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Should Zoo Foods be Chopped for Hornbills?

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Abstract

Zoo diets containing fruit and vegetables are commonly chopped into small pieces, and yet there is limited evidence as to why this is practiced. Species-specific studies are therefore needed to determine whether chopping food is a good use of time. Many hornbill species are primarily frugivorous, and they are popular in zoos globally. Studies, therefore, on hornbill food presentation and behaviour could have application for zoo diets worldwide. This study explores food presentation effects on the behaviour of two hornbill species (Visayan hornbill, *Penelopides panini* and von der Decken hornbill, *Tockus deckeni*) were studied at Sparsholt College. Both species' behaviour was observed utilising instantaneous focal sampling during chopped and whole presentation conditions. Food intake and the time taken to prepare each diet was also measured. Behavioural results showed a significant increase in natural behaviours such as social feeding, and a significant decrease in inactivity and aggression during whole presentation for both species. There was no significant difference in food intake and preparation time, suggesting whole presentation did not reduce intake, add wastage, or make diet preparation difficult. Therefore, this study evidences the use of whole presentation for both species as there was a definitive increase in natural behaviour, which signifies welfare improvement, with no negative impacts such as decreased nutrient intake or increased preparation time. Both species are threatened in their wild habitats; therefore, captive management is required, and improvements in husbandry may improve welfare. Increased sociality and decreased inactivity are important for captive animals, and swapping to whole presentation had no apparent effect for these species while saving keeper time. Future studies should replicate this on other hornbill groups to evidence a complete change of husbandry for these species and others to continue to evidence husbandry methods.

Keywords: Avian; Chopped Food; Diet Presentation; Hornbill; Natural Behaviour; Zoo Nutrition

Introduction

Zoo diets for captive animals should be nutritionally equivalent to a species' wild diet, allowing expression of natural behaviours in captivity [1]. However, a lack of species-specific research makes the development of zoo diets challenging for specialist species [2]. Additionally, most research on zoo nutrition concerns nutritional content in diets; however, food presentation and feeding behaviour are rarely incorporated [3]. It is important that both the nutritional value, and the behavioural value, of food is therefore considered [4].

Brereton JE, et al. [1] found an increase in food presentation studies since the seminal study by Plowman A, et al. [5] which highlights that correct food presentation can increase naturalistic behaviours and provide valuable enrichment in captivity [6]. Therefore, repeating these presentation studies on various species could vastly improve their welfare. Preparation and presentation methods, such as heating or cooling, can change a diet's nutritional value [7]. Additionally, chopping fruit increases nutrient breakdown; these studies require nutritional analysis [8,9]. However, presentation studies like Plowman A, et al. [5] focus on the size or visual image of food items, such as whether an animal should receive whole or chopped food.

Zoos commonly feed chopped diets to their animals [10,11], the reasoning behind feeding chopped diets includes reduced competition/aggression around larger items, increased foraging opportunities and better portion control [12]. However, one approach for one species may not be suitable for all [13]. A range of mammal studies Shora JA, et al. [10,14,15] suggest that whole foods increase natural behaviour and feeding duration, reducing inactivity. If zoos aspire to continue their recent movements towards evidence-based husbandry practices, more taxa must be covered [16].

Avian behaviour is understudied compared to mammals, yet they contain the most individual species of all taxa in zoos [17]. The need for more bird species to be researched separately has grown as more species require ex-situ conservation due to population decline [18]. Avian studies on food presentation, such as James C, et al. [19] have found that parrot species prefer to work for their food. If this is the case, chopping food items may limit cognitive enrichment [20]. Parrots are the most widely studied avian family due to their perceived intelligence [21]; however, studies of other families could expand knowledge on husbandry techniques for multiple species.

Hornbills (*Bucerotidae*) are unique birds, characterised by their casque and breeding strategy, which involves sealing the female with her eggs within a tree cavity [22]. Due to habitat loss, populations of varying hornbill species have significantly declined [23]. Monogamy, low reproductive success, and choosy nesting habits inhibit them from maintaining numbers when threats like deforestation are introduced to their natural environment [24]. Visayan tarictic hornbills (VTH) (*Penelopides panini*) (Boddaert, 1783) are endangered [25]; therefore, zoological collections such as the Zoological Society of London, have captive individuals to breed [26]. VTH are native to southeast Asia, where their diet consists of fruit and insects [27]. Natural feeding behaviours include swallowing small items whole or tearing large fruits apart [28]. Asian hornbills depend highly upon fruiting trees and nest availability to determine breeding opportunities [29]. Vital research on the breeding strategy of VTH by Lamperti AM, et al. [24] suggests that current chopped diets may be under-stimulating as varying-sized fruits with seasonal changes in diet promote breeding.

In addition to Asian hornbills, there are also lesser-studied African species [30]. The International Union for the conservation of nature's (IUCN) red list shows that most sub-Saharan Hornbill populations are decreasing [31]. Von der Decken's hornbill (VDH) (*Tockus deckeni*) (Cabanis, 1868) is currently rated least concern by the IUCN; however, their numbers have continued to decrease like the VTH [32]. There is also little published research on VDH; therefore, their dietary needs also lack detail [33]. Common behaviours studied in VDH show they soften hard food items by mashing them within their beak for prolonged periods [34]. This softening behaviour removes the fruit's flesh from centre stones [22]. This skill shows hornbills are capable of problem-solving like parrots, further highlighting the need for studies on suitable enrichment in captivity to provide mental stimulation [13].

VTH and VDH populations are progressively getting smaller [31,35]. Therefore, human intervention is required to prevent further population decline [36]. Creating the ideal environment for these species could change breeding success [37]. New research suggests chopped food is oversimplified and does not fully meet dietary needs [38]. Deciding whether whole or chopped food is optimal may add valuable detail to husbandry guidelines for hornbills [39].

Differing results can be attributed to varied methodologies [40]. Mathy JW, et al. [14] conducted 1-0 sampling due to the fast-paced recording of aggressive behaviours; therefore, positive behaviours were mainly neglected. Results showed a significant correlation between food size and aggression [14]. In contrast, Plowman A, et al. [5] found no significance when using continuous focal sampling for a broader range of behaviours for each individual. Although animals were sampled individually, data were analysed per group, potentially missing key individual differences. Shora JA, et al. [10] conducted instantaneous group sampling; therefore, results were formed on group average [40]. Thus, both studies Plowman A, et al. [5,10] may not show individual differences. When one individual was separately analysed by Plowman A, et al. [5], it was discovered that the subordinate individual obtained more food under the whole condition [5]. This finding links to Mathy JW, et al. [14] result that depletion time increased as dominant individuals focused on one food item for longer; therefore, preventing them from returning to take more food from lower-ranking individuals [41]. These mammalian studies have varied results, but all show that behaviour is affected by food presentation.

Chopped Versus Whole

Plowman A, et al. [5] concluded that the benefits of chopped food were unfounded, suggesting more studies need to be done on other species to potentially change husbandry methods. There is little literature on birds compared to mammals [4]. There is recent growth in avian research; this study also identified that research focuses on flagship species. This is evident in published avian presentation studies which mainly study parrots (*Psittaciformes*), renowned for attracting visitors with their colourful plumage and social behaviour [21]. Rozek JC, et al. [20] found orange-winged Amazonian parrots (*Amazona amazonica*) to prefer large pellets to regular ones; within this study, parrots were affected not only by a food's nutrients but also by food form.

James C, et al. [19] study on blue-and-gold macaw (*Ara ararauna*) found similar results to Rozek JC, et al. [20] but with fruit instead of pellets. James C, et al. [19] used a randomised feeding regime, which has been shown to prevent order effects [42]. Rozek JC, et al. [20] did not use this method; therefore, the results could be due to acclimatisation [43]. This method was used to determine whether macaws preferred chopped or whole fruit; results showed natural behaviour and feed time increased with whole foods. Neither study saw an effect on aggression, as seen in mammalian studies [10,44], however, this could be attributed to less detailed knowledge within literature on avian aggression compared to mammals [45]. However, Rozek JC, et al. [20] and James C, et al. [19] found no negative impact of whole food on birds, only positive. The display of natural behaviour is a positive welfare indicator [46]; therefore, visible increase in food manipulation resulting from large food items, as seen by Rozek JC, et al. [20] and James C, et al. [19] suggests improved welfare. These results indicate that replicate studies need to be performed on other avian families to determine whether others could also have their welfare in captivity improved.

Zoo Husbandry

Fidgett AL, et al. [6] state that chopped diets have many benefits and suggest chopped food is easier to weigh and distribute than the whole. Portion control is vital to ensure that animals maintain a healthy weight [47]. For species that lack the ability to know when their stomachs are full (limited leptin hormone), chopped food may be more appropriate [48]. However, it is stated by Friedman-Einat M, et al. [48] that birds stop eating when they are full; therefore, if hornbills were given whole items, they may eat a portion of the fruit and leave the rest for later. This, however, could lead to the suggestion that food wastage for zoos using the whole method could increase. Komdeur J, et al. [49] and Gonzalez JC, et al. [27] found that VTH and VDH feed socially so those whole items may be shared rather than wasted. Griffin B, et al. [50] found no significant difference in food wastage when turacos (T*auraco leucotis* and *Tauraco fischeri*) were fed whole food. Rojas TN, et al. [51] found frugivorous birds to be highly selective with the type of fruits eaten; brightly coloured fruits with high sucrose levels were favoured, suggesting food wastage may be more affected by food type rather than presentation. However, James C, et al. [19] found a decrease in wastage with whole presentation, suggesting that the presentation method may be more important for some species than others.

Zookeepers commonly chop most animal diets to weigh them easily [5,10]; however, Arbuckle K, et al. [3] states that this process is time-consuming. Multiple studies Plowman A, et al. [5,10,19] found that whole-feeding food reduced preparation time. Chopping diets may be necessary for some species which need to be scatter-fed [52]. Scatter feeding has been shown by Woods B, et al. [52] to increase foraging behaviours and feeding time. This may be appropriate for birds that commonly only have access to small, scattered food sources [53], but VDH and VTH feed from a far larger range of fruiting trees with varying-sized fruits, often abundant in one area [24]. Zoos may save money by feeding whole diets to some species as it may reduce costs associated with paying staff for diet preparation time [54]. Additionally, zoos could reduce wastage and improve animal welfare; whole diets may save time and money that can be focussed on conservation [1,55].

Hornbill Research

Hornbill and parrot husbandry are comparable [56]; nearly all are frugivorous, live in groups, and display social behaviours such as allo-feeding in the wild [57]. Despite these similarities, research on parrot diets has not been applied to hornbills [58]. Brereton JE. et al. [1] identifies that many avian taxa have been neglected, referring to the lack of diversity of zoo taxa covered in presentation studies. This study suggests fruit-eating birds such as *Bucerotiformes*, which include hornbills, should be studied as they could likely have similar results to *Psittaciformes* [1]. James C, et al. [19] also suggest that other frugivorous birds could benefit from whole food. For example, Griffin B, et al. [50] studied turacos and found increased food manipulation with whole presentation; however, this result varied between juveniles and adults.

There is no available research on food presentation in frugivorous hornbills; most papers focus on breeding strategy [22,24,27]. However, Lamperti AM, et al. [24] suggest that hornbill breeding depends highly on the available fruit types and quantity. Drupes (large, stoned fruits) are identified by Lamperti AM, et al. [24] to be the preferred fruits of African hornbills; this is similar to Meehan CL, et al. [59] who found parrots also prefer large fruit with centre stones. Schlegel ML, et al. [34] found that VDH mash large drupes in their beaks to break away the flesh from large seeds. Sherub K, et al. [22] also observe this mashing behaviour and state that this allows parent birds to tear away segments of fruit to share with offspring or partners.

Few studies are solely on VDH; however, limited information is available within broader hornbill studies, such as Kitamura S, et al. [60] focused on diets. Kitamura S, et al. [60] reviews Asian and African hornbill diets through a literature survey, finding wild hornbill diets to be far more diverse than what captivity can provide [60,61]. Kinnaird MF, et al. [25] builds on Kitamura S, et al. [60] research and describes VDH courtship as exchanging high-value food items such as large drupes. Riamon S, et al. [33] support Kinnaird MF, et al. [25] and state hornbill beaks have evolved to clamp down on fruits to compress them into an edible size; this study observed hornbills to work together to hold large fruits still whilst others tear away flesh. Viseshakul N, et al. [62] state that this cooperative behaviour has evolved to allow hornbills to consume a broader range of available fruits in their native habitats. These studies Kinnaird MF, et al. [25,33,60,62] show that VDH have the physiological means to consume large fruit.

VTH are larger than VDH, but their diets in captivity are made of the same constituents; tropical fruit and insects [24]. Reintar ART, et al. [63] has studied their natural behaviour, but this research mainly focuses on breeding strategy due to their endangered status [35]. This intense focus on breeding behaviour has overshadowed the need for studies on this species' dietary needs, which could improve conservation efforts [6]. Crissey S, et al. [64] highlights that for a diet to be suitable, animal preference needs to be considered. Fidgett AL, et al. [6] expands on this idea of preference and determines presentation and palatability to strongly affect animal behaviours towards their food. Regarding VTH, observation by Sinnott-Armstrong MA, et al. [65] shows they select large, brightly coloured fruits over small dull ones. Therefore, VTH shares this preference with VDH. Research such as Lamperti AM, et al. [24] on hornbill diets has not been replicated enough; therefore, without further research confirming similar results on more samples, these species' genuine preference remains just speculation.

The aim of this study is to fill a gap in the zoo food presentation literature, by conducting studies on two novel hornbill species. Here, the impacts of food presentation on behaviour, and the impacts of food presentation on keeper time, are investigated.

Materials and Methods

Study Subjects and Location

Before this study commenced, ethical approval was provided by the University Centre Sparsholt Ethical Review Committee (UCSEC 6022). This study utilised convenience sampling of two species of hornbill: *Penelopides panini* (VTH) and *Tockus deckeni* (VDH). Both groups were housed at Sparsholt's Animal Health and Welfare Research Centre. Two VTH and three VDH captive born subadult females were studied. Both groups were housed in thermostat-controlled indoor enclosures and unheated semi-natural outdoor areas. Enclosures allowed full visibility of the birds due to indoor and outdoor access (Figures 1-4). Staff provided individual bird profiles to differentiate between birds, including feather markings and beak abnormalities. VDH were all between two and three years old and VTH were both between 11 and 12 months old. Both species had previous exposure to human presence, as students and staff are in their vicinity multiple times a day. Therefore, the researcher's presence was not a hindrance [13]. During the study period, extraneous variables such as the outdoor temperature ranged from 14°C-31°C, and humidity was between 53% - 82%; these statistics were obtained from local met office data for the observed hour [66].

Figure 1: VDH indoor enclosure.

Figure 2: VTH indoor enclosure.

Figure 3: VDH outdoor enclosure.

Figure 4: VTH outdoor enclosure.

Data Collection

Data collection took place in summer 2022; this period was chosen to reduce the confounding effects of temperature change [67]. A total of 60 hours of observation was carried out, alongside 20 recordings of food intake per group and four weeks of diet preparation times. Observation hours were during morning feeds (9:30 am - 10:30 am), and staff were present to introduce food and provide access to indoor areas. Staff left the proximity of the enclosure during observation, limiting behaviour induced by the keeper's presence [50].

Behaviour Data Collection

There were no available species-specific ethograms for either VDH or VTH; therefore, an ethogram (Table 1) was created using related avian papers [50,68,69] on species with comparable behaviour. State behaviours were recorded using instantaneous focal sampling during minute intervals, whereas event behaviours were continuously recorded as a tally for all individuals [70]. All behaviour was recorded on paper record sheets and then converted into virtual copies on Microsoft Excel™.

Ethogram	
Behaviour	**Description**
State behaviours	
Allo-preen	Two or more individuals in close body contact, using their beaks to clean one another by picking through feathers.
Food manipulation	An individual uses their beak or feet to break apart, move and consume food items.
Social feeding	One individual feeds with or shares food with another.
Insect capture	An individual grasps an insect within their beak or feet and then consumes it.
Locomotion	Movement requiring the repositioning of the feet or flight.
Inactive/stationary	Bird remains stationary, with little movement. Eyes may be open or closed.
Out of sight	The observer can no longer physically see the individual.
Event behaviours	
Peck	One individual uses their beak to poke another individual.
Wing flap	Individual flares wings, accompanied by raised feathers.
Stealing	One animal forcibly takes an item from another, normally accompanied by loud vocalisations.

Table 1: The ethogram which was used for behavioural data collection.

Food Intake and Preparation Time

Dietary sheets were provided by staff before data collection began (Tables 2 & 3). Food types and quantities did not deviate from these diet sheets during the study. Before feeding, each type of fruit/vegetable and pellets were weighed using digital scales (0.1-gram sensitivity). At the end of each day, staff collected the remnants from both enclosures and weighed each food type. Weights were recorded in separate chopped and whole sections in a booklet provided by the researcher. Chopped food was described as under five centimetres in length and width, and whole was over 10 centimetres, and both were presented in bowls as usual. Pellets were included in food intake to ensure nutrient requirements were met; however, these did not change size. Chopped and whole food was alternated weekly to avoid order effects causing habituation [43,71-73]. An extra bowl for each condition was placed in a vacant enclosure; these were used to create a correction factor, accounting for desiccation [19,50]. For each condition, preparation time was recorded (seconds) on every observation day using a stopwatch; time started when the keeper gathered utensils and food and stopped after the equipment was washed and put away.

VDH	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
AM Feed	Grapes 10g	Strawberries 10g	Grapes 10g	Strawberries 10g	Grapes 10g	Strawberries 10g	Grapes 10g
	Plum 10g	Blueberries 10g	Plum 10g	Blueberries 10g	Plum 10g	Blueberries 10g	Plum 10g
	Red pepper 10g	Red pepper 10g	Red pepper 10g	Red pepper 10g	Red pepper 10g	Red pepper 10g	Red pepper 10g
	T16 Pellet 10g	116 Pellet 10g	116 Pellet 10g	116 Pellet 10g	116 Pellet 10g	116 Pellet 10g	116 Pellet 10g

Table 2: VDH diet sheet.

VTH	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
AM Feed	Parsnip 50g	Parsnip 50g	Parsnip 50g	Parsnip 50g	Parsnip 50g	Parsnip 50g	Parsnip 50g
	Squash 50g	Squash 50g	Squashe 50g	Squash 50g	Squash 50g	Squash 50g	Soponnese 50g
	Apple 50g	Apple 50e	Apple 50g	Apple 50%	Apple 50g	Apple 50e	Apple 50g
	Pesme 50gg	Pear 50p	Pear 50g	Postar 50p	Pear 50pc	Pear 50gr	Pear 50er
	Tornaller 50er	Tomales 50er	Tomales 50g	Tomato 50g	Tomato 50g	Tomalo 50e	Tomullo 50e
	Grapes 50g	Grapes 50g	Grapes 50g	Grapes 50g	Grapes 50g	Grapes 50g	Grapes 50g
	Banana 50er	Banana 50g	Banana 50g	Bamama 50g	Banana 50g	Banana 50er	Banmanman 50pg
	Blueberries 14g	Blueberries 14g	Blueberries 14g	Blueberries 14g	Blueberries 14g	Blueberries 14g	Blueberries 14g
	H116 Pellet 60g	H16 Pellet 60g	H16Pellet 60g	H16Pellet 60g	H16 Pellet 60g	H16 Pellet 60g	H16Pellet 60g

Table 3: VTH diet sheet.

Data Analysis

Data were compiled using Microsoft Excel™ (2021) and analysed using Minitab™ (2021). Individuals 1-3 were VDH, and 4 and 5 were VTH*.* Excel was used to create activity budgets for state and event behaviours for all birds, allowing comparisons between conditions and species [74]. Event behaviours were converted into a rate per hour. All hypotheses required differences to be analysed, and this study utilised a repeated measures design. Most state and event behaviours (state: allopreening, social feeding, locomotion, inactivity, event: pecking, wing flapping and stealing) were determined as parametric through probability plots, and both data sets had equal variance, supported by histograms. Although food manipulation and insect capture were non-parametric, data followed mostly normal distribution. ANOVAs are robust against violations of normal distribution [75,76] therefore, nine general linear models (GLMs) were run for state and event behaviours to compare conditions and species [77-79]. Behaviour was a random factor, and condition and species were fixed. The alpha p<value was set at $p< 0.05$ for all GLMs.

Both food intake and preparation were only tested for differences between conditions. Food intake was calculated by subtracting the weight of leftovers from the supplied weight for each condition. Correction factors were then applied. Food intake was determined as non-parametric, and a boxplot confirmed zero outliers. Therefore, a Wilcoxon-signed rank was run. Preparation time was normally distributed; therefore, a paired-sample t-test was used. Both the Wilcoxon and paired t-test significance/alpha levels were set at $p< 0.05$.

Results

Behaviour

Table four depicts mean and standard deviations for all GLM tests. Activity budgets (Figures 5 & 6) display differences in behaviour between chopped and whole presentations and between species. A significant difference ($p<0.05$ [*]) in state behaviour was found between presentation conditions for allopreening ($R^2 = 41.20$, $F(1, 59) = 6.71$), food manipulation ($R^2 = 65.52$, $F(1, 59) = 77.37$), social feeding ($R^2 = 45.69$, $F(1, 59) = 22.48$), insect capture ($R^2 = 15.54$, $F(1, 59) = 6.65$) and inactivity ($R^2 = 55.56$, $F(1, 59) = 65.27$); event behaviours of pecking ($R^2 = 35.31$, $F(1, 59) = 20.75$), wing flap ($R^2 = 17.31$, $F(1, 59) = 11.11$) and stealing ($R^2 = 19.05$, $F(1, 59) = 14.82$) were also significant (Table 5).

A significant difference between species' ($p<0.05$ [*]) state behaviour was identified for allopreening ($R^2 = 41.20\%$), $F(1, 59) = 36.62$) food manipulation ($R^2 = 65.52$, $F(1, 59) = 36.73$), social feeding ($R^2 = 45.69$, $F(1, 59) = 21.15$), locomotion ($R^2 = 11.79$, $F(1, 59) = 7.54$), insect capture ($R^2 = 15.54$, $F(1, 59) = 6.21$) and inactivity ($R^2 = 55.56$, $F(1, 59) = 10.50$). The event behaviour pecking ($R^2 = 35.31$, $F(1, 59) = 13.45$) was also significantly different between species (Table 6).

State behaviour	Chopped		Whole Chopped		VDH				VTH			
					Chopped		Whole		Chopped		Whole	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Allopreen	3.133	2.921	1.933	1.363	1.556	1.097	1.222	1.060	5.500	3.233	3.000	1.044
Food manipulation	14.630	6.170	26.800	7.400	17.830	5.190	30.440	5.530	9.830	4.090	21.330	6.530
Social feeding	3.533	2.560	7.333	4.751	2.111	1.491	5.222	3.422	5.667	2.060	10.500	4.810
Insect capture	0.433	0.774	1.067	1.172	0.667	0.907	1.333	1.138	0.083	0.289	0.067	1.155
Locomotion	13.430	5.760	11.467	4.666	15.170	5.890	12.611	4.118	10.830	4.650	9.750	5.080
Inactive	24.830	7.280	11.400	6.600	22.670	7.580	9.170	4.380	28.080	5.630	14.750	8.050
Event behaviour												
Peck	0.029	0.024	0.009	0.012	0.036	0.025	0.015	0.013	0.018	0.017	0.000	0.000
Wing flap	0.034	0.021	0.017	0.029	0.039	0.020	0.020	0.022	0.028	0.002	0.013	0.014
Steal	0.025	0.002	0.007	0.011	0.029	0.025	0.007	0.012	0.019	0.019	0.007	0.011

Table 4: Mean and standard deviation for all GLM models.

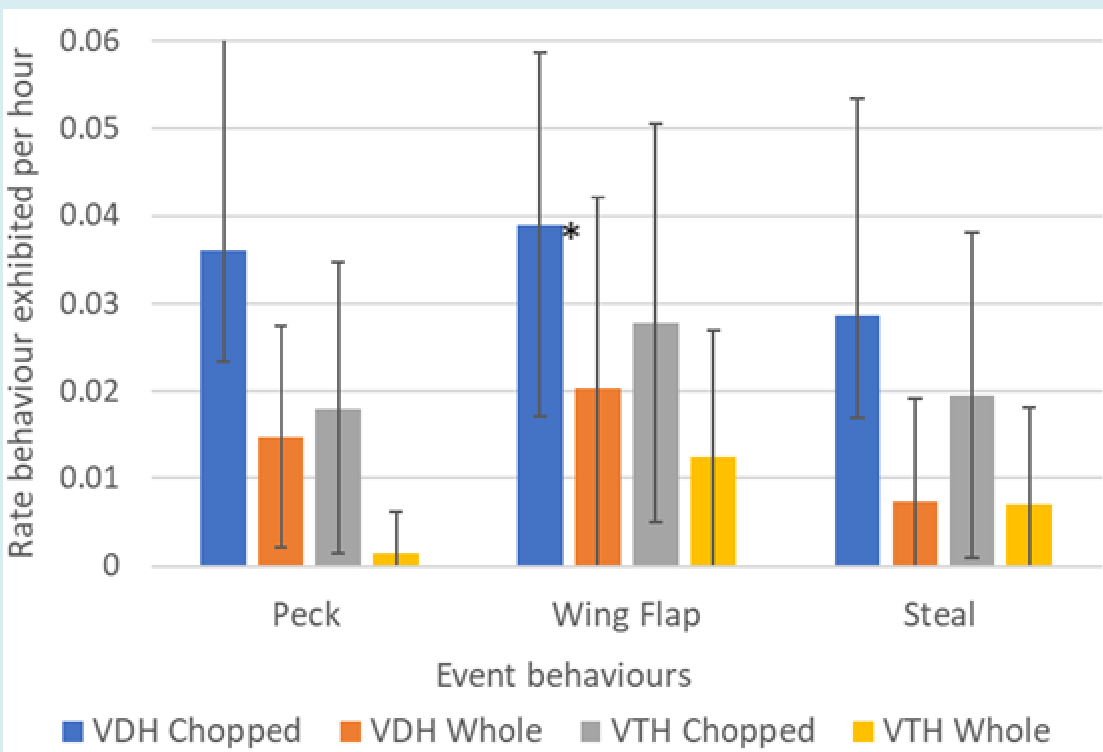

Figure 5: Activity budget for average time spent exhibiting each event behaviour under chopped and whole conditions (± standard error).

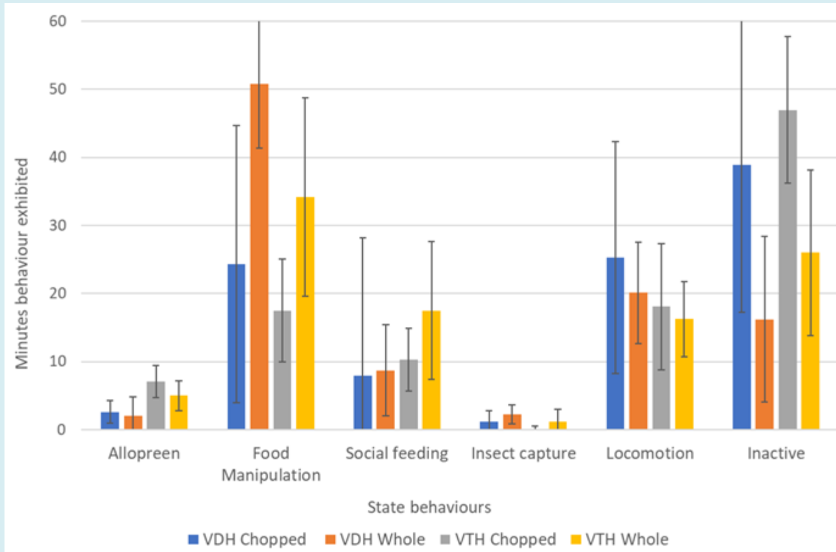

Figure 6: Activity budget for average time spent exhibiting each event behaviour under chopped and whole conditions (± standard error).

State behaviour	F- value	P-value
Allopreen	6.710	0.012*
Food manipulation	77.370	<0.001*
Social feeding	22.480	<0.001*
Insect capture	6.650	0.013*
Locomotion	2.350	0.131
Inactive	65.270	<0.001*
Event behaviour	**F- value**	**P-value**
Peck	20.750	<0.001*
Wing flap	11.110	0.002*
Steal	14.820	<0.001*

Table 5: General linear model outputs difference in behaviour between conditions (* Indicates significance).

State behaviour	F- value	P- value
Allopreen	36.620	<0.001*
Food manipulation	36.730	<0.001*
Social feeding	29.150	<0.001*
Insect capture	6.210	0.016*
Locomotion	7.540	0.008*
Inactive	10.500	<0.001*
Event behaviour	**F- value**	**P- value**
Peck	13.450	<0.001*
Wing flap	3.240	0.077
Steal	1.060	0.307

Table 6: General linear model outputs difference in behaviour between species (*Indicates significance).

Food Intake

A Wilcoxon signed rank test found no significance in food intake between chopped (*Mdn* = 190, range = 60 - 446) and whole (*Mdn* = 205, range = 60 - 379) conditions (z = -0.89, p = 0.929, p<0.005) (Figure 7).

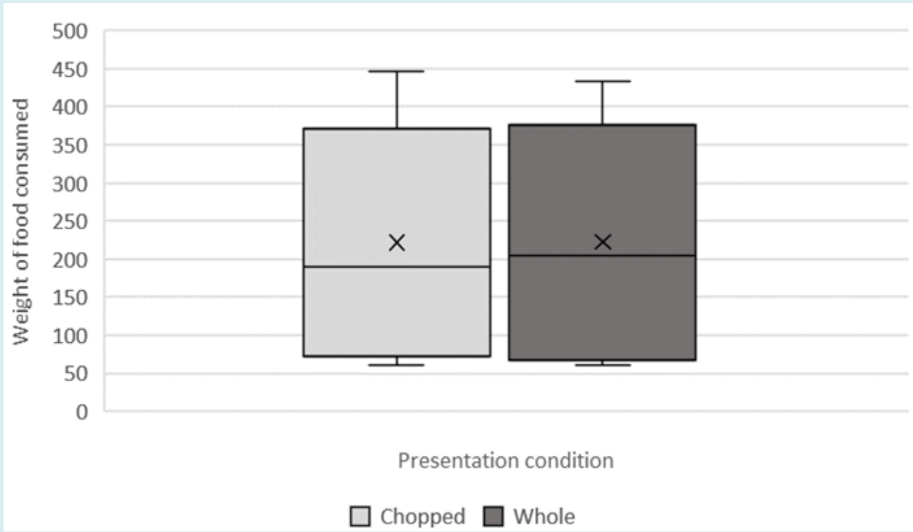

Figure 7: Boxplot of total food intake (in grams) for all individuals per presentation method.

Preparation Time

A two-sample t-test found no significant difference (p>0.05) in preparation time between chopped (M = 361.4, SD = 125.3) and whole (M = 265.3, SD = 98.4) conditions ($t(22)$ = 1.11, p = 0.278) (Figure 8).

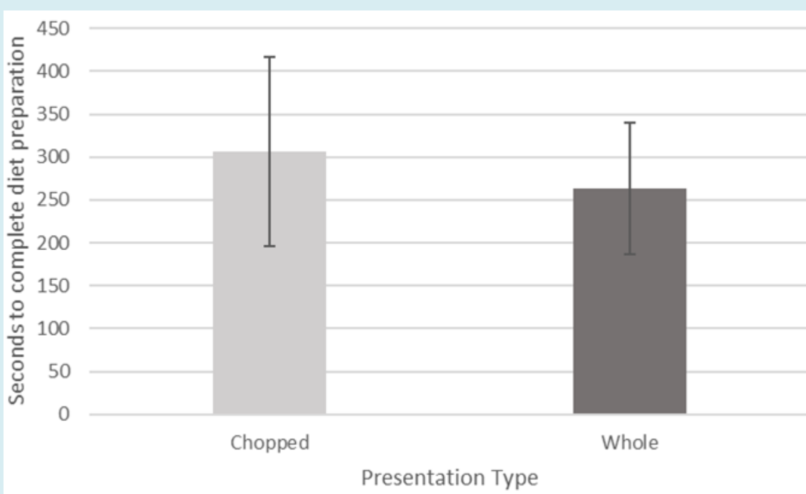

Figure 8: Average preparation time per presentation condition (± standard error).

Discussion

Results show that whole food significantly increased allopreening, food manipulation, social feeding and insect capture. Whole food also significantly decreased inactivity and all agonistic event behaviours (peck, wing flap and steal). Locomotion was not significantly different between conditions; however, the significant decrease in inactivity and increase in other behaviours requiring movement may account for this. Significant differences between species were also found for all behaviours other than wing flapping and stealing.

Behaviour

Both hornbill species showed significantly less inactivity, and more social and feeding behaviours (figure 5), suggesting they were affected positively by whole food presentation [46]. This is confirmed through the significant reduction of potentially aggressive behaviours such as pecking, wing flapping and stealing, suggesting large food items improved the overall temperament of both species during feeding (figure 6). However, aggression seen during chopped presentation was minor, similar to other studies [19,20]. This difference shows that this sample of VTH and VDH was not as reactive as other studied species, and more extreme comparisons of aggression have been found in primarily mammalian studies [10,14]. However, this could be due to the amount of available research on mammalian behaviour compared to avian; aggression in birds may be more subtle in comparison [1,45]. Studies such as Welsh O, et al. [44] suggest that whole food decreases aggression by preventing monopolisation; however, both James C, et al. [19] and Rozek JC, et al. [20] found no effect on aggression on their studied species of bird. VTH and VDH rarely displayed stealing and other aggressive behaviour during chopped conditions. Yet, there was still less during the whole presentation, confirming Welsh O, et al. [44] suggestion. These results suggest that whole food relieved boredom-induced stress by reducing aggression and increasing sociality [13].

Recent studies state that preventing stereotypical behaviour requires constant stimulation through movement, feeding and socialisation [59,80]. Therefore, this study's results agree with others [19,20,50], showing whole items encourage all the suggested positive behaviour for these individuals. Similar results were found by Lamperti AM, et al. [24] stating that this wiping behaviour is used to break apart drupes in the wild. These behaviours were accompanied by increased social behaviour, with individuals interacting significantly more to share and pull apart larger items [49].

Birds perform allopreening when attempting to form connections and reconfirm existing bonds; a significant increase in this behaviour was seen for both species. All individuals studied were female. However, improving communicatory behaviours is beneficial when introducing a male, as the females may be more receptive to courtship behaviour and pair bond [81], increasing the chance of breeding [37]. This is further supported by Kinnaird MF, et al. [25] as they suggested that high-value food items are exchanged in courtship, and this exchange of food items was seen in both species within this study. Increasing social bonds within captive groups have been found by Kemp LV, et al. [82] to improve breeding success. The added mental stimulation of large bright fruit has also been found to signify breeding season to female hornbills [6]. These findings are a promising development towards understanding the breeding requirements of these species in captivity. In addition to increased social behaviour, reduced inactivity is also ideal for the weight management of captive species [47,53,64]. Therefore, whole presentation could be an ideal method of weight management as it does not require food deprevation but increases exercise [56,12].

There was a significant difference in behaviour between species (table 6), which was expected as there were two VTH and three VDH. The three VDHs were more active and showed more aggressive behaviour; the possibility that group size affects intragroup dynamics is stated by Kinnaird MF, et al. [25] as the inability to pair up may cause greater friction within an avian group [67]. VTH were seen allopreening and social feeding more frequently, confirming Kinnaird MF, et al. [25] theory. In addition to different group sizes, VTH is an Asian species, and VDH is an African species [35,31]. Climatic differences between wild habitats may have caused significant differences [83,84]. Temperature and humidity varied for each observational period (appendix A and B), and VDH (African species) were observed to become more active in warmer temperatures [18,27]. Therefore, environmental conditions may have caused the difference between species, not the presentation method. Thus, behavioural results can be applied to both species.

Food Intake

No significant difference between presentation methods was found for food intake (Figure 7). This result is similar to Griffin B, et al. [50] who stated that neither over nor did under-consumption result from the change to whole food. However, long-term studies should be performed on both VDH and VTH to monitor the weight of the birds over time during whole presentation to ensure accumulative effects do not occur.

Komdeur J, et al. [49] state that social feeding decreases food wastage; this study confirms this suggestion as social feeding increased under whole presentation, limiting food wastage as large items were shared. No more was left over than chopped, generating a non-significant result. James C, et al. [19] found whole food decreased wastage, yet this result was also non-significant. It is suggested by Kitamura S, et al. [23] that hornbill species can be highly selective of food items, choosing brightly coloured, high-sucrose fruits [64,85]. Therefore, food intake may depend more on the type of foods provided and not the presentation method. Therefore, studies that fed more bland diets, such as Plowman A, et al. [5] may find different results to studies utilising brightly coloured sweet fruits [19,50]. However, this study's results show that neither presentation method made food items less desirable (figure 7); this could be attributed to that the same fruits were fed for both conditions.

According to James C, et al. [19] many bird species exhibit contra-freeloading behaviour; thus, they will choose foods requiring more effort [1], therefore chopping food items simplifies the process of feeding [12,20]. A minimal increase in intake was found during whole presentation; therefore, whole presentation may make foods more desirable by requiring more mentally challenging manipulation methods. This correlates with behavioural results, showing that food manipulation strategies significantly increased during the presentation.

T16 bird pellets were included in food intake calculations. These remained the same size for both chopped and whole conditions, and their consumption did not differ. Their inclusion in morning feeding was required on a nutritional basis [6,50]. However, had they not been included, the birds may have had a greater appetite for other food items, increasing their overall consumption, and could have caused a more significant result. As pellet consumption did not change between conditions, the results are likely accurate as all other food quantities remain comparable. The lack of difference in intake between conditions can be viewed as positive as neither species showed signs of neophobia [19,37,50]. However, behavioural indications of neophobia were not directly recorded; the increase in food manipulation does support the suggestion that neophobia was not an issue [44].

Preparation Time

There was no significant change in preparation time between chopped and whole conditions (figure 8). This result was unexpected as multiple other studies did find a significant difference [19,50]. However, the lack of difference shows that neither condition was more time-consuming; therefore, the most suitable presentation method for the species' welfare can be utilised with no extra effort from keepers [54]. Plowman A, et al. [5] suggest that keepers choose whole presentation, as it is easier to prepare and reduces nutrient breakdown [1]. This current study supports Plowman A, et al. [5] as whole food was no harder to prepare than chopped food, whole was also more stimulating; giving no reason for why whole may not be beneficial.

Studies such as James C, et al. [19] that found a significant difference were able to provide entire fruits to larger species which would require little to no preparation. This study required that whole items be substituted with 10cm pieces not to exceed nutritional needs [6,17,51]. Keepers suggested that it was difficult to know how many 10 cm-sized pieces made up the total weight within diet sheets, adding preparation time to whole preparation. Ideally, this study would have used whole fruits; however, the effect on food intake/wastage and behaviour was yet to be deciphered. If larger items were to cause increased aggression or intake, the less extreme change might have mitigated these adverse effects [86]. Nevertheless, results found decreased aggression and increased natural behaviour with no added wastage, suggesting that entirely whole fruits and vegetables may be provided in the future without the fear of extreme reaction from both species.

Future Research

Results from this study are compelling and suggest that whole presentation may advance these species' captive management and improve their welfare and conservation status. However, this study alone cannot influence change within the wider industry; a greater sample size is required to evidence a complete change to these species' management. The likelihood that similar results will occur is supported by other frugivorous bird studies which also find whole presentation to be the most practical way to mimic natural feeding within captivity. The behavioural data collection method used to find these results is robust as it has been utilised multiple times within presentation studies, with little criticism [5,42,70]. Therefore, once generalisability has been confirmed, change can be facilitated in multiple VDH and VTH zoological collections.

Behavioural data collection was performed on individual birds; however, results focussed on species, not individuals, like Plowman A, et al. [5] and Shora JA, et al. [10]. Using this method gives a specific answer per species as to the effect of each presentation method [40]. Furthermore, food intake could only be calculated as all birds were fed together and wastage was combined. Therefore, behaviours were combined per species: for behavioural results and intake to remain comparable. Individual preference is an extraneous variable not evaluated within this study; Bender IMA, et al. [85] state that this is common in frugivorous species and that preference changes seasonally. Food preference combined with its presentation would provide an in-depth view of every individual's desires [60,64]; however, catering to the specific preferences of each individual animal within a zoo environment with limited staff and financial resources may be unrealistic [55]. Conducting preference studies would be ideal for specialist breeding facilities for hornbills to improve breeding success [36,80]. However, this study aims to cater to the wider zoological community and provide evidence towards optimal husbandry, which can be applied to improve the welfare of all captive populations [87-89].

Both hornbill species were subjected to the same outdoor temperatures. The weather had a greater impact on behaviour than first expected; insect capture was a behaviour which significantly increased during the final week of behavioural observations (whole presentation); this was also the week with the highest temperatures. High temperatures increased the number of insects observed; therefore, this behaviour cannot be attributed to the change in food presentation. However, chopped and whole presentation were switched each week; therefore, there was one cooler week and one hotter week per condition (Appendix A). This mitigates the effects of the weather on the behavioural results as an average per condition was formed. This means this study's results do have biological significance. In future studies, individuals could be kept inside for the duration of the study to remove climatic factors. However, this could deprive the animals of the enrichment of outdoor stimuli [12] and vitamin D. At no point in this study was the welfare of the hornbills decreased due to research measures; therefore, results come from physically and mentally healthy individuals. Thus, these results can be applied to other healthy populations. However, separate studies would be required to assess the appropriate presentation method for birds in rehabilitation or with badly damaged beaks [33,56].

Conclusion

Results from this study suggest that food presentation significantly affects VDH and VTH behaviour. The effect of whole presentation is significant and provided welfare improvement, as key natural behaviours were increased. In addition, this presentation method had no significant impact on food intake or preparation time; therefore, whole presentation can be utilised without added complications. This result supports multiple other studies' results. Compared to mammals and other species of frugivorous birds, there remains a large gap within research on Bucerotiformes, many of which are endangered and complex to maintain in captivity. The lack of aggressive behaviour and display of natural behaviour shows that the current welfare standard of the sampled individuals is high. However, this could be further improved by switching to whole presentation. These findings provide species-specific

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