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RESEARCH ARTICLE

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A preliminary global investigation into potential impacts on successful captive breeding for two species of *Rhyticeros* hornbill

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Abstract

Asian hornbills have limited ex situ breeding success, yet these species are some of the most threatened of birds, in need of managed breeding programs. To optimize breeding and increase the sustainability of such populations, it is necessary to assess and improve their husbandry and welfare. Evidence to improve reproduction can be gathered through global husbandry surveys. A survey was sent out to all European Association of Zoos and Aquaria and Association of Zoos and Aquarium holders of the wreathed hornbill (*Rhyticeros undulatus*) and Papuan hornbill (*R. plicatus*) to determine predictors for ex situ breeding success. This research found that pairs that have spent more years together (p = .016) and that adding additional proteins to the diet (p = .006) are two significant predictors of breeding success for wreathed- and Papuan hornbill pairs. This paper found a general trend that successful hornbill pairs prefer nest boxes that are situated outside (p = .054). The behaviors of calling to each other and sitting in close proximity showed a general trend and were observed more frequently in successful pairs and, therefore, could be good indicators of bonded pairs. We recommend that ex situ institutions allow their hornbill pairs time to form strong bonds, and that pair compatibility is monitored regularly to ensure that such interactions are positive and not consistently negative. An increase in the percentage of dietary proteins, prior and during the breeding season appears to stimulate pairs to breed. If the management and husbandry alterations presented in this study are implemented, the sustainability of *Rhyticeros* hornbill populations may be enhanced.

KEYWORDS

breeding success, evidence-based husbandry, Papuan hornbill, questionnaire, wreathed hornbill

1 | INTRODUCTION

Accredited or membership zoos and aquariums (hereafter "zoos") are committed to wildlife conservation and aspire to lead efforts to protect species around the world (BIAZA Conservation Policy, 2021; Conservation—AZA, 2023; Conservation Strategies—WAZA, 2006; EAZA Code of Ethics and Conduct, 2023) by supporting, initiating, and managing in situ and ex situ conservation projects (Gilbert et al., 2017; Gusset & Dick, 2010). Zoos support ex situ conservation by breeding endangered species, often through regional or global managed breeding programs initiated by zoo associations like the European Association of Zoos and Aquaria (EAZA) Ex situ Program (EEP), the Species Survival Plan, and the Global Species Management Plan. However, for these programs to thrive, ex situ populations must be viable and sustainable (Lacy, 2013; Lynch & Snyder, 2013). A sustainably managed ex situ population should retain its full utility for their defined roles of modern zoos; conservation, education, research, and entertainment (Conde et al., 2011; Rose & Riley, 2022). Sustainable ex situ populations are achieved if the scientific and husbandry knowledge exists to breed species at desired numbers to maintain appropriate population sizes (Che-Castaldo et al., 2021; Lees & Wilcken, 2009; Powell et al., 2019; Putnam et al., 2022), and if populations remain genetically diverse for the long-term (Che-Castaldo et al., 2021; Powell et al., 2019; Putnam et al., 2022).

Birds are among the most species of vertebrate taxa currently housed in zoos (Brereton & Brereton, 2020; Rose et al., 2019). Research within EAZA bird EEPs showed that 36% of the species kept within the EAZA region consisted of 50 individuals or fewer, and 73% of species have a reproduction rate of 25% or lower (Leus et al., 2011). A survey of 110 produced Association of Zoos and Aquarium (AZA) Breeding and Transfer Plans for avian programs showed that 43% of the species examined have demonstrated an average trend of decline over the 5 years before these most recent management plans (Lynch & Snyder, 2013). To optimize ex situ breeding and increase the size of these populations, it is necessary to assess and improve the welfare of birds kept ex situ (Mellor et al., 2018; Swaisgood, 2007). One way evidence to improve ex situ breeding can be gathered is by conducting global husbandry surveys. Through these surveys, gaps in current husbandry knowledge can be identified, aspects of good practice recognized and outcome for further development be provided (Fuller et al., 2012; Harley et al., 2021; Rose & Roffe, 2012; Rowden & Rose, 2016), which, in turn, provides the foundation for species-specific best-practice guidelines for all holders to follow.

One example of a taxonomic bird group in need of further husbandry evidence are hornbills (*Bucerotidae*), Thirty-four hornbill species are kept within AZA and EAZA collections (Brouwer et al., 2020; ZIMS, 2022a). Although hornbills are commonly kept in zoos, they remain challenging to breed in captivity (Beilby, 2022; Kozlowski et al., 2015; Rose et al., 2020). Especially the larger Asian species have limited breeding success in zoological institutions and these species are generally the most threatened and most in need of ex situ breeding programs (Beilby, 2022; Brouwer et al., 2020).

Research highlights

- Hornbills are difficult to breed in captivity.
- A husbandry survey revealed that dietary proteins and strong pair bonds influence breeding success.
- Future studies should focus on behavioral outputs and nest box characteristics and parameters.

Although ex situ breeding results are scarce, there is anecdotal evidence found in the literature suggesting how to improve the breeding results in these species. One of these suggestions, is the increase of the percentage of proteins in the diet, prior and during the breeding season to stimulate pairs to start breeding (Galama et al., 2002; Gregson, 2001; Morrier & King, 2014). Another proposal suggested to motivate pairs to breed is the provision of artificial rain showers that could stimulate hornbill pairs to start performing reproductive behaviors, while simultaneously improving humidity in the nest box (Galama et al., 2002). Galama et al. (2002) also states that the nest itself and nest-related behaviors are extremely important for breeding success of hornbills, and therefore, parameters like nest entrances, sealing material, nest lining, and an ability to perform reproductive behavior (such as courtship) are important stimulants to overall reproductive success in zoos.

It is, therefore, important to assess the reproductive activity of these hornbill species in zoological institutions, to find predictors of breeding success, improve the ex situ reproduction success, and to focus on advances in bird husbandry and management and novel population-management techniques. This then will hopefully lead to an increase in the sustainability within these ex situ populations.

This paper focusses on two species of the genus *Rhyticeros*, the wreathed hornbill (*Rhyticeros undulatus*) and the Papuan hornbill (*Rhyticeros plicatus*). The wreathed hornbill is currently classified as Vulnerable with a decreasing population trend according to the IUCN Red List of Threatened Species (BirdLife International, 2018; Krishna et al., 2012; Setha, 2004), therefore, supporting a viable and self-sustaining ex situ insurance population is warranted (Brouwer et al., 2020). The Papuan hornbill, however, is listed as Least Concern but is decreasing in population size (BirdLife International, 2020). Nevertheless, the ex situ population of Papuan hornbill is still considered of conservation value relevant to in-range capacity building and conservation education, especially in rescue centers, as husbandry and other management experiences can be shared (Brouwer et al., 2020). It could potentially serve as a model species for testing and trailing aspects of animal care needed for similar species that do require conservation planning (Kerr, 2020; Rose, 2021), like the wreathed hornbill. The use of model species and proxies for developing husbandry and conservation would align captive hornbill management with the IUCN's One Plan Approach to Conservation (Byers et al., 2013) which encourages a sliding scale of management for a species wherever it is found. Furthermore, the primary forests that the Papuan hornbill inhabits are also among the most threatened in the world (White et al., 2021), which could result in this species becoming of conservation concern in the future.

Although information on wild ecology and habitat selection is limited for both species, literature suggest that both species have a comparable ecology and inhabit primary evergreen forests extending into secondary forests (Kemp & Boesman, 2020; Kemp & Kirwan, 2020). Both species are mainly frugivorous, with a substantial portion of the diet consisting of fig (*Ficus* spp.) species (Kinnaird et al., 2008). However, these hornbills are also known to forage on live prey, including invertebrates (e.g., insects and crustaceans), birds, and small reptiles (Hadiprakarsa & Kinnaird, 2004; Kemp & Boesman, 2020; Kemp & Kirwan, 2020). Live prey are mainly consumed during the breeding season (Kemp, 2001; Kemp, 1995; Kemp & Boesman, 2020), which occurs from January to October and corresponds with the rain season and, therefore, also the peak fruiting season after the rain season (Kemp & Boesman, 2020; Kemp & Kirwan, 2020; Kinnaird et al., 2008). Both species are monogamous, which is a trait shared across these birds (Kemp, 1995; Kinnaird et al., 2008). These two hornbill species exhibit a range of different breeding behaviors to cement their pair bond. Individuals within a pair increase the frequency, duration, and intensity of calls and displays to each other, which are usually the first signs of breeding (Kemp, 1995). Furthermore, courtship-feeding between birds is a well-described behavior (Kemp, 1995) and suggests a pair is compatible. Like all Asian hornbills, both species utilize cavities in large mature trees for nesting, where the female seals herself within this cavity during incubation and chick rearing, while the male provides food for both her and the chicks (Kemp & Boesman, 2020; Kemp & Kirwan, 2020; Kinnaird et al., 2008).

The key aim of this investigation was to summarize the information, applicable to future standardization of species-specific husbandry practices for two representative species of wreathed hornbills globally, and to identify potential predictors of breeding success in wreathed- and Papuan hornbill pairs kept ex situ. It is predicted that there are significant predictors of breeding success to be found within the ex situ management for the wreathed and Papuan hornbills.

2 | MATERIALS AND METHODS

2.1 | Survey participants and selection

All holders of the wreathed hornbill and Papuan hornbill within EAZA and AZA institutions were contacted and additional holders outside of these associations were suggested by the EEP coordinator and contacted by the author. The contact details of wreathed hornbill and Papuan hornbill holders were sourced through Species360 or were provided by the EEP coordinator. The survey was sent to the 27 holders of the wreathed hornbill and 31 holders of the Papuan wreathed hornbill. For the wreathed hornbill, 21 holders responded (77.78% of holders contacted), the survey was filled in for 23 pairs as two holders held multiple pairs within their collection. One response was excluded from data analysis because the holder housed only a single bird over the last 5 years. Data for 22 pairs were included in the analysis. For the Papuan hornbill, 27 holders responded (87.1% of holders contacted). Seven responses were excluded from data analysis because the holder housed a single bird in the last 5 years, the pair had not yet been housed together, or due to incompleteness of the data. Data for 20 pairs were included in the analysis. Institutions responding to the survey were located in Europe, the United States, the Middle East, and Asia (see Table 1, a complete overview of the study population can be found in Supporting Information S1: Data 1).

2.2 | Data collection

Data were collected through the distribution of a husbandry and reproduction survey consisting of 68 questions and was provided in a Microsoft Word document (Supporting Information S1: Data 2; Survey: Reproductive and husbandry management of *R. plicatus* and *R. undulatus* in zoological institutions). Each holder was asked to complete the survey for all wreathed hornbills and/or Papuan hornbills housed within their collection. The survey was divided into six sections with the following subjects: (1) Pair background, including Zoological Information Management System (ZIMS) ID (to extract age and sex

TABLE 1 Overview of the study population of hornbills for both species included in the survey with information relating to the age range, age difference between the pair, and the years the pair has been together.

Species	Min. age	Max. age	Mean (±SD) age	Min. age difference between pairs	Max. age difference between pairs	Min. years together	Max. years together
Wreathed hornbill males	2	29	14.6 ± 8.62)	0	22	1	28
Wreathed hornbill females	3	32	15.25 ± (9.60)	0	22	1	28
Papuan hornbill males	5	24	13.52 ± (6.16)	0	16	3	30
Papuan hornbillfemales	4	25	14.28 ± (8.)	0	16	3	30

Note: A full overview of all individuals can be found in Supporting Information S1: Study population.

of individuals), and the time the pair has been housed together; (2) nutrition, including nonbreeding and breeding diet, frequency of feeding and ways in which the diet was offered to the birds; (3) physical environment, including enclosure size, time spent in the enclosure, temperature, foliage cover and rain showers; (4) health, including predation, annual health checks and vaccinations; (5) behavioral interaction, including breeding behaviors, aggressive behaviors, hornbill-keeper interactions, interactions between the hornbills and other species housed within the enclosure or adjacent enclosure, husbandry practices, enrichment and training; (6) breeding success, including breeding forms occurring over the last 5 years (2017–2021), breeding information (e.g., date of sealing, hatching, and fledging), nest box information and measurements and monitoring practices. The survey was compiled of a mix of open- and close-ended questions, including multiple-choice questions. All multiple-choice questions in the survey included an "other" option, and open-ended responses were asked to be specified in a comment box. Data were collected from the April 27, 2022, until the August 21, 2022. Reminder emails were sent to recipients every 2 weeks; from the July 14, the EEP coordinator sent out reminders to all zoos that did not respond to the survey thus far. If survey responses were incomplete or answers were unclear, the respondent was contacted with these follow-up questions. This study was ethically approved by the University Centre Sparsholt Ethics Committee (Code: USCEC 8421).

2.3 | Data analyses

The key aim of this research project was to find predictors of ex situ breeding success in wreathed and Papuan hornbills. The statistical program Minitab v.19.2020.1 (Minitab, 2022) was used for all statistical tests in this study. To analyze the effect of the bird-based and environmental predictors on the ex situ breeding success of the wreathed hornbill and the Papuan hornbill, Binary Logistic Regressions were utilized. Data were rationalized to allow data analysis. Data on breeding over the last 5 years (young successfully fledged) were extracted and converted into binary answers. Predictors without any variance within the data points, or with only one divergent data point, were not considered as potential predictors of breeding success and were, therefore, excluded from statistical analysis to allow the model to run the statistical tests. For example, all individuals were fed in a bowl and, therefore, this predictor was excluded from analysis. For all analyses, individual responses were given for each sex of hornbill, but species were combined into one data set due to the small overall sample. Age of both male and females were extracted from ZIMS and the age difference between the individual birds were calculated.

2.4 | Bird-based model

To determine any impact of bird-based factors on the success (or not) of fledging young, a binary logistic regression was run. The outcome variable was "young successfully fledged" over the last 5 years, with yes/no as the binary outcome, and the predictors included were "Age difference", "Years together," "Calls and displays," and "Sitting in close proximity of each other." The variance inflation factor (VIF) for this model's factors were all below 2 and so all factors were kept in the model. The r^2 of this model was 0.0822 meaning that 8.22% variation was captured by the factors that were used. Predictors were split between bird-based and environmental-based factors as it considers individual differences that are animal-specific, whereas the environment is the same for each individual bird at that specific institution.

2.4.1 | Environmental-based model

Differences between nonbreeding and breeding diet were extracted and compiled into binary answers, yes if there was an increase in the amount, no if diets stayed the same or there was a reduction in the amount. The predictor increase in proteins during the breeding season was extracted from the predictors increase meat during the breeding season and increase insects during the breeding season. As there are no zoos that reduce the amount of protein prior or during the breeding season, this predictor was also converted into binary answers. The provision of sealing material and nest lining were both converted into binary answers of yes or no. Predictors were either categorized in either binary answers or grouped into three categories (e.g., natural, rectangle, and other) to allow for statistical analysis.

The environmental model was originally going to include the following predictors ("Increase in dietary proteins prior and during the breeding season," "Provision of artificial rain," "Average indoor temperature," "Outdoor foliage density," "Nest box type," "Nest box floor," "Nest box location, "Nest box entrance hole shape," "Provision of nest lining," and "Provision of sealing material"), as these are potential predictors contributing to ex situ breeding success described in literature. However, due to a quasi-complete separation of data points, only the following predictors were included in the model "Increase in dietary proteins prior and during the breeding season," "Provision of artificial rain," "Nest box type," "Nest box floor," "Nest box location," "Provision of nest lining," and "Provision of sealing material." With the outcome variable "young successfully fledged" over the last 5 years, with yes/no as the binary outcome. The VIF for this model's factors were all below 2 and so all factors were kept in the model. The r^2 of this model was 0.1338 meaning that 13.38% variation was captured by the factors that were used.

3 | RESULTS

The survey provides information on 44 individual wreathed hornbills in 20 zoological institutions worldwide (EAZA = 13 institutions, AZA = seven institutions, Other = one institution). For the Papuan hornbill, the survey provides information on 40 individuals in 20 zoological institutions worldwide (EAZA = 14 institutions, Other = six institutions).

3.1 | Ex situ demographic and population information

For the wreathed hornbill population, there were 22 females and 22 males included in this data analysis (Figure 1). Most animals were in the middle (between 11 and 15 years old) age group (*N* = 10). Four birds within the sample size are of unknown age. Half of the pairs have been kept together 5 years or less (*N* = 11). Five pairs were kept together for more than 15 years.

For the Papuan hornbill population, there were 20 females and 20 males included in this data analysis (Figure 1). For the majority of individuals, the age is unknown (*N* = 13). The age group 6–10 contains the most individuals of which the age is known. More than half of the pairs have been kept together 5 years or less (*N* = 13). Three pairs were kept together for more than 15 years.

3.2 | Regression analyses of bird-based factors on ex situ breeding success

Table 2 illustrates the full model output results of the Binary Logistic Regression model testing for a relationship between several bird-based factors of the population surveyed and the overall fledged young in the last 5 years as the response variable. The model found that the years that a pair has spent together is a predictor of successful breeding ($\chi^2 = 5.83$; SE = 0.0502; $df = 1$; $p = .016$). The other three predictors: age difference, the behavioral outputs: Calls and displaying and sitting in close proximity of each other were not significant predictors of ex situ breeding success in this model.

3.3 | Regression results of environmental-based factors on ex situ breeding success in wreathed and Papuan hornbills

The Binary Logistic Regression testing for a relationship between environmental-based predictors and the overall fledged young in the last 5 years as the response variable found one significant predictor of breeding success. Table 3 illustrates the full model output results for the environmental-based model. The predictor: Increase in dietary proteins prior and during the breeding season was found to be a significant predictor of breeding success for these two hornbill species ($\chi^2 = 7.56$; SE = 0.891; $df = 1$; $p = .006$). The predictor of the nest box being situated in the outside enclosure showed a general trend ($\chi^2 = 3.72$; SE = 0.750; $df = 1$; $p = .054$) and is worthy of further study. The type of nest box, the shape of the nest box floor, and the provision of artificial rain, sealing material, or nest lining were found to be nonsignificant in the final logistic regression model. However, for both behavioral outputs there is a descriptive trend which will be illustrated in Section 3.4.

3.4 | Behavioral outputs of hornbill pairs

Although model outputs for time spent sitting together and time spent vocalizing were nonsignificant, descriptive analyses reveal that for both of these behavioral outputs, a trend can be observed for the

TABLE 2 Model output of the Binary Logistic regression testing for a relationship between bird-based factors and successfully fledged young in the last 5 years for wreathed and Papuan hornbills.

Predictor	SE coefficient	*df*	χ^2	Deviance R^2 (adj)	*p* Value
Age difference	0.0545	1	2.97	-	.085
Years together	0.0502	1	5.83	-	.016[a]
Calls and displays		1	0.30	-	
Yes	0.750				.586
Sitting in close proximity of each other		1	1.61	-	
Never	1.03				.555
Occasionally	0.849				.352
Overall model output	0.968	60	65.98	0.0822	.278

[a]Values are significant.

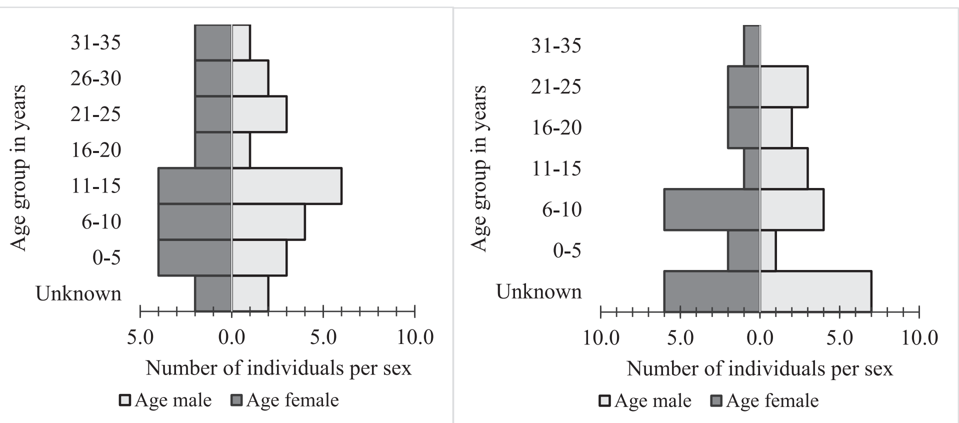

FIGURE 1 Demographic of the wreathed hornbill (left), and Papuan hornbill (right) ex situ population.

subpopulation of birds that have successfully reared young. Birds that have successfully bred can be observed seen sitting in close proximity more often (77.78%) (Figure 2) and these birds were more likely to be calling and displaying to each other (50%) (Figure 2).

TABLE 3 Model output of the Binary Logistic regression testing for a relationship between environmental-based factors and successfully fledged young in the last 5 years for wreathed and Papuan hornbills.

Predictor	SE coefficient	*df*	χ^2	Deviance R^2 (adj)	*p* Value
Increase in dietary proteins prior and during the breeding season					
Yes	0.891	1	7.56	-	.006[a]
Provision of artificial rain					
Yes	0.827	1	0.80	-	.372
Nest box type					
Natural	1.12	3	0.47	-	.715
Rectangle	0.813				.869
Other	1.11				.761
Nest box floor					
Sloped towards the middle	0.821	1	0.97	-	.324
Nest box location					
Outside	0.750	1	3.72	-	.054
Provision of sealing material					
Yes	0.910	1	1.32	-	.250
Provision of nest lining					
Yes	0.958	1	2.01	-	.126
Overall model output	1.51	74	70.87	0.1338	.582

[a]Values are significant.

3.5 | Nest box characteristics

Results revealed (Table 4) that wooden barrels (*N* = 7) and rectangle wooden boxes (*N* = 7) were the most commonly provided nest box types for the wreathed hornbill. For the Papuan hornbill, the most commonly provided nest box was a rectangle wooden box (*N* = 12). The mean entrance hole length wreathed hornbill: 0.27 ± (0.07), Papuan hornbill: 0.26 ± (0.07), and width wreathed hornbill: 0.17 ± (0.07), Papuan hornbill: 0.16 ± (0.05) differed by only 1 cm between the two species. Nest boxes for the wreathed hornbill were offered more than a meter higher than for the Papuan hornbill. The distance between the entrance hole and the floor of the nest box was more substantial with the Papuan hornbill nest boxes compared to the wreathed hornbill nest boxes. The floor of the nest box was flat for the majority of pairs of both species (wreathed hornbill: *N* = 19, Papuan hornbill: *N* = 14). The entrance hole shape was oval for the majority of nest boxes provided to both species (wreathed hornbill: *N* = 14, Papuan hornbill: *N* = 15).

4 | DISCUSSION

These results represent an in-depth analysis of wreathed- and Papuan hornbill husbandry, management, and reproduction success across North American, European, and Asian institutions. This research has shown that pairs that have spent more years together (*p* = .016) and that adding additional proteins to the diet (*p* = .006) are two significant predictors of breeding success for wreathed- and Papuan hornbill pairs. This study found that only 18% of wreathed hornbill pairs and 25% of Papuan hornbill pairs reproduced successfully in the last 5 years.

Pair-bonding through courtship behavior is suggested in the literature as essential for the development of strong and successful pairs (Kemp, 1995; Kinnaird et al., 2008), and it may be that pairs that have been housed together for only a few years have not yet had the opportunity to form strong pair bonds or are not yet of breeding age.

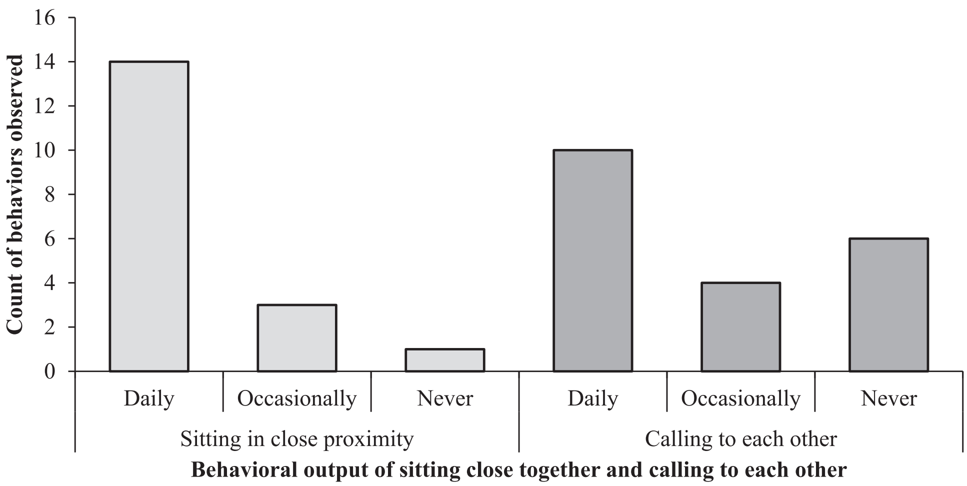

FIGURE 2 Behavioral outputs, for hornbills that have successfully nested, of sitting in close proximity of each other and calling and displaying to each other. "Occasionally" includes birds that exhibit the behavior less then daily.

TABLE 4 Mean and (SD) of the nest box characteristics offered to the wreathed hornbill and Papuan hornbill pairs.

Nest box type	Nest box length (m)	Nest box width (m)	Nest box height (m)	Nest box entrance hole length (m)	Nest box entrance hole width (m)	Nest box height placement (m)	Distance between entrance hole and floor of the nest (m)
Wreathed hornbill (*n* = 44)	0.65 ± (0.16)	0.65 ± (0.22)	1.00 ± (0.22)	0.27 ± (0.07)	0.17 ± (0.07)	3.35 ± (3.02)	0.22 ± (0.08)
Papuan hornbill (*n* = 40)	0.61 ± (0.25)	0.56 ± (0.12)	0.92 ± (0.19)	0.26 ± (0.07)	0.16 ± (0.05)	2.23 ± (1.49)	0.30 ± (0.20)

An ex situ study into the reproductive behavior of the great hornbill (*Buceros bicornis*) suggests that pair bonds may strengthen and the probability of successful reproduction may increase, the longer individuals are kept together (Kozlowski et al., 2015). However, there is also evidence that repairing individuals that did not reproduce for years resulted in reproduction success within a few months (Galama et al., 2002; Macek, 1997). As the study period was 5 years, a further investigation of past and more recent reproductive behavior of pairs would further clarify the length of time a pair typically needs to become reproductively active and how behaviors and degree of success progress. This would allow better decision-making regarding repairing of individuals, including evaluating whether older individuals have become reproductively senescent. It is of paramount importance that young and unsuccessful pairs are monitored and evaluated each year to identify bonded and potentially successful pairs and repair pairs that are not interested in each other and are, therefore, deemed unsuccessful.

Although the majority wild hornbill diets consists of fruit and figs (Kinnaird et al., 2008; Poonswad et al., 2004), both species of hornbills are also known to forage on live prey (Hadiprakarsa & Kinnaird, 2004; Kemp, 2001; Kemp & Boesman, 2020; Kemp & Kirwan, 2020; Kinnaird et al., 2008), but evidence on the percentage of proteins consumed in both the nonbreeding and breeding diet vary (Kinnaird et al., 2008; Poonswad et al., 2004). Results show that the predictor of increase in dietary proteins prior and during the breeding season, has proven to be significant factor for breeding success (p = .006), which corresponds with the literature that live prey are mainly consumed during the breeding season (Beilby, 2022; Kemp, 2001; Kemp, 1995; Kemp & Boesman, 2020; Poonswad et al., 2004). It is, therefore, important to increase the percentage of proteins in the diet, prior and during the breeding season to stimulate pairs to start breeding, as also is suggested by Galama et al. (2002), Gregson (2001), and Morrier and King (2014). Figs are an important source of food for Asian hornbill species (Kinnaird et al., 2008; Poonswad et al., 2004), these fig species are reliant on pollinators such as fig wasps (*Agaoninae*, *Agaonidae*, *Chalcidoidea*), which, in turn, lay their eggs in these figs (Borges, 2015; Harrison, 2005). Therefore, these wasp eggs within the figs are likely to provide wild hornbills with additional dietary protein, as noted for other bird species (Mackay et al., 2018). Zoos could replicate this phenomenon by adding mealworms or other small insects into large pieces of fruit. Stimulating seasonal change within captive hornbill diets is clearly needed to stimulate breeding but caution is recommended when adding extra dietary protein as iron storage disease (ISD) or secondary hemochromatosis, caused by high dietary iron levels (Gamble et al., 2012; Schlegel & Howenstein, 2013; Sheppard & Dierenfeld, 2002) is noted in these species. As invertebrate proteins contain lower iron levels (Galama et al., 2002) when compared to vertebrate proteins there may be less of a risk but the iron content of captive hornbill diets should not exceed 50–100 ppm dry matter to prevent ISD (Galama et al., 2002; Schlegel & Howenstein, 2013).

This paper found a general trend that successful hornbill pairs prefer nest boxes that are situated outside (p = .054). This could be because these nest boxes are exposed to the elements and, therefore, maintain more natural temperature and humidity levels within the nest (Kinnaird et al., 2008; Rahayuningsih et al., 2022; Utoyo et al., 2017). Maintaining humidity levels similar to those found in natural habitats (90%) might positively affect breeding success ex situ (Galama et al., 2002) and, therefore, it could be important that zoos replicate the nest characteristics found in the wild as close as possible. Providing foliage in indoor areas close to the nest box could also provide additional humidity and may help individuals feel more secure in enclosure areas that may be less furnished and less naturalistic.

Although this paper did not find significant behavioral outputs for successful pairs due to a small sample size, the behaviors of calling to each other and sitting in close proximity showed a general trend and were observed more frequently in these successful pairs and, therefore, could be good indicators of bonded pairs. Kozlowski et al. (2015), found that vocalizations by male great hornbills were the most frequently observed courtship behavior prebreeding season and suggests that the amount of time pairs spend in proximity, may help evaluate compatibility and the likelihood of successful reproduction for pairs of great hornbills. Calling and displaying are also described by Kemp (1995) as among the first breeding behaviors occurring. Therefore, the behavioral trends observed in this paper are similar to known behaviors of wild hornbill pairs. Although literature suggests that most Asian hornbills are monogamous (Kinnaird et al., 2008), both the wreathed and the Papuan hornbill are observed to flock together outside of the breeding season, occasionally in groups of over 1000 individuals at communal roosts (Kemp, 2001; Kemp & Boesman, 2020; Kemp & Kirwan, 2020; Naniwadekar et al., 2021; Zheng et al., 2020). Therefore, this flocking likely serves a social function by enabling maturing birds to find and evaluate potential partners or provides a mechanism for already successfully breeding adults to change breeding partners in these communal flocks for subsequent seasons. While this hypothesis has yet to be formally tested (Kinnaird et al., 2008), social choice is evidently an important aspect of a hornbill's life history and behavioral ecology and one that zoos are recommended to try and replicate if breeding results are still poor following other husbandry interventions. Multi-institutional research on the behavioral predictors of reproduction and mate choice in wreathed and Papuan hornbills could further provide evidence on the role of social and courtship behaviors, and how they might predict successful reproduction (Kozlowski et al., 2015).

Dimensions of the nest entrance are of immense importance for most hornbill species (Ponsawat et al., 1987; Rahayuningsih et al., 2017; Sibarani et al., 2020). A small entrance helps to keep intruders out and is easier to seal (Galama et al., 2002). The entrance does not have to be much wider than the width of the female from shoulder to shoulder when the wings are drawn in (Kemp, 1995). This research found that the mean width of the entrance hole provided to wreathed hornbill pairs ex situ was 17 cm, which compared to data from the wild is 7 cm wider than the wild mean width (Rahayuningsih et al., 2017). This larger mean entrance hole width could cause a nesting female hornbill to feel insecure and, therefore, not commence breeding. Although similar in situ data on nest characteristics for Papuan hornbills are not available, a noteworthy observation is that the mean width of the entrance hole of the Papuan hornbill pairs is only 1 cm smaller than the mean entrance width of the wreathed hornbills. The mean body mass of the Papuan hornbill is 790 g smaller for males and 283 g smaller for females compared to wreathed hornbills (male: 2510 g, female: 1950 g) (Kemp, 1995; Kinnaird et al., 2008). This would indicate that Papuan hornbills need a smaller entrance hole to feel secure and to be able to properly seal their nest entrance. Smaller nest entrances might also prevent males from entering the nest box while the female is incubating as this has been observed as disturbing for successful reproduction (Galama et al., 2002).

A limitation of any husbandry survey is the balance between the scientific validity of data collected and the time constraints of those working in zoos to fill in such a questionnaire thoroughly. Comparably, the behavioral data gathered through this questionnaire have been filled in by numerous zoo staff and, therefore, the scoring of these behaviors might differ between individual respondents. Furthermore, these data rely on the recollection of behaviors observed by the respondent or by the person inputting these data onto ZIMS. These variables described above may also explain the low r^2 values, captured by the Binary Logistic Regression models. Therefore, this type of study would benefit from in person data collection at multiple institutions (Kozlowski et al., 2015; Lemos de Figueiredo et al., 2021) or by requesting video footage as an extension of our research, which might improve reliability and validity of data and outcomes. Another method to extend this research could be to identify holders with repeated breeding success and conduct a series of qualitative interviews to identify additional predictors of ex siu breeding success for these species of hornbills (Karlsdóttir et al., 2021). This method would be a valuable tool as it allows for experts to express their thoughts on topics that might otherwise not be evaluated within a questionnaire (Brinkmann & Kvale, 2015; Bryman, 2016).

It may also be important to consider the latitude of the zoo holding tropical species and how the zoo's global location may impact on animal responses to the environment. If captive animals are exposed to an external environment that markedly differs from their range states (e.g., day length, temperature, and humidity), breeding success may be reduced (Heldstab et al., 2020; Schulte-Hostedde & Mastromonaco, 2015). As our study is only preliminary, we would encourage further research that comprises visiting zoos holding these hornbills to assess the degree of outdoor access these individuals may have and compare any associated differences in climatic conditions that may impact the performance of reproductive behavior.

Furthermore, ex situ populations of both species are relatively small and although the response rate for this survey was high (82.76%), more data may have given significant findings on compatibility. As our statistical analysis only utilized a binary outcome as the response variable (as most pairs only produced one chick in the last 5 years) it was not possible to grade reproductive success between pairs. Extending this research for a longer period of time may provide more data on instances of successful breeding that would allow for a change in modeling away from a yes/no perspective. Further study across species, could also illuminate what causes successful breeding and provide further identification of predictors to use in such analysis. Zoos are encouraged to monitor the behavioral development of their birds, consider how much time pairs spend together and match this alongside natural dispersal and mate choice activities in the wild.

These data could also be enhanced by repeating the same research on another species of Asian hornbill, similar in size and ecology (Kemp, Boesman & Sharpe, 2020) with a relatively large ex situ population (ZIMS, 2023), the wrinkled hornbill (*Rhabdotorrhinus corrugatus*). This additional data could then be added to the already existing sample size and the statistical analysis repeated.

5 | CONCLUSIONS

We recommend that ex situ institutions allow their hornbill pairs time to form strong bonds, as it may take several years for pairs to successfully breed. Hornbill pairs, therefore, need to be monitored and their compatibility evaluated each year to identify bonded (and, therefore, potentially successful) pairs, and to then repair birds that are not compatible or show little interest in nesting. An increase in the percentage of dietary proteins, prior and during the breeding season appears to stimulate pairs to start breeding. Further research should focus on developing reliable protocols using behavioral outputs such as calling, displaying, and sitting in close proximity of each other as predictors of pair bonding and breeding readiness. Further research on the measurements and internal environmental parameters of nest boxes for wreathed- and Papuan hornbills is recommended to determine the most successful nest box design for these birds.

If the management and husbandry alterations presented in this study are implemented for ex situ hornbill populations, the sustainability of such *Rhyticeros* hornbills may be enhanced and add further value (from a conservation and avicultural perspective) to their place in living collections globally.

AUTHOR CONTRIBUTIONS

Kees Groot and James E. Brereton developed the concept of the manuscript. Kees Groot and Catherine E. King completed the survey design, and its distribution, and collected all data. Kees Groot and Paul Rose undertook the analysis and drafted the original text. All authors contributed to review and editing of the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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