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Male Southern Yellow-billed Hornbill successfully raises chick despite death of female inside nest

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Abstract

Although many biparental bird species divide provisioning responsibilities relatively equally, hornbills are characterised by male-biased provisioning. Even after departing the nest cavity, female Southern Yellow-billed Hornbills *Tockus leucomelas* do not provision offspring at the same rates as their mates. Given that males provide food for the female during her period of incarceration within the nest cavity (which corresponds to the pre-laying, laying, incubation and early chick-rearing stages), a lack of provisioning on the part of the female during the weeks after she has left the confines of the cavity suggests that males could potentially perform 100% of the provisioning. In 2018, I followed the fate of a nest in which the breeding female died shortly before she was due to leave the nest box. The male continued to feed the chick inside which fledged approximately one month later.

Keywords: hornbill, provisioning, paternal care.

Although biparental care is the norm for most bird species, parental care is not always shared equally between males and females (Lack 1968, Cockburn 2006). A great deal of theoretical and empirical research has focused on the question of how birds should respond to reduced investment by their partners (Trivers 1972, Houston and Davies 1985, Lessells 1991, 2012, Parker et al. 2002). For example, Whittingham et al. (1994) showed that female Tree Swallows *Tachycineta bicolor* increased their provisioning rate to compensate for missing mates but not for temporarily handicapped mates. Griggio and Pilastro (2007) found that female Rock Sparrows *Petronia petronia* were more likely to fully compensate for an absent male and males typically only partially compensated for an absent female. In fact, the payoffs for increasing, reducing, or maintaining the level of effort may be different for the two sexes (Szentirmai et al. 2007) and may also vary over the breeding season (Székely et al. 1999). Perhaps not surprisingly, responses to mate handicapping and mate removal are highly variable (see Table 4 in Sanz et al. 2000, Cantarero et al. 2019).

In some species, males regularly contribute far more to chick-rearing than do their mates. Although this is the case among polyandrous species (Owens 2002), sex-biased provisioning can also occur within socially monogamous species. Among owl species, males typically do most of the hunting (Newton 1979, Eldegard and Sonerud 2009, 2010). In fact, in the Boreal Owl *Aegolius funereus*, female desertion has evolved as a strategy for females to maximise their fitness (Eldegard and Sonerud 2009, 2010). Although mate desertion sometimes lacks a sex bias (see the Snail Kite *Rostrhamus sociabilis*, Beissinger and Snyder 1987), up to 63% of female Boreal Owls desert their nests when food availability is above average (Eldegard and Sonerud 2009, 2010).

Although hornbills (Family Bucerotidae) do not practice mate desertion (Kemp 1995), some aspects of their breeding biology are similar to that of many owls (see Newton 1979, Eldegard and Sonerud 2009, 2010, 2012). As with many owls, female hornbills perform all of the incubation and brooding of offspring. Both owls and hornbills exhibit extreme hatching asynchrony within their broods. Moreover, as in owls, female hornbills conduct the direct feeding of nestlings, which takes place during the period when most brood reduction occurs. Finally, as in many owls, female hornbills tend to contribute substantially less than their mates (i.e. after they have departed the nest cavity – see Kemp 1995, Finnie 2012). Although differences in mean genetic relationship to offspring has been invoked in some species to explain

the greater motivation of females to provision offspring (Schroeder et al. 2016), research has demonstrated that hornbills tend to be genetically monogamous, such that both male and female parents are equally related to the offspring in their nest (Stanback et al. 2002, Kinnaird and O'Brien 2020).

Male hornbills are completely responsible for providing food to the female during the pre-laying, egg-laying, incubation, and the first part of the chick-rearing stages (Kemp 1995, Stanback et al. 2002). Given the extensive male investment observed in hornbills, the question of whether males could successfully raise offspring without female assistance is valid. Here, I report a case in which a male Southern Yellow-billed Hornbill *Tockus leucomelas*, successfully raised a chick after the death of the female relatively early in the breeding cycle.

On 12 January 2018, at my study site at the Cheetah Conservation Fund near Otjiwarongo, Namibia, I found that a breeding female *T. leucomelas* had recently died of natural causes inside her nest box (#135) during the chick-rearing stage. She was last observed alive in the nest box on 8 January 2018. Her death occurred several days before the time she would have left the nest. She had been losing weight prior to her death (max mass = 212 g on 25 December 2017), but such weight loss is not unusual for female hornbills, so I had taken no action. At this time, the larger chick (which hatched on approximately 16 Dec 2017) had a mass of 135 g, and the smaller chick (which hatched on approximately 18 December 2017) had a mass of 91 g (both masses typical for chicks at this stage of nesting). Given that I was unsure of the fate of the chicks with a single parent, I opted to remove the larger chick and place it in another nest with a single chick to which it was closer (though smaller) in mass. I also removed the female's carcass. Although the 91 g chick was near the lower threshold of size that could survive without a female present, I allowed the male at box 135 to attempt to raise this single chick by himself. I did not supplement the nest in any way. Although the disappearance of the smaller chick is more standard in hornbill nests, I have documented cases where the larger of two chicks die for reasons unrelated to starvation. I continued to measure the single chick regularly (every 2-4 days) for nearly another month. Its growth rate did not differ noticeably from other hornbill chicks at the same stage of growth (the sibling that I removed and placed elsewhere ultimately starved before fledging). I last measured the chick in box 135 on 7 February 2018. I could not check the box around the time of fledging, but an inspection of the nest box and nest plug on 17 February 2018 indicated that the chick fledged successfully.

Although raising a single chick solo may not be a noteworthy accomplishment in many years, the effort required to do so in the breeding season of 2017/18 was presumably substantial. Due to a lack of rain (and hence scarce food resources) that summer (Stanback et al. 2021), relatively few *T. leucomelas* attempted to breed, and no Monteiro's *T. monteiri* or Damara Red-billed *T. damarensis* hornbills nested (compared to 38 *T. monteiri* and 17 *T. damarensis* nests the summer before). Of the 13 other *T. leucomelas* nests I followed in the 2017–2018 breeding season, the mean number of chicks fledged was 1.0 (with four nests fledging no young), suggesting that food availability was limited. The summer before, *T. leucomelas* nests produced an average of 2.12 fledglings (range 0-3). Although I did not observe the nest in box 135 to see if additional *T. leucomelas* provisioned, it is unlikely that the male would have recruited a new female willing to assist with the provisioning of offspring of his former mate (such behaviour is virtually unknown in birds). My observation does not necessarily imply that the provisioning conducted by female hornbills is unimportant to reproductive success. However, it suggests that male *T. leucomelas* may be capable of performing all chick provisioning. This is similar to the case of a lone female Wandering Albatross *Diomedea exulans* that successfully raised a chick despite the death of the male early in the chick-rearing phase (Brown and Adams 1984). In fact, during the 2019/2020 breeding season, one *T. leucomelas* female re-entered her nest box (to double-brood) when the penultimate chick from her first brood left the nest (Stanback et al. 2021). From then on, her mate was the only adult provisioning any of the three juveniles from the first brood.

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