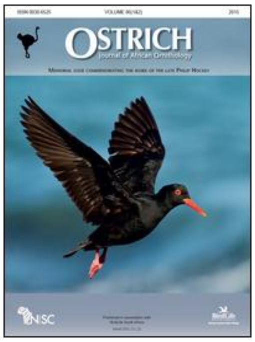

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Short Note

The simultaneous moult of female hornbills is not triggered by the darkness of their nest cavity

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A verbal model from 1937 proposed that the darkness of the nest cavity acts as a proximate trigger for the simultaneous moult observed in female hornbills. Although never tested, the plausibility of this hypothesis has allowed it to be cited frequently. We tested the role of darkness on the moult of *Tockus* hornbills by providing females with either opaque wooden nest boxes or translucent plastic ones. Most females underwent a simultaneous moult of their remiges and retrices following clutch completion, regardless of the amount of time they had spent in the nest. More importantly, the variation in the simultaneity of the flight feather moult was unrelated to box type. These results suggest that darkness does not act as a proximate cue for the simultaneous moult of female hornbills.

La mue simultanée des femelles Calao n'est pas déclenchée par l'obscurité de la cavité de leur nid

Un modèle datant de 1937 propose que l'obscurité de la cavité du nid agisse comme un facteur déclencheur de la mue simultanée chez les femelles Calao. Bien que jamais testée, la plausibilité de cette hypothèse lui a permis d'être régulièrement citée. Nous avons testé le rôle de l'obscurité sur la mue de Calao *Tockus* en fournissant aux femelles aussi bien des nids opaques dans des boites de bois que des nids dans des boites translucides en plastique. La plupart des femelles ont entrepris une mue simultanée de leurs rémiges et des rectrices juste après la ponte quelque soit la période de temps passée dans le nid. Plus important encore, les variations dans la simultanéité de la mue des plumes de vol n'étaient pas liées aux types de boites. Ces résultats suggèrent que l'obscurité n'agit pas comme une cause directe du déclenchement de la mue simultanée chez les femelles Calao.

Keywords: hornbill, simultaneous moult

Hornbills (Bucerotidae) exhibit a highly unusual breeding habit, wherein the female seals herself into her nest cavity prior to oviposition and remains ensconced inside until her chicks are half-grown (Kemp 1995). The consequences of this sealing behaviour are numerous. For example, females must store sperm within their reproductive tract to fertilise eggs that may be laid up to several weeks after their last copulation (Stanback et al. 2002). In addition, because of the confinement of females, males must single-handedly provide food to fuel egg production, incubation and chick growth (Kemp 1995; Stanback et al. 2002; Klaassen et al. 2003; Mills et al. 2005). This burden on the male is further exacerbated by the fact that while sealed in the nest cavity, the female undergoes a nearly simultaneous moult of all of her flight feathers (primaries, secondaries and retrices) (Kemp 1995; Stanback et al. 2002; Klaassen et al. 2003; Mills et al. 2005). Because this dramatic moult occurs out of sight of human eyes, little is understood about the proximate factors triggering it. Indeed, untested hypotheses from the early twentieth century (Stonor 1937) explaining this unusual moult are still cited online (Wikipedia contributors 2018).

Stonor (1937) described the breeding behaviour of a pair of captive Trumpeter Hornbills *Bycanistes bucinator* in London. In addition to making extensive observations, he produced several hypotheses concerning the unusual breeding biology of hornbills. Stonor's most detailed conjecture was that the darkness of the nest cavity somehow stimulated the simultaneous moult of females. His only support was in the form of a lengthy description of a practice in Japan at the time known as 'Yogai' in which captive songbirds were exposed to prolonged light to stimulate singing. More particularly, he noted that the cessation of the light treatment resulted in moult. He emphasised the following: 'the extremely delicate balance between the light intensity and the moult and, secondly, the statement that the greater the reduction in the light the more rapid is the moult' (Stonor 1937: 94).

It is quite clear that female hornbills in the genus *Tockus* do live in darkness while sealed in their nest (Kemp 1995).

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Moreover, these birds not only seal the nest entrance (with the exception of a small slit through which they receive food and defecate), they also seal every hole, crack and seam in the nest cavity (MTS pers. obs.). Consequently, there is little variation among females in the levels of darkness that they experience. It is thus not surprising that Stonor (1937) posited a role for this relatively sudden loss of light.

Although it is difficult to refute a role of darkness in the simultaneous moult of female hornbills, the loss of feathers appears to be more linked to the cessation of oviposition than the darkness of the cavity. For example, for female Monteiro's hornbills *Tockus monteiri*, the time period between their entering the cavity and the laying of their last egg ranges from 7 d to well over three weeks (MTS unpublished data). Despite this variation, the moult of the remiges and retrices always occurs immediately after the completion of the clutch – and is thus apparently unrelated to the time spent in darkness (MTS unpublished data).

Such data, although critical, cannot alone refute a role of darkness in the simultaneous moult of female *Tockus* hornbills. As part of our study of the breeding biology of *Tockus* hornbills in Namibia, we incorporated both traditional wooden nest boxes and translucent plastic nest boxes. These latter boxes were modified screech-owl nest boxes obtained from the Barn Owl Box Company (Pittsburgh, PA, USA). All of our plastic boxes were installed in shady trees to prevent overheating. Despite the shade, the boxes tended to be very bright inside, even after hornbills smeared faeces and mud over parts of the inner surface. Moreover, these plastic boxes had multiple ventilation holes that were unreachable by female hornbills. These holes not only helped prevent overheating of the boxes, they also allowed additional light into the box. If the simultaneous moult of remiges and retrices is at all dependent on the female experiencing darkness, we would expect females nesting in well-lit boxes to differ in the simultaneity of their flight feather moult from females nesting in the darkness of a sealed wooden nest box.

In the 2017 and 2018 breeding seasons, we monitored hornbill nests at our study site (Cheetah Conservation Fund) near Otjiwarongo, Namibia. Our study species were Monteiro's Hornbill *Tockus monteiri*, Southern Yellow-billed Hornbill *Tockus leucomelas* and Damara Hornbill *Tockus damarensis*. Most of our data come from the 2017 summer breeding season. Our only nests in the 2018 breeding season were 14 nests of *T. leucomelas* that were initiated in the spring (October/November) of 2017. Unfortunately, the rains of early 2018 were insufficient to initiate summer breeding of hornbills. Of 28 monitored nests of *T. monteiri*, 11 were in plastic boxes; of 23 monitored nests of *T. leucomelas*, two were in plastic boxes; and of 14 monitored *T. damarensis* nests, four were in plastic boxes. All females of all species underwent a successful moult of their remiges and retrices following the completion of egg-laying. Females differed, however, in the simultaneity of their moult.

Given that moult was not the focus of our overall study, we did not collect detailed moult data from every female. However, we were able to record the number of females that underwent a simultaneous flight feather moult vs those exhibiting a less-than-simultaneous moult. We inspected the moult of each female several times during their nesting cycle (between clutch completion and their departure from the nest). We considered a female as having a non-simultaneous moult if she (1) retained an unmoulted wing or tail feather while new ones were at least half-grown or (2) exhibited a new flight feather that was at least 10 cm shorter than any others of its type. We are quite aware that our descriptions of moult lack the precision typically demanded by students of moult. Indeed, moult terminology continues to divide researchers otherwise eager to describe moult variation in an evolutionary framework (Humphrey and Parkes 1959; Rohwer et al. 1992; Howell et al. 2003; Wolfe et al. 2014).

The translucency of our plastic boxes rendered the interior of these boxes relatively bright. In an attempt to quantify this brightness, we used a Galactica Luxmeter on an Apple iPhone to measure the lux value inside plastic boxes. The lux is the SI unit of illuminance, measuring luminous flux per unit area. Because we were unable to use the iPhone inside a closed wooden box, we have no lux values for those conditions. However, the interior of a wooden box with a hornbill nest plug is quite dark. To measure the brightness of plastic boxes, we placed an unoccupied but formerly used plastic box (with mud and faeces smeared on the inside) in partial shade (under a tree) and in full shade (adjacent to a building) as well as in full sun. Over the course of two days (7–8 January 2018), we recorded the brightness of the reflectance of a sheet of white card stock placed inside the nest box. We recorded the lux values at multiple times of day (hourly from 09:00 to 17:00) under both clear and overcast conditions.

We used a Fisher's exact test to determine whether females nesting in opaque and wooden boxes differed in the simultaneity of their moult.

Light levels in our plastic box varied substantially. Combining values for clear (eight sampling times) and cloudy conditions (five sampling times) across both days of measurement, our test box had higher lux values when fully exposed (mean = 943 lux, SE = 108) compared with when in partial shade (mean = 281 lux, SE = 33) or full shade (mean = 197 lux, SE = 40). Because the plastic boxes installed for hornbills were never placed in full sun, we can confidently conclude that the light levels experienced by hornbills nesting in our plastic boxes routinely exceeded 200 lux. For comparison, architects recommend lux values of 100–300 for lighting in hallways and rooms in which concentrated visual tasks are not performed (Adams 2018). More importantly, in none of the three species did we find a relationship between box type and the simultaneity of flight feather moult: females using wood (dark) boxes did not exhibit greater simultaneity in wing or tail moult than did females in plastic (bright) boxes (Table 1).

The simultaneous moult of breeding female hornbills is without comparison among birds. Although it is superficially similar to the simultaneous wing molt experienced by ducks (see Pyle 2005), the fact that this hornbill moult occurs only in females and only within the confines of the nest cavity (females who fail to nest undergo a male-like moult) suggests that the proximate cues for the moult are unique. Consequently, given the known effect of the removal of light stimulation (Yogai) on avian molt, Stonor's

Table 1: Occurrence of simultaneous and non-simultaneous flight feather moult in three species of *Tockus* hornbills nesting in opaque (wood) vs translucent (plastic) nest boxes

Species	Box type	Simultaneous (*N*)	Non-simultaneous (*N*)	Fisher's exact *p*
Tockus monteiri	Wood	14	3	1.00
	Plastic	9	2	
Tockus damarensis	Wood	10	0	1.00
	Plastic	4	0	
Tockus leucomelas	Wood	13	8	0.52
	Plastic	2	0	

(1937) hypothesis invoking the darkness of the nest cavity is understandable. However, several observations support our conclusion that the darkness of the nest cavity has no significant proximate effect on moult of *Tockus* hornbills. First, as we report in Table 1, box type (light regime) had no effect on the simultaneity of moult. Second, the simultaneous moult of females appears to be associated with clutch completion, regardless of the amount of time the female has spent ensconced in the darkness of the nest cavity: in no case did a female begin her moult prior to the completion of her clutch.

Our finding that darkness is not the primary trigger for the moult of breeding female hornbills is certainly not the end of the story. Why is it that female hornbills that double-brood are able to undergo such moults twice in a single breeding season (H Bohme unpublished data)? And how is it that females who skip breeding can moult like males? It remains to be seen what aspect of clutch completion acts as the proximate cue for the unusual moulting behaviour of female hornbills.

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