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RESEARCH ARTICLE

Seasonality, Social Structure and Age Predict Conspecific Aggression in Captive Breeding Southern Ground-Hornbills (*Bucorvus leadbeateri*)

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ABSTRACT

Southern Ground-hornbills (SGHs) are listed as Vulnerable globally, and Endangered in South Africa, Namibia and Swaziland, due to poisoning, habitat loss and persecution. Successful conservation breeding and rearing of redundant second-hatched chick protocol has been established to supplement natural SGH populations in an attempt mitigate a declining population. However, captive rearing is costly and susceptible to loss of birds through conspecific aggression. Maximising the efficacy of reproductive output in captive settings and ensuring successful reintroductions of captive-reared birds to wild populations is of paramount importance if this species is to persist. Therefore, it is important to untangle the predictors of what drives mortalities in captive birds, particularly, through conspecific aggression. Using a database of captive SGH mortalities collected over 46 years we investigated whether variables such as season, age, relatedness, sex and husbandry predicted the occurrence of conspecific aggression in SGH. Aggression among adult, non-related birds particularly during SGH breeding season (austral spring) was the most predictable form of conspecific aggression. It was inferred that aggression is normally directed at non-related birds outside of already established social groups or at younger, related birds that are not dispersing from groups when reaching sexual maturity. Variables such as season, age, relatedness and husbandry were therefore all useful for predicting the potential and avoidable occurrence of an aggression event. Male birds were most often the aggressors. Making use of such variables to manage birds in a captive setting, move birds before sexual maturity and maintaining birds in known and accepted social structures could greatly improve management in SGH breeding facilities and optimise the efforts for re-establishing natural SGH populations.

1 | Introduction

Aggression, both intra- and inter-specific is well documented across multiple taxa and forms a central role in moulding social structures, maintaining territories and partitioning resources (Evans 1970; Grether et al. 2013; Tóth et al. 2009). At times beneficial, aggressive acts may be costly and potentially fatal. This is true for both the aggressor and the victim, particularly, when considering the energetic cost and time invested and most critically potential injuries, which reduce fitness and increase the probability of fatalities. Aggression is unlikely a stochastic event, but rather deterministic, meaning aggressive interactions

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Summary

- Conspecific trauma accounted for approximately 7.80% of all recorded Southern Ground-hornbill (SGH) mortalities.
- Seasonality significantly influenced aggression, with more attacks in austral spring compared to autumn.
- Breeding status did not affect aggression frequency; non-breeding individuals were more often involved.
- Males were not significantly more aggressive than females or pairs, but non-breeding individuals were most aggressive in austral winter and spring.
- Victim sex or attacker sex did not predict aggression likelihood.
- Age and sex determined onset of attacks with majority of attacks been adult birds and females (8.8 ± 8.3 years) been attacked earlier then male (9.1 ± 8.9 years).
- Group size did not significantly influence attack frequency.
- Moon phase did not affect aggression occurrence.

may be predictable. Essentially aggression may be a consequence of one or more predictable environmental conditions (both natural and anthropogenic), especially in a captive setting. For instance, among captive American (*Phoenicopterus ruber*—Bildstein, Frederick, and Spalding 1991) and Chilean flamingo—(*Phoenicopterus chilensis*—Perdue et al. 2011) aggression was shown to increase in response to season often resulting in serious injuries, disruptions in the reproductive cycle and at times death, all of which, in turn, reduce breeding success. Identifying drivers of conspecific aggression is important for understanding biological systems and especially important for successfully managing both wild and captive species. This is especially true for captive-based breeding efforts for Vulnerable and Endangered species, which aim to supplement dwindling natural populations. For instance, disappearing keystone species such southern African vultures (four of six species listed as Critically Endangered) have become reliant on captive breeding efforts as one of the conservation tools to bolster populations and avoid regional extinction (Hirschauer et al. 2022). Such projects, while challenging, are critically important for maintaining ecological functionality and preserving diverse, stable and resilient ecosystems (Estes et al. 2011; Kuussaari et al. 2009). Minimising conspecific aggression injuries and fatalities within such breeding facilities is thus important.

Southern Ground-hornbills (*Bucorvus leadbeateri*), hereafter referred to as SGH, are such a species that is at risk of going extinct without human intervention due to anthropogenic activities: persecution, poisoning and landscape transformation (Kemp 2000; Kemp and Webster 2008). One of two species described in the genus *Bucorvus*, the SGH feature among the largest flying hornbills (species average = 3.8 kg; males = 4.2 kg and females = 3.3 kg; Hockey, Dean, and Ryan 2005) and are endemic to sub-Saharan Africa with a distributional range that extends from Kenya south to the Eastern Cape province of South Africa (Kemp et al. 2020). Terrestrial and occupying a wide variety of habitats including savanna, grassland and mixed woodland thickets (Hockey, Dean, and Ryan 2005), SGH are long-lived, generalist carnivores. These ground-hornbills breed cooperatively and support a complex family/social structure (Hockey, Dean, and Ryan 2005). Family groups normally comprise three to five individuals, which include a dominant breeding pair (i.e., alphas) and helpers (usually non-breeding adult or immature males from previous breeding years) (Hockey, Dean, and Ryan 2005; Kemp and Kemp 1980). Male helpers fulfil various roles including territorial defense and feeding the nest-bound female during incubation(Carstens et al. 2019b). Female birds generally disperse from their family groups after 1–3 years. Groups of SGH are highly territorial and usually, depending on habitat composition, defend large areas (80–250 km^2) and as such (Kemp et al. 2020), naturally occur at low densities. Declining populations are exacerbated by slow breeding groups do not breed every year, and only a single chick is ever reared per group per year due to obligate brood reduction (Jordan 2011, Hockey, Dean, and Ryan 2005).

Globally Vulnerable and Endangered in South Africa, Namibia and Swaziland, without human intervention, SGH faces regional extinction (Taylor, Peacock, and Wanless 2015). Rapid declines in SGH population size are linked to life history traits coupled with increasing anthropogenically driven landscape transformation, decreasing nesting sites, resource availability and increased human persecution (Carstens et al. 2019b, Koeppel and Kemp 2015; Theron et al. 2013). Rapid declines in SGH population size motivated the establishment of the 'National Single Species Recovery Plan for South Africa' (Jordan 2011) whose aim is to address and mitigate the known hindrances to the re-establishment of the South African SGH population. The plan aspires to implement effective conservation management practices in the hopes of eventually stabilising and increasing the SGH population, motivating the downgrading of the conservation status of SGH. One of the strengths of the 'Recovery Plan', is the captive-rearing programme which reintroduces captive-reared SGH individuals into the wild to bolster natural populations. However, in order for this complex process to be successful, and logistically and financially viable, the breeding programme must be refined and optimised to maximise survival (Kemp 2017; Kemp et al. 2020).

Historically conservation efforts have largely focused on the reintroduction of captive-reared animals to bolster vulnerable natural populations. This approach has been particularly successful for species such as the SGH (Combrink et al. 2020). However, for this approach to be successful long-term, it is pertinent that an informed stance regarding optimal housing conditions is established for successful breeding yields to be achieved in a captive setting (Carstens et al. 2019b). In recent years, there has been a growing appreciation of how an understanding of the basic reproductive processes may aid in species management and conservation (Schwarzenberger and Brown 2013). Optimising the reproductive performance of populations under threat requires a multifaceted approach and a thorough understanding of reproductive behaviour and endocrinology, as both factors may have a significant influence on the level of aggression between individuals (Schwarzenberger and Brown 2013). Multiple reports suggest that the reintroduction efforts of SGH have been largely hindered by mortalities brought about by conspecific aggression prior to release (Danel, Rebout, and Kemp 2023). To date, drivers of conspecific

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aggression specifically within SGH are not well understood. Determining which factors drive conspecific aggression is pertinent to conservation success and could have major benefits for the management strategies of global captive-bred SGH populations.

This study, therefore, aims to determine whether aggression in captive SGH is predictable based on known variables such as age, sex, relatedness, husbandry and season. Such information would be valuable for informing managers on how to optimise SGH breeding success. It was predicted that:

1. Aggression will be higher between non-related individuals.
2. Aggression will increase approaching and during the breeding season.
3. Aggression will be initiated by adults involved in social groups, defending against birds from outside of the established social framework.
4. Male helpers and alpha pairs would therefore be more likely to attack birds outside of the family group regardless of sex.

2 | Methods and Materials

2.1 | Data Compilation and Study Sites

Data were collected between 1975 and 2021 among multiple captive SGH breeding and rearing facilities. Birds included in the study were held captive at various reserves and establishments: the Mabula Ground Hornbill Project (MGHP) and Mpumalanga Tourism and Parks Agency Alliance Baobab Conservation Rearing Centre (25.40274, 29.27988), National Zoological Gardens (−25.73579, 28.19049), Ubhetyan O′ Africa (−25.52062, 29.55843), Hoedspruit Endangered Species Centre (−24.51348, 31.03352) and Johannesburg Zoo (−26.16744, 28.03824).

Mortality data for SGH in South Africa was recorded opportunistically in a national mortality database, of which the MGHP is the curator. Fatalities were reported, with details specific to each victim and aggressor when known. In most cases, a recorded mortality in a facility was followed up by a post-examination by the veterinary scientists at the National Zoological Gardens or the University of Pretoria Faculty of Veterinary Science. These post-mortems allowed for the cause of death to be determined. In cases where carcasses were discovered in enclosures where trauma was indicated as cause of death, conspecific aggression was specified in the national mortality database. Conspecific aggression-related injuries requiring veterinary attention, so not necessarily leading to mortality, were also included in the data set.

2.2 | Survey

An online survey was undertaken, which required participants to complete several questionnaire sections related to aggressive behaviour among SGH at their facilities (Supporting Information). The survey consisted of seven components, the first of which asked if aggressive interactions had ever been encountered and if so, whether the participant was willing to share such data. The following five sections dealt with each variable related to the study, namely the sex, ages, group dynamics and husbandry, as well as information related to time and season of the interactions. The final question in the survey asked participants that had recorded no aggressive interactions to write a short note on the management practices at their respective facilities to fully assess possible factors that negate aggressive interactions.

2.3 | Data Sorting

Mortalities listed as conspecific were extracted from the national mortality database and imported into a separate spreadsheet for data analysis. Analytical variables were extracted for both the individual that was attacked and the aggressor and included sex, age and season at the time of the aggressive interaction. If a bird died, and no age was specifically stated, age was calculated as date of birth to date of death. The composition (sex, relatedness, age) of birds housed within the enclosure where the attack took place were included as variables. Aggressors were classified as breeding if they had produced a chick or egg in the past. Data were categorised for both victims and aggressors. Victims included birds that had fallen victim to an aggressor, while aggressors were birds that initiated and/or participated in the conspecific attacks. Birds that survived attack due to human intervention were included into the database.

Age was categorised into adult (> 6 years), sub-adult (2–5 years) and juvenile (0–2 years) (Hockey, Dean, and Ryan 2005) as consistent with the recording protocol used to construct the national mortality database. Data were further classified into age in years for each of the data points for both aggressors and individuals, providing a finer temporal scale and/or specific time at which animals in each age category were attacked.

Total number of attacks that occurred for each month of the year was recorded and plotted onto a bar graph (Figure 1a). Months were further categorised into austral seasons (spring, summer, autumn and winter) (The South African Weather Service 2022) (Table 1). Number of attacks per season were recorded and a bar graph plotted (Figure 1b).

Variables such as the sex, breeding history and rearing history was also added into the data set. Furthermore, the dynamics of the enclosure was also added as a variable, so that individual relationships could be assessed, and group dynamics could be interpreted.

2.4 | Data Analysis

All data were analysed in the R 4.0.5 (R Core Team 2020) environment, using RStudio 3.6.1. Significance was assessed at $\alpha < 0.05$ and values are presented as mean ± SD. Analysis was conducted for males, females and/or combined. Values were converted to binary values for instance *males* = 1, *females* = 2 or *attacker* = 1, *victim* = 2. We conducted a Kruskal–Wallis test

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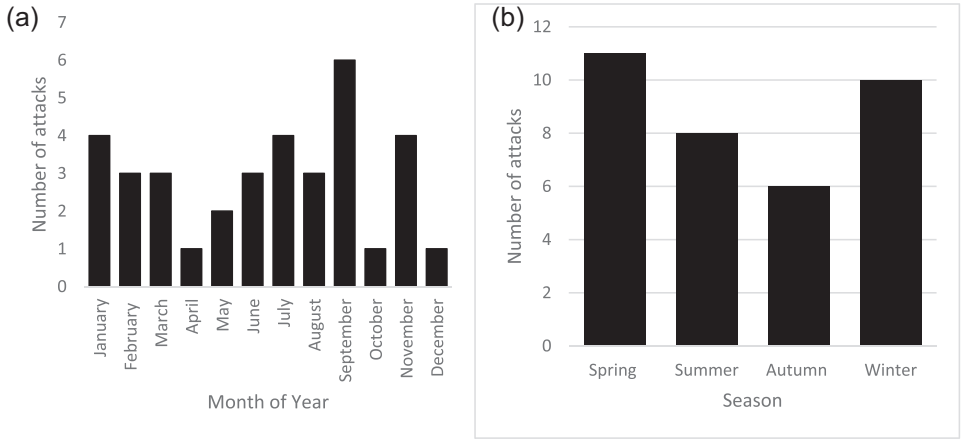


FIGURE 1 | Bar graphs illustrating incidents where conspecific aggression was recorded for (a) months and (b) season among southern Ground-hornbills between 1975 and 2021.

TABLE 1 | The classification of seasons in the Australian southern hemisphere according to the classification stipulated by the South African National Weather Services (The South African Weather Service 2022).

Season	Months of the season
Spring	September–November
Summer	December–February
Autumn	March–May
Winter	June–August

was performed to determine whether the season was a predictor of number of conspecific aggression incidents. A Dunn's post-hoc test was then used to determine pairwise comparisons. A one-way ANOVA was used to determine whether the number of attacks per month differed between attackers of different breeding statuses. A one-way ANOVA was also used to determine if the number of attacks per month differed between group sizes. A *t*-test was used to compare the averages ages of male and female birds which were attacked. Mixed effects logistic regression models (Bates et al. 2015) were used to determine whether our binary predictor variables had a significant effect on the age of the victim and the sex of the victim (fixed variables: season, victim age, attacker age; random variable: victim ID). A mixed linear mixed effects model with Poisson adjustments was used to determine the effects of predictor variables on number of attacks per month (fixed variables: season, victim sex, attacker sex, victim age, attacker age; random variable: attacker ID). A χ^2 test for independence was used to compare the frequency of attacks initiated by each sex, the number of each sex attacked, the number of females attacked by each sex, the number of males attacked by each sex and the number of juveniles and sub-adults which were attacked. A χ^2 test for independence was also used to compare the frequency of related and non-related birds attacked, the number of eggs laid in each season, the number of attacked birds reared in each condition and the number of attacks that were initiated by different group sizes. A Cramer's V test was used to see if moon phase, considered as a disturbance in an aviary at night in the dark, leading to blind attack on any cage mates, was a predictor of aggression. Analyses were conducted to detect for autocorrelation among predictor variables (Durbin–Watson test) and assessed the normality of residuals for the model using a Shapiro–Wilk test. Residuals were found to be normally distributed (Shapiro–Wilk normality test: $p = 0.13$).

3 | Results

Conspecific trauma contributed to 23 death (10%) ~7.80% of all recorded SGH mortalities ($n = 230$) from 1975 to 2022. There was a total of 46 attacks with 23 (50%) resulting in mortality either during attack or shortly after, an average of 0.53 ± 1.43 (mean $\pm$ SD, 95% CI = 0.41%) attacks were recorded each year. Of the 46 recorded incidents of aggression, 35 had sufficient data (all relevant variables) to allow for further analysis.

3.1 | Seasons and Breeding

Season was a significant predictor of conspecific attacks ($p = 0.002$). Occurrences of aggression were more likely to occur in Spring (11 attacks, 31.4%) (months include September, October and November) than in Autumn (six attacks, 17.1%) (Bonferroni adjusted $p = 0.003$). Attacks per month increased in frequency toward the onset of Spring, with the number of attacks on the rise from May and reaching the peak in September.

There were no significant differences (F-value = 1.71, $p = 0.20$) in attacks executed by breeding individuals versus non-breeding individuals. Of the aggressors that attacked helpers, only eight (21.1%) individuals were breeding at the time that attacks were recorded. In contrast 30 individuals (78.9% of recorded aggression records) were non-breeding at the time that attacks were recorded. Breeding individuals tended to be more aggressive in summer (three attacks recorded), while the highest number of attacks from non-breeding individuals was recorded in spring and winter (nine attacks for each season). Conspecific aggression by breeding individuals was also not concentrated within a specific month and occurred sporadically between January and December. Among breeding birds, there was no evidence that a

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specific sex or pairs (composed of an alpha male and female or male–male pair) were more likely to initiate an attack. Regarding non-breeding individuals, males were no more likely to initiate aggressive interactions (26.3%) relative to females (13.2%) ($\chi^2 = 1.80$, $df = 1$, $p = 0.18$) or pairs (7.8%) ($\chi^2 = 2.58$, $df = 1$, $p = 0.11$).

In general, non-breeding individuals seemed to be most aggressive in winter and spring with nine recorded aggressive interactions in both seasons. Breeding individuals were seen to be most aggressive in summer, with three recorded aggressive interactions in that season.

The sex of the victim (coefficient = -1.74 ± 1.31, z-value = -1.325, p-value = 0.19) and the sex of the attacker (coefficient = -1.02 ± 1.09, z-value = 0.94, p-value = 0.35) were not significant predictors of whether conspecific aggression was likely to take place on a bird of a certain age. When comparing aggression among victims and aggressors, there were no significant difference between males (20) and females (15) that fell victim to conspecific aggression ($\chi^2 = 0.02$, $df = 1$, $p = 0.89$). There was no difference in the number of individual males (21) and females (14) who initiated aggressive encounters ($\chi^2 = 2.63$, $df = 1$, $p = 0.11$) ($t = 0.07$, $df = 29.1$, $p = 0.95$). The highest frequency of aggressive behaviour from males were recorded in September and November (4 each) followed by July (3). Aggression by females was seen throughout the year, with a slight increase in January, March, August and September (2 attacks per months). There was no difference in whether female victims were attacked by males (50%) or females (50%) ($\chi^2 = 0.00$, $df = 1$, $p = 1.00$). There was no difference in whether male victims were attacked by males (73%) versus females (26%) ($\chi^2 = 3.27$, $df = 1$, $p = 0.07$). In eight instances, aggressive interactions were initiated by pairs of birds, which consisted of both a male and female attacker (22%).

3.2 | Age

The average age of victims was 8.92 ± 8.49 years old. The results suggest that although most of the attacks were directed toward adult birds, the frequency of attacks directed toward juvenile and sub-adult birds were very similar (17.1% and 14.3%) ($\chi^2 = 0.09$, $df = 1$, $p = 0.76$). A single attack was recorded where a fostered neonate was the victim. The average age of males (9.1 ± 8.9 years) compared to females (8.8 ± 8.3 years) at the time they were attacked did not differ ($t = 0.07$, $df = 29.0–3$, p-value = 0.94) (Figure 2a).

The average age of adults that initiated attacks was 19.0 ± 8.66 years. The oldest bird to initiate an attack was a 35-year-old female, and the youngest bird was 5 years old. Regarding the different sexes, the average age at which males tended to initiate or partake in aggressive encounters was 17.6 ± 6.8 years, while the average age in females was 20.6 ± 10.4 years (Figure 2b).

3.3 | Relatedness and Husbandry

We found that there was a higher number of non-related individuals that were attacked, versus related individuals, although in captivity hornbills are sometimes raised together which are not related but behave as if they are related. More individuals were attacked by birds that they were not related to (32%–91.4%), compared to individuals that were attacked by genetically related birds (3%–8.6%) ($\chi^2 = 21.51$, $df = 6.37$, $p < 0.00$). More than half of the attacks (23/35) was carried out by five individuals (three males and two females) shown in Figure 3.

The rearing history of the birds that were attacked was also investigated. It was found that of the birds that fell victim to aggression, attacks were most frequently recorded on birds that were hand-reared (29 birds, ~83%), versus birds raised by parents (3 birds, ~8.6%) and wild-caught birds (3 birds, ~8.6%) ($\chi^2 = 2.075$, $p = 0.35$), where wild-caught birds that came into captivity post rearing due injury or disease.

The number of individuals per cage was also investigated to determine if group size played a role in the frequency of aggressive interactions. There was no significant difference between the group sizes per enclosure when and the frequency of attacks ($p = 0.53$). Similar number of attacks occurred if there were two or three birds in enclosure (15 vs. 14 attacks) with lower attacks in enclosures containing four birds (five attacks).

Moon phase did not significantly affect the occurrence of aggression (Cramer's $V = 0.97$).

4 | Discussion

The findings suggest that conspecific aggression among captive SGH does occur and can be anticipated and mitigated by factoring in season, age of birds, allowing for dispersal of young adult and being cautious with altering social frameworks with already established alpha pairs and helpers. The prevalence and frequency of conspecific aggression events based on recorded protocols was, however, lower than expected. In most recorded cases, SGH attacks were fatal (25 of 35 attacks, ~71.4%), but whether conspecific related fatalities such as this are unique to captive settings or also occur in natural systems has yet to be determined, with some documented incidences of serious attacks in the Kruger National Park, and in reintroduced groups (MGHP unpublished data). Certain captive individuals have shown high incidence of aggression and should not be used for introductions to the wild or in captive breeding programmes. Further investigation into natural conspecific aggression may further untangle the drivers of aggression within this species and would likely also be useful for informing captive breeding programmes.

Season was a significant predictor of conspecific attack prevalence in captive conditions. The likelihood of an attack was found to increase in the period approaching and peak during spring, where 11 out of 35 of our aggression incidents were recorded. At a finer temporal resolution, it was found that the frequency of attacks began gradually increasing during austral winter (June–August) and reached its peak in September. The initiation of the SGH breeding season (Wilson and Hockey 2013) largely overlaps with this detected 'aggression period' and as such the prediction that conspecific aggression

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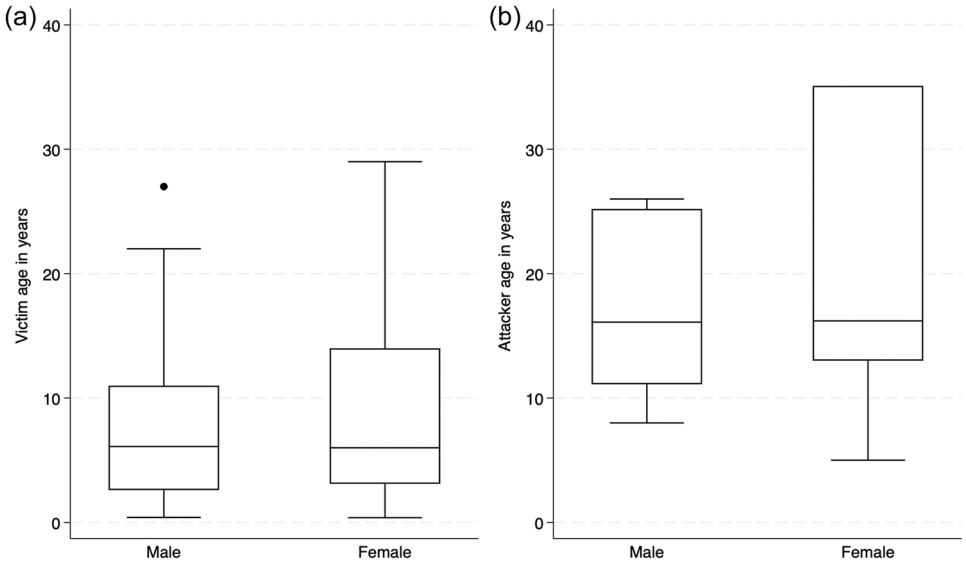


FIGURE 2 | Boxplots of (a) victims and (b) attackers illustrating the age in years for both males and females for Southern Ground-hornbills between 1975 and 2021. • Indicates single outlier.

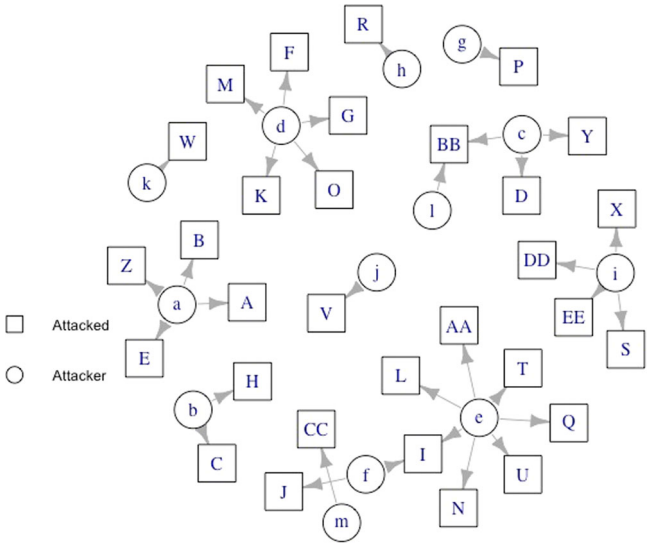


FIGURE 3 | Network analysis of attacks of Southern Ground-hornbills. The attackers are denominated by the letters a, c, d, e and i in the network analysis highlighting that conspecific aggression is instigated by specific birds.

would likely increase approaching breeding periods appears to hold merit. In cooperative breeders such as starlings testosterone increases up to threefold in breeding males during the incubation period leading to heightened aggression (Pikus, Guindre-Parker, and Rubenstein 2018). A similar finding of aggression correlated with breeding season was found by Hinton et al. (2013), where leading up to and during breeding season, aggression in captive American flamingos (*P. ruber*) increased due to competition for nesting sites and mating partners. Such inferences may be highly relevant to SGH, which are similar to *P. ruber* in terms of their highly territorial nature and their breeding history, offering advanced insight into breeding aggression among captive birds. As such, increased monitoring for behavioural shifts within enclosures among group members during, and approaching, the breeding season could reduce and avoid conspecific driven mortalities among SGHs.

It is important to note though that while season was found to be a predictor of conspecific aggression, incidents were not exclusively limited to the breeding season. Incidents of conspecific aggression occurred sporadically across the year. It has been well documented that many bird species, including song sparrows (*Melospiza melodia morphna*), European starlings (*Sturnus vulgaris*) and spotted ant-birds (*Hylophylax naevioides*), displayed aggression, specifically territorial aggression, during both the breeding and non-breeding seasons (Caldwell, Glickman, and Smith 1984; Canoine and Gwinner 2002; Hau, Stoddard, and Soma 2004). Therefore, unpredictable aggressive interactions outside of the breeding season may be more difficult to anticipate and avoid.

The likelihood of male (57%) and female (43%) SGH falling victim to conspecific aggression were similar. This conclusion was surprising, considering females experience raised aggression at an early age to encourage dispersal in the wild. Female SGH's tend to disperse on average at 11 months of age, relative to males which disperse at 8 years (Carstens et al. 2019a). The lack of aggression being weighted towards a specific sex, may be attributed to captive females generally being moved to new groups before they reach sexual maturity (Unpublished observation, Nel, N; MGHP). Regardless of sex it is suggested that helpers be moved out at 3 years but keepers should be vigilant of any social disturbance from 2 years onwards.

Males and females both initiated attacks at the same rate and there was no difference in the sex that they attacked which is different to flamingos where male *P. ruber* were generally more aggressive relative to female birds (Schmitz and Baldassarre 1992). Furthermore, among free-living and captive spotted antbirds (*H. naevioides*) and African stonechats (*Saxicola torquata*), it was found that intruders of the same sex

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elicited increased aggressive displays and behaviour (Gwinner, Rödl, and Schwabl 1994; Hau, Stoddard, and Soma 2004). Raised detection of intra-sexual aggression may arise more commonly among monogamous species, (i.e., SGH), with same-sex intruders (i.e., males) competing for their mates and resources (Seibert and Crowell-Davis 2001).

Adults were found to have committed 100% of aggressive interactions (35 records). Victims were mostly adult birds ($n = 23$, 65.7%), but also included sub-adults ($n = 5$, 14.3%) and juveniles ($n = 6$, 17.1%) and one chick (3%). The chick was killed in a failed fostering attempt with an aggressive bird (Figure 3—attacker a). Aggression between adults was likely a consequence of competition between birds for breeding partners, space and resources as seen in Hinton et al. (2013), where a similar significant positive correlation between age and aggression in male *P. ruber* was detected. The authors cited that experience plays a critical role in aggression and dominance. As such, ensuring adult birds in the same captive enclosures are known helpers, or to be a part of the breeding SGH social framework, is important for decreasing the likelihood of aggression to foreign birds.

With regard to lowered aggression towards juvenile and sub-adult birds, it is possible to speculate that these limited aggressive interactions were due to SGH breeding cooperatively and being reliant on helpers to rear chicks and defend territories, specifically young male birds. In cooperatively breeding species aggressive behaviour between adults and subordinates generally occurs when helpers seek to become breeders (Snowdon and Pickhard 1999). Male SGH are thought to only start breeding past 8 years of age (median 13.52, range 9.05–26.83) (PAAZA 2021). From these data, mean male victim age was ~9.1 years suggesting aggression towards males at this age serve as an effective mechanism to limit breeding competition by evicting potential competitor males from the group. Removing male helpers from the enclosure before they reach sexual maturity would reduce aggression.

In captivity, the extent of the aggressive interactions (death) on male birds reaching maturity, may be due to the lack of dispersal potential due to being confined. Relatively older birds falling victim to aggression could be the result of unpredictable 'social rejection' where birds are placed in enclosures with established pairs and helpers, possibly resulting in failed social integration. Female aggressors were also found to be much older (~20 years) and thus the alpha females. Seibert and Crowell-Davis (2001), found that aggression in captive adult cockatiels (*Nymphicus hollandicus*) was correlated with dominance rank, which is associated with experience and age. Similarly, Cloutier, Beaugrand and Laguë (1995), found that subordinate individual chicken (*Gallus gallus*) hen pairs were less likely to engage in aggressive behaviour during altercations when compared to pairs of dominant hens. Keeping groups of young hornbills together without a dominant pair may reduce aggression within the group but then they lose the benefits of learning from experienced mentors.

Most documented attacks in this study were between non-related individuals (91%). One possible explanation for this may be that related individuals are charged with the task of rearing and defending their family groups, therefore, aggression among family members would be misplaced and more beneficial when directed toward intruders, to protect breeding pairs and resources. Higher aggression was seen in flamingos in socially bonded groups towards other flamingos (Perdue et al. 2011). Although aggression toward related individuals was rare among SGH in this study, the few instances where it was recorded were assumed to be linked to dispersal or lack thereof of younger birds. A male alpha SGH attacked two of his offspring, a male sub-adult and juvenile. The offspring were of an age when dispersal would have been appropriate, and as such the aggression may have been a result of inappropriate social group management. Similarly, a second known related attack was perpetrated by an adult alpha female on a female juvenile bird.

Interestingly, hand-reared SGH were more susceptible to conspecific aggression than parent-reared or wild-caught birds. Limited exposure to normal social interactions may reduce individuals' ability to assess/detect and avoid aggressive advances. In hand-reared ravens (*Corvus corax*) the relationships formed with other members of their group was weaker than relationships established in parent-reared birds, showing that the rearing method had a direct effect on social interactions (Boucherie, Blum, and Bugnyar 2020).

Aggressive encounters decreased as group size increased in this study. Although there was no significant difference in the frequency of attacks and group sizes, it was found that aggressive interactions decreased as group sizes increased. Such findings may be similar to that Snowdon and Pickhard (1999), seen in domestic fowl with reduced threats and pecking in larger group sizes (Estevez, Keeling, and Newberry 2003). Aggression in captive groups may be a reflection of the processes related to dispersal in wild animals, which is nearly impossible in captive settings.

It should be noted that some birds in the study were deemed to be too aggressive to house with any other birds. In such instances, attempts at introducing new individuals were completely abandoned and birds were housed alone. Such cases may also need to be further investigated to determine the cause of such behaviour to mitigate future problems. Sexual maturity was seen from around 9 years in current study but has been seen from earlier age in the Northern Hemisphere so including more records from captive collections around the world might improve the understanding of the drivers of aggression. Note on more detailed breeding behaviour such as presence of eggs should also be included.

As this was a retrospective study on aggression not all of the variables were recorded for all aggression incidences, especially for older records. Future studies should focus on prospective data collection efforts in both instance of conspecific aggression and instances/periods of non-aggression to develop predictive models to identify which captive conditions reduce the likelihood of attacks.

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Ethics Statement

This work was endorsed by the Mabula Ground Hornbill Project and only retrospective data was used in analysis.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Regional Studbook PAAZA Number: PP1 31 5 21Published March 2021.

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