Parental Provisioning in Captive Red-billed Hornbills (*Tockus erythrorhynchus*)

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Introduction

The level to which parents provision offspring varies across species and may be influenced by factors such as brood size, care requirements of offspring, and the cost of parental investment. For example, a clutch of eggs of some species of fish may require little or no care at all, whereas female mammals incur very high costs during both gestation and lactation (Davies et al., 2012). Birds typically employ bi-parental care in raising their broods. Because the female does not lactate, both parents can provide resources to the young, which greatly increases the overall survival of offspring, especially with altricial young (Davies et al., 2012).

In some bird species, such as the great kiskadee, both parents participate equally in delivering food to chicks during the nesting period (Llambas, 2003). However, males may spend more time providing care if the female's ability to provide care is compromised or heavy predation requires the male to protect the nest (Markman et al., 1995; Fraser, 2002). The saddle-billed stork also employs bi-parental care of eggs and chicks, however females provide substantially more care than males (Elston et al., 2010).

Hornbills (Bucerotidae) have a distinctive nesting behavior that may influence the patterns of caregiving of males and females. The mating pair chooses a small cavity in their environment as their nesting site and, after the female enters the nest, covers the entrance with spackle (a mixture composed mainly of food material, with some fecal matter), and leaves a slit the width of their bills in the spackle. For the entire nesting period (approximately two months in the red billed hornbill), the female remains in the nest cavity, relying on the male for food (Moreau, 1937). After one month of brooding chicks, the hornbill mother will emerge from the nest box and the chicks reseal the hole. Then, both parents deliver food to the chicks. After approximately one to two weeks, depending on clutch size, the chicks will widen the slit in the spackle and emerge from the nest box. Following emergence, the parents will continue to feed the chicks outside of the nest box (A. Waier, pers. comm.).

Producing eggs and remaining in the nest box during the nesting period can be costly to the female, which could decrease the resources she has available to provide care for her brood after incubation. This would imply that the male, having more resources available, might spend more time provisioning after the female leaves the nest box (Liker and Székely, 2005). On the other hand, while the females are sealed in the nest box, males are the primary provider of food to both the female and the brood. Because the male decreases his time spent caring for himself during this time, he may spend more time recovering lost resources once the female leaves the nest box and is able to deliver food to the chicks on her own (Stanback et al., 2002). Alternatively, the female and chicks may form a close bond during incubation that continues as they leave the nest box, leading her to spend more time provisioning.

There may also be certain characteristics of chicks that can result in differential provisioning by their parents. Slagsvold (1997) found that sibling rivalry could be a major factor in the proportion of care an individual chick receives. Larger chicks in this case are expected to receive more frequent parental care compared to smaller chicks because they are able to push the smaller chicks out of the way and obtain attention from the parents. On the other hand, it has been observed that chicks that hatch last in a brood have a smaller body mass as well as increased begging behavior, which may elicit more food from the parent(s) (Siano et al., 2001). However, no bias may be evident if the brood is small, and thus it is advantageous for the fitness of the parents to provide care equally among all chicks in the brood. Although sex-biased provisioning is seen in some avian species (Ligon and Hill, 2010), there is no literature on the effects of chick gender on the distribution of care by hornbills.

This study aimed to determine if the frequency of parental care differs between the mother and father in a pair of captive red-billed hornbills at the Milwaukee County Zoo. In addition, we investigated whether either parent showed a bias for any specific chick.

Methods

Subjects and exhibit

Our focal subjects are an experienced mated pair of captive red-billed hornbills, *Tockus erythrorhynchus,* housed in the aviary building at the Milwaukee County Zoo, WI. The exhibit dimensions are 6m x 3m x 3m with a nest box located centrally on the ceiling that could be accessed via branches. The outer facing wall of the exhibit is made of tightly spaced vertical tension wires. The wall separating the focal exhibit from its neighboring exhibit is made of nylon zoo mesh, while the other two are made of painted plaster. The exhibit also contains various plants, a shallow pool of water, artificial and natural rocks/boulders of varying sizes, and a torpedo sand floor. Two food dishes are provided to the subjects daily and live crickets are provided daily and most often during our sampling periods. All subjects were individually recognizable based on colored plastic leg bands.

Nesting timeline

The nesting timeline was similar to that observed by Moreau (1937). The mother was sealed within the nest box on July 24th, 2013. Although it was impossible to determine the specific date of hatching, keepers used chick vocalizations to estimate that the three chicks hatched on or around August 24th. On September 25th, the mother left the nest box and the chicks re-sealed themselves inside. On October 2nd, the first two chicks emerged from the nest box, followed by the third chick on October 7th. Since actual hatching order was not observed, it was assumed that the order of emergence was also the order or hatching (A. Waier, pers. comm.).

Chick sex was determined via analysis of blood samples. The sex of the chicks was not revealed to the observers until all data had been collected in order to prevent any observer bias. Chicks are referred to

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by their estimated hatching order followed by their sex (in parentheses).

Chick removal

This pair of red-billed hornbills has raised eight clutches to date. In each of the first seven clutches (2006 - 2012) the breeding male attempted to drive the female chicks from his territory once they were fully fledged (at about two months of age). Once the breeding male started chasing his female chicks, the entire clutch of chicks (males and females) were removed from the exhibit and placed off exhibit for their safety and to provide companionship for each other. The eighth clutch produced by the red-billed hornbill pair in 2013, (the subject of this paper) produced a different outcome. The adult male began to relentlessly chase and displace chick 2 (later determined to be a male) 10 days after fledging. Knowing that chick 2 had started self-feeding at a very young age, the aviary staff decided that he did not need his mother to help him obtain food. He was quickly removed from his enclosure for his own safety on October 10th. He was placed in the adjacent exhibit to allow him to continue to interact with the family.

Data collection

Data were collected from September 26th through November 14th, 2013, on Thursday afternoons in 45-minute sessions with approximately 5 minutes between sessions. All occurrences of feeding behavior were recorded during each session. Feeding behavior was defined as one parent carrying food in his/her beak and depositing (or attempting to deposit) it in the nest box or directly in the mouth of a chick, regardless of whether the chick accepted the food offered. Which parent fed and which chick received the food was recorded when possible. Thirty total hours of data were collected. On each day of observation, no more than three sessions (135 min) were conducted. We tested for inter-observer reliability (defined as 85% similarity between data collected during one session) prior to the start of data collection and after 15 observer-hours of data collection. Each observer collected data on one focal bird and the focal bird was alternated between observers for each session to reduce any potential bias.

Data analysis

All data were analyzed using SPSS. All sessions were treated as independent measures of behavior within a case-study design. Differences in mean number of feedings per session between parents as well as between weeks were analyzed using a 2-way between subjects analysis of variance (ANOVA). Post hoc analyses were made using Tukey's B. Since chick 2 (M) was removed after the third week of data collection, we analyzed the potential parental biases both before and after his removal. A 2-way between subjects ANOVA was also used to analyze potential chick biases for each parent before the removal of chick 2 (M). Since only two chicks remained after the removal of chick 2 (M), parental biases were analyzed using an independent sample t-test. For all figures, error bars represent one standard error.

Results

Influences of parental gender

There was a significant main effect of parental gender on the average number of feedings per session each week ($F_{(1, 24)} = 6.592$, $p < 0.05$). The father's overall feeding rate was higher than that of the mother (fig 1). We also found a significant main effect of week ($F_{(1, 24)} = 14.713$, $p < 0.05$). Post-hoc tests showed that both parents significantly decreased their feeding rate after weeks one and two. Interaction between factors was not significant ($F_{(7, 24)} = 1.380$, $p = 0.259$).

Biases towards chicks

We found no significant bias towards a specific chick by the father ($F_{(2, 17)} = 1.176$, p=0.335, fig. 2a) before or after (t=0.660, p=0.516, fig. 2b) the removal of chick 2 (M). Similarly, there was no significant bias towards a specific chick by the mother either before ($F_{(2, 17)} = 1.607$, p=0.233; fig. 2a) or after (t= -2.007, p=0.056, fig. 2b) the removal. The mother tended to direct more care toward chick 3 (F) than to chick 1 (F), but this difference was not statistically significant, most likely due to the small number of observations. Anecdotally, chick 3 (F) seemed to be the smallest chick.

Discussion

Our results indicate that the father did, on average, feed the chicks more often per session than the mother. Our data suggest that the father provides this higher frequency of care for a longer period of time than the mother (fig 1), extending into the fourth, and possibly fifth, week. In contrast, the mother seems to reduce her high frequency of feeding at the third week. This appears to support the findings of Liker & Székely (2005) who found that because males do not incur the high costs of producing eggs and remaining in the nest box, they are more likely to have the resources available to provide more care after the emergence of the chicks. Since red-billed hornbill females spend over two months in the nest, it is likely that high costs are incurred while producing, laying, and incubating eggs that may hinder the mother's ability to continue

feeding her chicks for an extended period of time.

Due to high levels of aggression by the father towards chick 2 (M), chick 2 (M) was removed from the flock and placed in a neighboring exhibit. Interestingly, this type of forced male-dispersal is uncommon in monogamous species like the red-billed hornbill (Perrin and Mazalov, 2000) since there is minimal local mate competition. Although before the removal of chick 2 (M) the father did tend to feed the male chick less than the two females, the difference was not statistically significant. Although we found no statistically significant bias by the mother towards any chick, her allocation of feedings tended to correlate with the estimated hatching order. Since chick 3 (F) was the last to hatch and appeared to be the smallest, this correlation suggests that the mother may be employing a form of parental compensation. Parental compensation is a strategy in which a parent will allocate the most resources (feedings, for our study) to the youngest or smallest chick in order to reduce hierarchical competition between chicks. This type of care provisioning may also increase the overall survival of all members of the brood (Shizuka and Lyon, 2013).

In order to increase the success of captive breeding, one must take into account the differences in parental care strategies employed by each parent, as has been exemplified in this study. In captivity, forced dispersals prove very problematic and may require the removal of certain individuals from the family unit. When these issues arise, it is important to understand the amount of care provided by each parent in order to ensure the health of all chicks in the brood. Although this research provide some insight into the parental provisioning of captive red-billed hornbills, further research is needed to determine if these findings can be generalized to other captive pairs.

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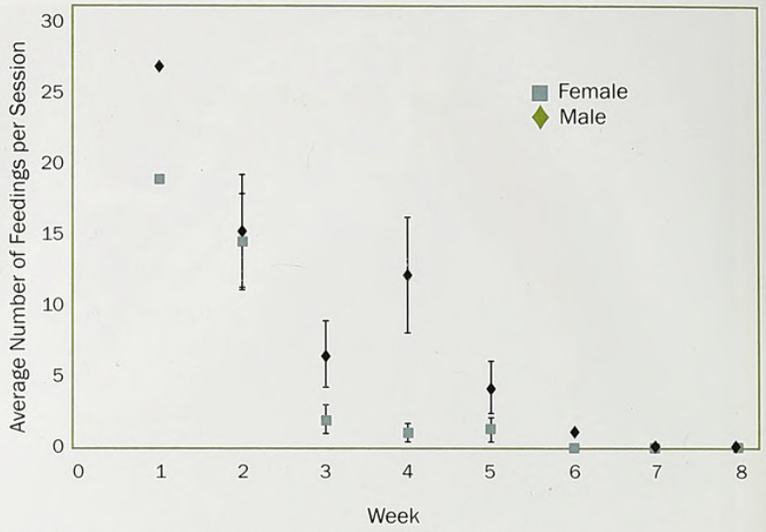

Figure 1. Overall, the male provided more care each week than the female (ANOVA, $p<0.05$) and average feedings per session for both parents decreased significantly after weeks 1 and 2 (ANOVA, $p<0.05$). The male also provided care for a longer period of time than did the female.

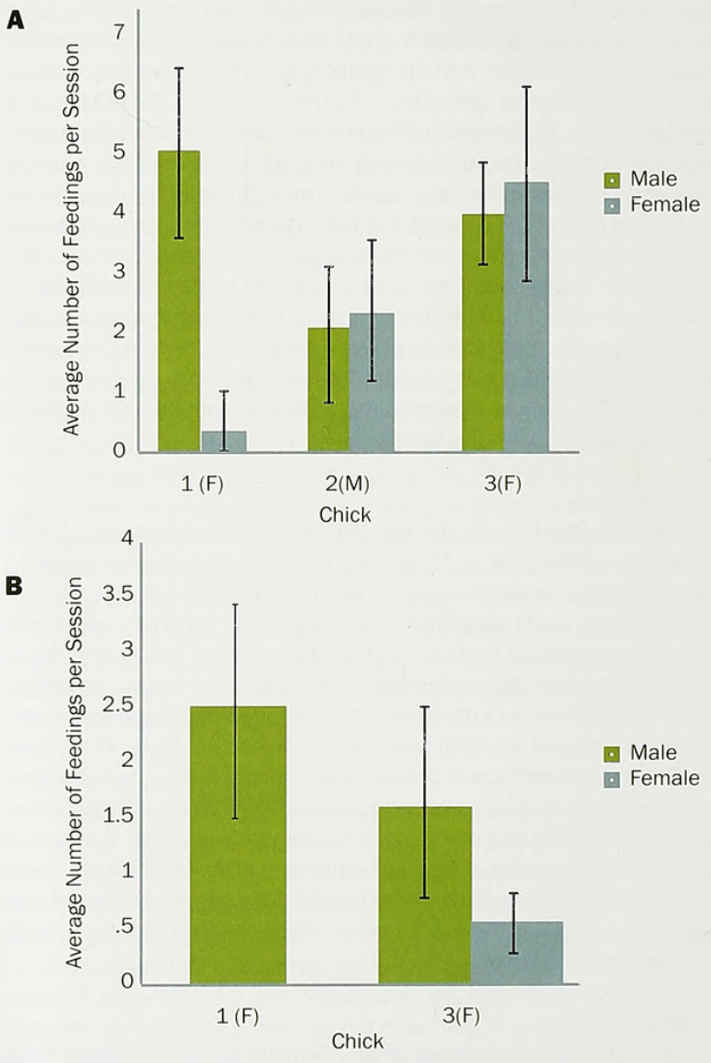

Figure 2. Neither parent had any bias towards any individual chick both before (a) or after (b) the removal of chick 2 (p_f=0.23, p_m=0.34 and p_f=0.68 and p_m=0.52, respectively).

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