-brooding in birds of prey: South African Black Sparrowhawks *Accipiter melanoleucus* extend the boundaries. *Ibis* 147: 11–16. <https://doi.org/10.1111/j.1474-919x.2004.00311.x>.
- Dean WRJ, Barnard P, Anderson MD. 2009. When to stay, when to go: trade-offs for southern African arid-zone birds in times of drought. *South African Journal of Science* 105: 24–28. <https://doi.org/10.1590/S0038-23532009000100016>.
- Eldegard K, Sonerud GA. 2009. Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proceedings. Biological Sciences* 276: 1713–1721. <https://doi.org/10.1098/rspb.2008.1775>.
- Fargallo JA, Blanco G., Sotolargo E. 1996. Possible second clutches in a Mediterranean montane population of the Eurasian Kestrel (*Falco tinnunculus*). *The Journal of Raptor Research* 30: 70–73.
- Funk C, Peterson P, Landsfeld M, Pedreros D, Verdin J, Shukla S, Husak G, Rowland J, Harrison L, Hoell A, Michaelsen J. 2015. The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. *Scientific Data* 2: 150066. <https://doi.org/10.1038/sdata.2015.66>.
- Geupel GR, DeSante DF. 1990. Incidence and determinants of double brooding in Wren Tits. *Condor* 92: 67–75. <https://doi.org/10.2307/1368384>.
- Hoffmann J, Postma E, Schaub M. 2015. Factors influencing double brooding in Eurasian Hoopoes *Upupa epops*. *Ibis* 157: 17–30. <https://doi.org/10.1111/ibi.12188>.
- Humphrey PS, Parkes KC. 1959. An approach to the study of molts and plumages. *Auk* 76: 1–31. <https://doi.org/10.2307/4081839>.
- Husby A, Kruuk LEB, Visser ME. 2009. Decline in the frequency and benefits of multiple brooding in Great Tits as a consequence of a changing environment. *Proceedings. Biological Sciences* 276: 1845–1854. <https://doi.org/10.1098/rspb.2008.1937>.
- Immelmann K. 1973. Role of the environment in reproduction as source of 'predictive' information. In: Farner DS (Ed.) *Breeding Biology of Birds*. Washington DC: National Academy of Sciences. pp 127–147.
- Jacobs AC, Reader LL, Fair JM. 2013. What determines the rates of double brooding in the Western Bluebird? *Condor* 115: 386–393. <https://doi.org/10.1525/cond.2013.120085>.
- Jamieson SE. 2011. Pacific Dunlin *Calidris alpina pacifica* show a high propensity for second clutch production. *Journal of Ornithology* 152: 1013–1021. <https://doi.org/10.1007/s10336-011-0691-4>.
- Johns ME, Warzybok P, Bradley RW, Jahncke J, Lindberg M, Breed G. 2017. Age, timing, and a variable environment affect double brooding of a long-lived seabird. *Marine Ecology Progress Series* 564: 187–197. <https://doi.org/10.3354/meps11988>.
- Kemp AC. 1995. *The Hornbills: Bucerotiformes*. London: Oxford University Press.
- Kjellen N. 1994. Moulting in relation to migration in birds – a review. *Ornis Svecica* 4: 1–24.
- Kroodsma DE, Verner J. 2020. Marsh Wren (*Cistothorus palustris*), version 1.0. In: Poole AF (Ed.) *Birds of the World*. Ithaca: Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.marwre.01>.
- Lack D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.
- Lloyd P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. *Ibis* 141: 637–643. <https://doi.org/10.1111/j.1474-919X.1999.tb07371.x>.
- Maclean GL. 1970. The breeding seasons of birds in the southwestern Kalahari. *Ostrich* (suppl. 8): 179–192.
- Maclean GL. 1974. Arid-zone adaptations in southern African birds. *Cimbebasia* 2: 163–176.
- Malan G, Crowe TM, Biggs R, Herholdt JJ. 1997. The social system of the Pale Chanting Goshawk *Melierax canorus*; monogamy v polyandry and delayed dispersal. *Ibis* 139: 313–321. <https://doi.org/10.1111/j.1474-919X.1997.tb04630.x>.
- Marchant S. 1960. The breeding season of some SW Ecuadorean birds. *Ibis* 102: 349–381. <https://doi.org/10.1111/j.1474-919X.1960.tb08415.x>.
- Marks JS, Perkins AEH. 1999. Double brooding in the Long-eared Owl. *Wilson Bulletin* 111: 273–276.
- Martin-Vivaldi M, Palomino JJ, Soler M, Soler JJ. 1999. Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching. *Bird Study* 46: 205–216. <https://doi.org/10.1080/00063659909461132>.
- Mendelsohn J. 1983. Social behaviour and dispersion of the Black-shouldered Kite. *Ostrich* 54: 1–18.
- Mendelsohn J. 1989. Population biology and breeding success of Black-shouldered Kites *Elanus caeruleus*. In: Meyburg B-U, Chancellor RD (Eds), *Raptors in the modern world*. Berlin: World Working Group on Birds of Prey. pp 211–225.
- Mendelsohn J, Jarvis A, Roberts C, Robertson T. 2010. *Atlas of Namibia: A Portrait of the Land and its People* (3rd edn). Cape Town: Jonathan Ball Publishing.
- Mills MS, Boix-Hinzen C, Du Plessis MA. 2005. Live or let live: life-history decisions of the breeding female Monteiro's Hornbill *Tockus monteiri*. *Ibis* 147: 48–56. <https://doi.org/10.1111/j.1474-919X.2004.00340.x>.
- Moore DJ, Morris RD. 2005. The production of second clutches in the common tern: proximate effects of timing and food supply. *Waterbirds* 28: 458–467. [https://doi.org/10.1675/1524-4695\(2005\)28\[458:TPOSC\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2005)28[458:TPOSC]2.0.CO;2).
- Nagy LR, Holmes RT. 2005. To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). *Auk* 122: 902–914. <https://doi.org/10.1093/auk/122.3.902>.
- Newton, I. 1979. *Population ecology of raptors*. Berkhamsted: T and AD Poyser.
- Newton I. 2009. Moulting and plumage. *Ringing & Migration* 24: 220–226. <https://doi.org/10.1080/03078698.2009.9674395>.
- O'Brien EL, Dawson RD. 2012. Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. *Oecologia* 172: 689–699. <https://doi.org/10.1007/s00442-012-2544-0>.
- Ogden LJE, Stutchbury BJM. 1996. Constraints on double brooding in a neotropical migrant, the Hooded Warbler. *Condor* 98: 736–744. <https://doi.org/10.2307/1369855>.
- Parejo D, Danchin E. 2006. Brood size manipulation affects frequency of second clutches in the Blue Tit. *Behavioral Ecology and Sociobiology* 60: 184–194. <https://doi.org/10.1007/s00265-005-0155-z>.
- Renfrew RB, Frey SJK, Klavins J. 2011. Phenology and sequence of the complete prealternate molt of Bobolinks in South America. *Journal of Field Ornithology* 82: 101–113. <https://doi.org/10.1111/j.1557-9263.2010.00312.x>.
- Saino N, Calza S, Ninni P, Moller AP. 1999. Barn Swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* 68: 999–1009. <https://doi.org/10.1046/j.1365-2656.1999.00350.x>.

- Stanback MT, Millican D, Visser P, Marker L. 2018. The simultaneous moult of female hornbills is not triggered by the darkness of their nest cavity. *Ostrich* 89: 373–375.
- Stanback MT. 2020. A plywood nest box for hornbills and other large cavity-nesters. *Hornbill Natural History & Conservation* 1: 35–40.
- Stearns SC. 1992. *The Evolution of Life Histories*. London: Oxford University Press.
- Stouffer, PC. 1991. Intra-seasonal costs of reproduction in Starlings. *Condor* 93: 683–693. <https://doi.org/10.2307/1368200>.
- Underhill LG, Prys-Jones RP, Dowsett RJ, Herroelen P, Johnson DN, Lawn MR, Norman SC, Pearson DJ, Tree AJ. 1992. The biannual primary moult of Willow Warblers *Phylloscopus trochilus* in Europe and Africa. *Ibis* 134: 286–297. <https://doi.org/10.1111/j.1474-919X.1992.tb03811.x>.
- Verboven N, Verhulst S. 1996. Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology* 65: 264–273. <https://doi.org/10.2307/5873>.
- Verboven N, Tinbergen JM, Verhulst S. 2001. Food, reproductive success and multiple breeding in the Great Tit *Parus major*. *Ardea* 89: 387–406.
- Verhulst S. 1998. Multiple breeding in the Great Tit: the costs of rearing a second clutch. *Functional Ecology* 12: 132–140. <https://doi.org/10.1046/j.1365-2435.1998.00165.x>.
- Verhulst S, Hut RA. 1996. Post-fledgling care, multiple breeding and the costs of reproduction in the Great Tit. *Animal Behaviour* 51: 957–966. <https://doi.org/10.1006/anbe.1996.0099>.
- Verhulst S, Tinbergen JN, Daan S. 1997. Multiple breeding in the Great Tit: a trade-off between successive reproductive attempts? *Functional Ecology* 11: 714–722. <https://doi.org/10.1046/j.1365-2435.1997.00145.x>.
- Wyndham E. 1986. Length of birds' breeding seasons. *American Naturalist* 128: 155–164. <https://doi.org/10.1086/284551>.
- Yom-Tov Y. 1987. The reproductive rates of Australian Passerines. *Australian Wildlife Research* 14: 319–330. <https://doi.org/10.1071/WR9870319>.