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Research article

Enhancing welfare in a mixed exhibit: The impact of dispersed whole food on activity levels and feeding behaviours of Mexican military macaws and red-billed curassows

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Abstract
Presenting chopped food in a bowl is a traditional feeding technique in zoos worldwide. However, it may not provide sufficient stimulation for many species to satisfy their behavioural needs. Recent studies suggest that dispersing food within enclosures may be a better alternative, especially in mixed exhibits where food competition is a concern. In this study, nine Mexican military macaws *Ara militaris mexicanus* and two red-billed curassows *Crax blumenbachii* were observed in a mixed exhibit to assess their behaviour when presented with chopped food in a bowl versus dispersed whole food. A total of 165 hr of behavioural observations were conducted using instantaneous scan sampling. Food consumption and preparation time were recorded for each food presentation type. With dispersed whole food, macaw behaviour changed with an increase in foraging (from 3.33% to 5.11%) and walking (1.70% to 2.39%) ($P<0.01$); a decrease in resting (59.50% to 55.78%), feeding behaviour (3.37% to 1.95%) and beak manipulation (68 instances to 32.7) ($P<0.001$). With dispersed whole food, curassow behaviour changed with an increase in walking (17.83% to 20.52%) and a decrease in beak manipulation (70.6 instances to 6.9) ($P<0.05$). No difference was observed in the amount of food eaten between types of food presentation. Zookeepers spent 2 min less per day preparing whole food than chopped food ($P<0.001$). Providing dispersed whole food in a mixed exhibit appeared to benefit activity levels in both species, promoted more balanced feeding manipulation techniques in macaws and functioned as a species-specific feeding practice. Further research on food presentation with other frugivores in zoo mixed exhibits may show enhanced welfare of coexisting species.

Introduction

Chopped food

Presenting chopped fruits and vegetables (hereafter produce) to certain herbivore, omnivore and frugivore species is a common practice in zoos and aquariums worldwide (Plowman et al. 2008). A common belief is that chopped food increases variety in ingested diets, food consumption and ease of manipulation for zoo-kept animals (Brereton 2020). Additionally, it is assumed to reduce aggression among coexisting species by ensuring ample availability of all food types (Plowman et al. 2008). Moreover, zookeepers have reported that scattering chopped food in the enclosure may help stimulate natural foraging behaviours (Plowman et al. 2008) and preparing chopped food in advance saves time for other daily tasks (Brereton 2020). Nevertheless, the time required for chopping produce will add up to a substantial sink of manpower when calculated, for example, on an annual basis (Plowman et al. 2008). Although the perceived advantages of chopping food may seem convincing enough to promote this feeding practice, such a belief often overlooks species-specific needs and natural behaviours. In fact, animals may have different foraging and food manipulation needs due to intrinsic or extrinsic factors (Amdam and Hovland 2011). Hence, it is crucial to consider each species individually and tailor food presentation accordingly to optimise their feeding experience.

If presentation is not properly considered, chopped food may not exhibit its purported benefits. For example, serving

chopped food at only one feeding site can simulate food scarcity. Thus, it may cause dominant individuals to monopolise the feeding site, resulting in an unbalanced distribution of food and potential aggression within the group (Young 1997). In a group of captive bongos *Tragelaphus eurycerus,* clumped food instigated competitive behaviours that determined privileges to access food (Ganslosser and Brunner 1997). As a result, not all bongos had access to a balanced diet. On the contrary, providing multiple feeding stations may help to improve feeding behaviours. By increasing the number of feeding stations for psittacine birds, Edinburgh Zoo prevented dominant individuals from restricting food access to conspecifics, simultaneously reducing group aggression (Field and Thomas 2000). Therefore, careful arrangement of chopped food presentation is key to prevent aggression within animal groups.

Lastly, chopping food can be time-consuming for zookeepers, especially when managing multiple enclosures (Plowman et al. 2008). The feasibility of preparing chopped food in advance is also dependent on daily schedules. Therefore, further research is needed to explore alternative feeding husbandry practices that benefit both animals and zookeepers.

Whole food

Recent studies on food presentation investigated the use of whole produce or larger pieces as an alternative approach. This type of presentation aims to enhance stimulation and engagement in captive animals. Studies on mammals report that serving produce in its entirety is more beneficial than serving chopped food. For instance, when a choice was given, a group of ring-tailed lemurs *Lemur catta* had a greater preference for whole food over chopped food, leading to an increase in daily feeding and foraging behaviours (Welsh et al. 2022). A group of ring-tailed coatis *Nasua nasua* had a higher interaction rate with dispersed whole food than with chopped food (Shora et al. 2018). Similar results were also observed in psittacine species. Presenting whole food in a bowl to blue and gold macaws *Ara ararauna* increased their feeding time and stimulated them to be more dexterous with their beaks (James et al. 2021). Comparably, feeding time and foraging behaviours also increased in Fischer's turacos *Tauraco fischeri* when handling whole food (Griffin and Brereton 2021).

The practice of providing whole food is still under investigation and should be explored in other species as behaviours related to food change across species. Nevertheless, the potential of this practice to encourage activity and increase behavioural diversity in zoo animals appears quite promising. For instance, Edinburgh Zoo implemented this feeding husbandry practice for their psittacine species by providing various food sizes placed inside enrichment devices to encourage more time spent feeding and foraging (Field and Thomas 2000). However, providing whole food implies less available pieces for the animals. Therefore, factors such as group size and diet composition (e.g., solely produce, a mixture of dry food and produce or produce as enrichment/supplement) should be taken into account before implementing this practice. This may prevent the development of aggressive behaviours within the group, as reported in a study with captive rhesus macaques *Macaca mulatta* (Mathy and Isbell 2002). Zookeepers may also benefit from providing whole food to animals. Recent studies report that zookeepers were able to save twice the time when preparing whole food compared to chopped food (Griffin and Brereton 2021; James et al. 2021).

Expanding food presentation studies in macaws

Similar to other wild macaw species, the Mexican military macaw *Ara militaris mexicanus* has been observed to live in vertical cliffs and canopies of tall trees in tropical deciduous forests and tropical dry forests (Contreras-González et al. 2009; Ragusa-Neto and Fecchio 2006; Rivera-Ortíz et al. 2008). Contreras-Gonzalez et al. (2009) suggest these macaws seasonally adapt to changing food resources, foraging mostly on seeds, fruits, leaves and latex from flower stems. This macaw belongs to the genus *Ara*, identified for their strong zygodactyl feet and beak (Botelho et al. 2014; Navalón et al. 2019) that are constantly used when foraging and feeding. Overall, parrots are distinguishable by their dexterity when using tongue and beak during food manipulation, and simultaneously stabilising themselves with their legs and feet (Sugasawa et al. 2021). Given these characteristics, macaws in captivity may require high levels of stimulation through enrichment, foraging opportunities or more complex feeding situations (e.g., challenges and choices) (Mason 2010; Mellor et al. 2015, 2021) to help them perform natural feeding behaviours and promote welfare. Lack of appropriate stimulation may increase the likelihood that macaws perform self-harming behaviours (Rodríguez-López 2016; van Zeeland et al. 2013). Thus, further feeding behavioural research is needed in different macaw species, including the Mexican military macaw.

Importance of food presentation in mixed exhibits

Mixed species exhibits in zoos are enclosures highly vulnerable to conflicts between species due to shared living space or food. Nonetheless, they can be successful when planned appropriately. Placing naturally associating species in a single exhibit has been the most successful combination (Buchanan-Smith 2012) and increases educational value (Kaandorp 2012; Leonardi et al. 2010; Probst and Matschei 2008). However, mixed exhibits have also been successful due to other factors such as placing non-associating sympatric species together (e.g., arboreal species with terrestrial, diurnal with nocturnal) (Daoudi et al. 2017); for companionship or space reasons (Baker 1992; Daoudi et al. 2017); and to provide larger enclosures to increase physical activity, social complexity and cognitive challenges (Buchanan-Smith 1999; Buchanan-Smith et al. 2013; Leonardi et al. 2010; Probst and Matschei 2008). However, these goals may be compromised when food placement is not taken into account. It is important to implement appropriate feeding strategies for each species in mixed exhibits to minimise the risk of interspecies conflict. Yet, the complexity of this task grows as the number of individuals sharing an enclosure increases (Daoudi et al. 2017).

Curassows in mixed exhibits

Various curassow species are commonly hosted in mixed exhibits; given that they are mainly terrestrial, they are compatible with arboreal species. However, little attention has been placed on their highly innate territorial behaviour observed in the wild (Bertsche 2006; Lafleur et al. 2014). Therefore, they may be a compatibility risk in mixed exhibits. Curassows also pose a risk given their flexible diet. In the wild, they are frugivores, occasionally eating seeds, leaves, insects or small vertebrates, which they mostly pick up from the forest floor (Leite 2020; Muñoz and Kattan 2007; Srbek-Araujo et al. 2012). Given the currasow's diet flexibility and likelihood of sharing an enclosure with other species, compatibility and diet similarity should be considered when managing a mixed exhibit. It may also be useful to identify feeding behaviour to understand similarities and differences with their wild conspecifics and how this may affect compatibility with other species. Additionally, there is little behavioural data available for captive curassow species, therefore studies on these species are beneficial for research and zoo purposes.

This study aimed to examine the impact of two different diet presentations (dispersed whole food versus chopped food in a bowl) in a mixed exhibit of Mexican military macaws and red-billed curassows *Crax blumenbachii* on the following aspects: 1) behavioural repertoire, 2) location of curassow feeding behaviour,

3) consumption of food provided, and 4) time spent by zookeepers preparing the food.

Methods

Ethical statement

This study was conducted in compliance with relevant Belgian and European legislation and in agreement with international scientific standards and guidelines. Due to the non-invasive nature of the study and absence of any potential discomfort, it does not meet the definition of an animal experiment as mentioned in Chapter I, Article 16 of the Belgian 'Act on the protection and wellbeing of animals' (Wet van 14 augustus 1986 betreffende de bescherming en het welzijn der dieren gesynchroniseerd met de wet van 27 December 2012). Therefore, the Royal Zoological Society of Antwerp waived the requirement for formal ethical approval of this study.

Case study in Zoo Antwerpen

A new feeding husbandry practice was implemented at Zoo Antwerpen (Belgium) in a mixed exhibit hosting two species: Mexican military macaws and red-billed curassows. Initially, the zookeepers responsible for this aviary followed the traditional method of providing chopped food in a bowl. However, the aim was to transition from serving the macaw produce and pellet diet in the indoor enclosure to only serving the pellet portion indoors and the produce portion outdoors. The new feeding practice also consisted of offering whole and dispersed food.

The curassows in this exhibit were fed a pellet diet in their indoor enclosure and this husbandry feeding practice was meant to remain the same. However, given that fresh produce is considered part of the curassow's natural frugivorous diet, it was unclear whether the curassows would show any attempts to reach and monopolise new feeding sites and in turn affect the macaws' behaviour. Therefore, the behaviour of both species was monitored to understand the impact of introducing new feeding sites for the macaws in a mixed exhibit and the potential effectiveness of this change.

To help the macaws acclimate to the new feeding husbandry practice, chopped food in a bowl was provided outdoors for two weeks before the start of the study. This was necessary given they were accustomed to the previous feeding location and neophobia is common amongst parrots (Fox and Millam 2007). Once the study began, both chopped and whole food were provided in a random alternating pattern.

Enclosure and subjects

The outdoor aviary consisted of two sections (76 m^2 and 79 m^2) that were connected. This space was shared by nine male Mexican military macaws and two red-billed curassows (male and female) (Table 1). Each species had indoor enclosures for shelter available at any time (43 m^2 for the macaws and 26 m^2 for the curassows). The aviary contained a variety of vegetation from natural soil, sand and grass to shrubs and trees, along with perches at various locations and heights.

Behavioural observations

Behavioural data for each species was collected at the group level. The observation period was from February to May 2022. Outdoor temperature was recorded and ranged from 2 to 22 °C across the study duration. The sessions began around the morning feeding time between 0900 and 1000 and ended between 1600 and 1630. Behavioural data for both species as well as data on curassow feeding locations were recorded on ZooMonitor (version 4.1, Lincoln Park Zoo 2022). Instantaneous scan sampling was used with an interval at 3 min to record state behaviours for a total of ten sessions of 30 minutes each. Five sessions were performed in the morning and five in the afternoon. All-occurrence sampling was performed for event behaviours during each session. A total of 165 observation hours were recorded for both species.

The ethogram (Table 2) was adapted from James et al. (2021) and used for both species. Based on preliminary observations,

Table 1. Age, sex and duration of time lived by the Mexican military macaws and red-billed curassows at Zoo Antwerpen

Species	Sex	Age (years)	Years lived in Zoo Antwerpen
Mexican military macaw *Ara militaris mexicana*	Male	34	34
	Male	20	2
	Male	16	2
	Male	13	2
	Male	15	2
	Male	7	4
	Male	13	3
	Male	10	2
	Male	10	2
Red-billed curassow *Creax blumenbachi*	Female	2	2
	Male	2	2

podomanipulation was excluded for the curassows and continuous intraspecific aggression was added for the macaws.

Provision of food

Both macaws and curassows were fed the same diet implemented with the new feeding husbandry practice before the start of the study. The macaws' diet consisted of 75–80% Nutribird P15 Tropical pellets (Versele Laga, Deinze, Belgium; see Appendix for nutritional composition) and 20–25% produce. The produce schedule alternated daily (Appendix Table A1) to serve a total of 360 g; 120 g of one type of fruit (e.g., apple, pear, papaya, orange) and 240 g of types of vegetables (e.g., chicory, beetroot, celery, carrot, cucumber, broccoli, courgette, sweet potato). Pellet consumption was not included in the study as it was offered indoors and therefore out of view of the observer. The curassows' diet consisted of Show 3 for poultry and Versele Laga T16 pellets (Versele Laga, Deinze, Belgium), while produce was not provided. Similarly, this was not part of the study as it was given indoors. Therefore, observations occurred solely when the macaws' produce diet was provided outdoors. Water was provided ad libitum for both species.

Diet preparation and presentation

Produce was prepared and presented in two different ways: chopped and in one bowl (50 cm × 40 cm × 150 cm) or whole and dispersed around the enclosure. For each condition, the time spent cutting the food was recorded.

The chopped diet was prepared by cutting the produce into 1 cm × 1 cm pieces and it was presented in one container. The whole diet was prepared by leaving the produce whole or occasionally cut in half. The latter option was dependent on the total number of available pieces, as this differed with the type of produce. It was necessary to maintain an equal number of pieces for all the macaws. Whole food pieces were either randomly pricked on nails installed on tree branches or on two small feeding devices to ensure food was dispersed. All were higher than the bowl height (Figure 1, Appendix Figure A1). For both conditions, the unfinished produce was collected the next morning to determine the average amount of food eaten per day. Produce was weighed using a scale (3000g B3C GX Pro IP65) which gave measurements to the closest 0.2 g. The two conditions (chopped in bowl and whole dispersed) were equally divided based on the predetermined observation days and were randomly assigned before the start of the study (Appendix Table A2). There was only one treatment per day. The food presentation schedule was randomised to prevent habituation. A total of 16 days of data for the chopped presentation and 17 days of data for the whole presentation were collected. The difference in days between diet presentations was due to the unavoidable cancellation of one observation day.

Statistical analysis

Statistical analyses were performed using SAS 9.4 (SAS Institute Inc., Cary, NC, USA). Data were tested for normality and the criterion for statistical significance was established at $P<0.05$. The group was the experimental unit. Allo-picking, auto-picking and interspecific aggression behaviours in both species, as well as allo-feeding, chewing and climbing behaviours in curassows only, were not included in the final analysis as there were limited observations. One macaw was an outlier due to its abnormal feeding behaviour and was excluded to avoid skewing the results.

Data were analysed using linear mixed models according to the nature of the variables (i.e., MIXED procedure when assumption of normality was met and GLIMMIX procedure with Poisson distribution and log link function when it was not). Behaviour

Table 2. Ethogram used for this study and adapted from James et al. (2021)

Event behaviour	Description
Allofeed	Food from the beak of one bird is seen passing to the beak of a conspecific who then swallows the food.
Allopick	Bird is seen plucking the feathers of a conspecific or allospecific followed by visual falling of the feather and potential vocalisation of the victim.
Autopick	Bird is seen plucking own feathers followed by visual falling of the feather.
Beak manipulation	Flesh of the diet item is removed from its skin using the beak.
Interspecific aggression	Bird pursues or attempts to bite an allospecific in the exhibit.
Intraspecific aggression	Bird pursues or attempts to bite a conspecific housed in the exhibit.
Podo-manipulation	Holding of and interaction with food items using a foot. The macaw may also use its beak to feed on the food during this time.
Chew	Opening and closing of beak on non-edible items in enclosure including bars and branches.
State behaviour	
Allopreen	Bird is seen preening the feathers of the other conspecific using beak.
Autopreen	Bird is seen preening own feathers using beak.
Climb	Movement of the feet and/or beak resulting in a vertical change of location.
Feed	Bird is seen swallowing a type of food.
Fly	Movement of wings resulting in elevation off the ground and moving location.
Forage	Use of feet or beak to interact with objects to search for food items.
Walk	Movement of the feet to result in a horizontal change of location.
Continuous intra-aggression	Bird is seen performing serious repeated attacks towards another conspecific.
Out of sight	Inability to see where the bird is situated; behaviour is unknown.
Rest	A lack of movement; can be resting on perch, bars or other features of the enclosure.

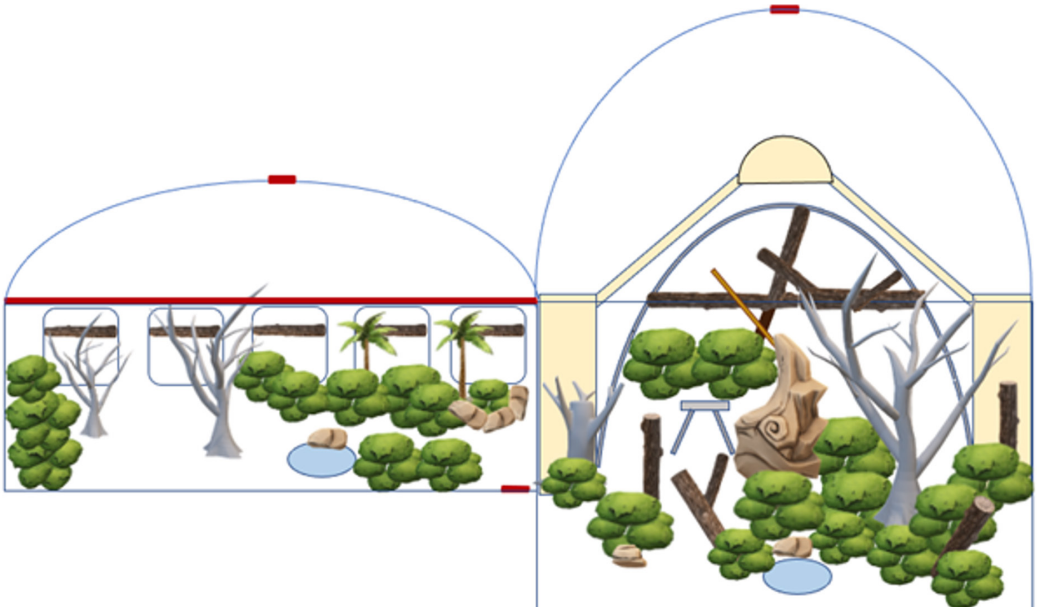

Figure 1. Enclosure layout showing bowl stand and trees where nails were installed; left side measuring 76 m² and right side 79 m². Red lines signify three levels in aviary: level 1, ground level; level 2, feeding areas; level 3, highest points of aviary.

counts, either in absolute counts per day or in percentage of observed time, were used as dependent variables. Food presentation (i.e., chopped versus whole) and temperature were included as fixed effects, whereas day was included as a random effect to account for repeated measures. Results are presented as least squares means±SE. Wilcoxon signed-rank tests were used to investigate differences between food presentations for the amount of food eaten and time spent preparing it.

Table 3. Average number of event and state behaviours per day in Mexican military macaws between food presentations (chopped in a bowl versus dispersed whole)

	Chopped		Whole		
	LS mean	SE	LS mean	SE	P-value
Event Behaviours					
Beak manipulation	67.97	6.702	32.73	6.502	0.0021
Podomanipulation	26.72	3.608	23.85	3.501	0.5767
Allofeed	17.76	3.445	20.58	3.342	0.5662
Chewing	81.69	7.927	83.89	7.689	0.8412
Intra-aggression	0.54	0.216	0.60	0.224	N/A
Allopick	0.09	0.073	0.41	0.237	N/A
Inter-aggression	0.25	0.188	0.03	0.034	N/A
Intra-aggression	39.06	4.253	46.23	4.126	0.2467
State Behaviours					
Allopreen	30.79	3.602	40.26	3.494	0.0804
Autopreen	61.62	4.580	67.07	4.443	0.4077
Climb	83.47	13.399	81.97	12.998	0.9373
Feed	26.79	2.592	15.30	2.517	0.0030
Fly	29.74	2.155	30.91	2.091	0.6936
Forage	26.76	2.940	35.91	3.823	0.0005
Walk	13.12	1.186	17.62	1.441	0.0052
Out of sight	39.56	6.643	37.18	6.234	0.2578
Continuous intra-aggression	3.35	0.972	5.14	0.943	0.1853
Rest	468.57	13.955	435.56	13.932	0.0006

Results

Macaw behaviour

With dispersed whole food, macaws showed a decrease in feeding behaviour (from 3.37% to 1.95%), resting behaviour (from 59.50% to 55.78%) and beak manipulation (from 68.0 to 32.7 times) per day (P<0.001). There was also an increase in foraging (from 3.33% to 5.11%) and walking (from 1.70% to 2.39%) per day when whole dispersed food was available (P<0.01). No significant changes were observed for all the remaining behaviours between food presentations. Results are presented in Figure 2 and Table 3.

Curassow behaviour

Curassows tended to show less resting behaviour (from 37.51% to 32.75%, P=0.078) and feeding behaviour (from 2.59% to 1.89%, P=0.067) per day with dispersed whole food. On average beak manipulation decreased from 70.6 to 33.4 times per day with dispersed whole food when compared to chopped food in a bowl (P<0.001). Walking increased (from 17.93% to 20.52% per day, P=0.051) when dispersed whole food was provided. No significant changes were reported for all the remaining behaviours between food presentations. Results are presented in Figure 2 and Table 4.

One area of concentrated curassow feeding behaviour was observed at the macaw feeding site when food was provided chopped in a bowl (Figure 3a), whereas multiple areas of low curassow feeding behaviour concentration are seen below macaw feeding sites when food was provided as whole and dispersed (i.e., produce was pricked on nails on tree branches or small elevated feeding devices; Figure 3b).

Amount of produce

There was no significant difference in produce eaten between dispersed whole food (294 g, SD=70.09) and chopped food in a bowl (320 g, SD=47.39) (S=25.5, m=25.70; P=0.243).

Food preparation time

On average, zookeepers spent significantly less time preparing whole food (2 min, SD=0.56) compared to chopped food (4 min, SD=1.05) (S=1.28, m=2.09; P=<0.0001; Figure 4).

Discussion

Effect of diet presentation on behaviour: Macaws

Overall, this study demonstrates that dispersed whole food is a promising alternative for enhancing activity in captive parrots and yields positive welfare outcomes in mixed exhibits. Dispersed whole food influenced the macaws to forage 1.8% more and walk 0.7% more daily in comparison to chopped food, indicating a more diverse behavioural repertoire (Miller et al. 2020). This pattern aligns with findings from other studies involving Fischer's turacos and ring-tailed lemurs, which also observed increased activity

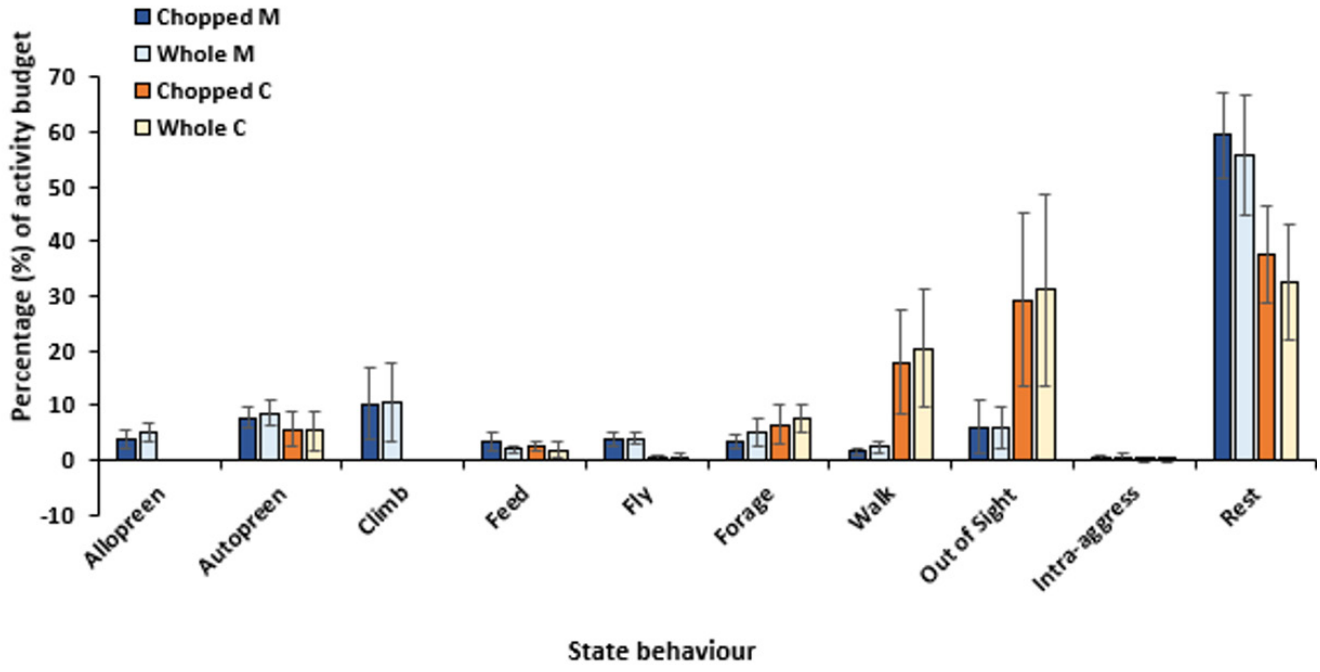

Figure 2. Daily activity budget of Mexican military macaws (M) and red-billed curassows (C) when provided with food either chopped in bowl or dispersed whole

Table 4. Frequency of daily behavioural events and states in red-billed curassows between food presentations (chopped in a bowl vs. dispersed whole). N/A = data were collected but not analysed as there were zero or limited observations

	Chopped		Whole		
	LS mean	SE	LS mean	SE	P-value
Event Behaviours					
Beak Manipulation	70.56	7.071	33.37	6.875	0.0007
Allofeed	0.00	0.000	0.00	0.000	N/A
Chewing	0.01	0.004	0.01	0.008	N/A
Autopick	0.00	0.000	0.00	0.000	N/A
Allopick	0.00	0.000	0.00	0.000	N/A
Inter-aggression	0.69	0.375	0.52	0.291	0.3320
Intra-aggression	0.00	0.00	0.00	0.00	N/A
State Behaviours					
Allopreen	0.00	0.000	0.00	0.000	N/A
Autopreen	11.45	1.705	10.16	1.654	0.5961
Climb	0.00	0.000	0.00	0.000	N/A
Feed	5.05	0.577	3.66	0.561	0.0673
Fly	0.64	0.234	1.02	0.314	0.2144
Forage	12.22	1.198	14.17	1.313	0.1409
Walk	30.91	4.262	34.95	4.771	0.0514
Out of Sight	52.37	6.900	55.18	7.230	0.2863
Rest	74.77	4.799	62.78	4.568	0.0782

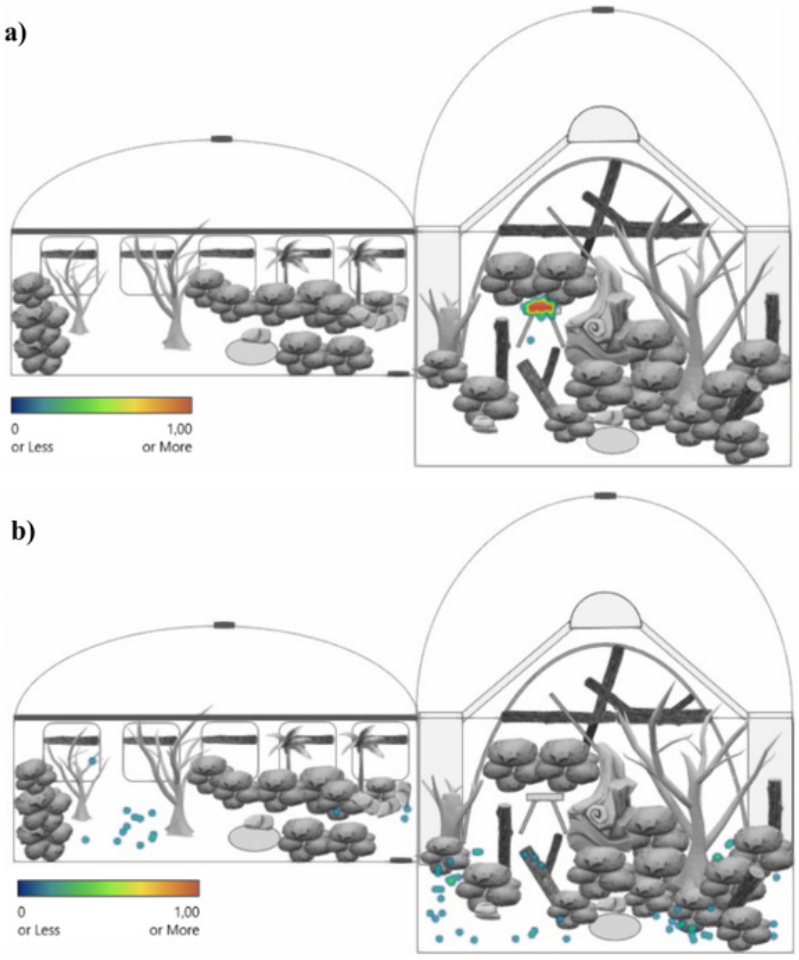

Figure 3. Heat maps generated by ZooMonitor, showing location of curassow feeding behaviour counts per day when (a) feeding from macaws' food under condition 'chopped in a bowl' (one area of high concentration in the aviary); and (b) feeding from macaws' food under condition 'whole and dispersed' (low concentration areas spread throughout the aviary). Red indicates areas where curassows spent most time feeding and blue indicates areas where they spent least time feeding.

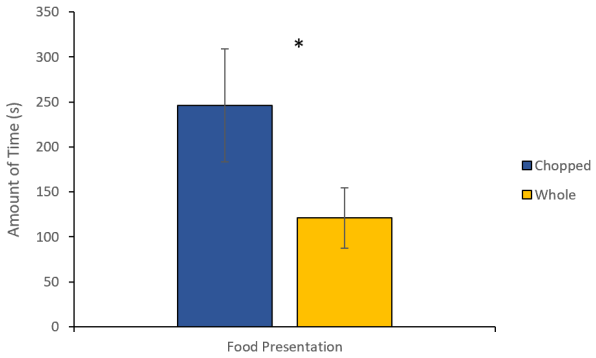

Figure 4. Average time (min) spent by zookeepers to prepare food for the macaws as either chopped or whole food; * denotes P<0.0001.

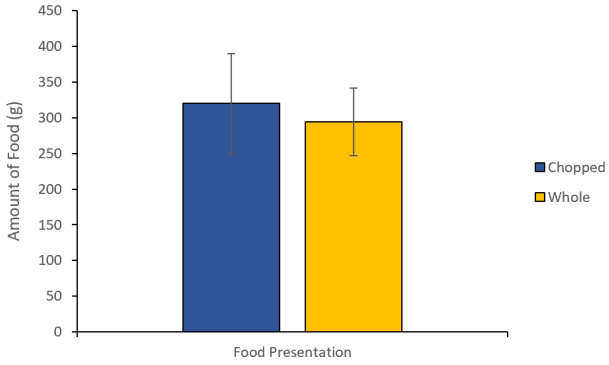

Figure 5. Average amount of food eaten by the macaws as either chopped or whole food.

levels with whole food diet presentations. The greater challenge of searching for and consuming whole food likely contributed to an increase in physical activity.

Unlike previous studies on whole food in parrots (Griffin and Brereton 2021; James et al. 2021), a 1.42% decrease in feeding behaviour was observed in macaws. This may be linked to macaws spending more time foraging under this condition. Whole food required more time to find given that its positioning on trees made feeding sites harder to access, therefore leaving less time for feeding during the day. However, it is important to highlight that a decrease in feeding behaviour should not be seen as a sign of poor welfare. In fact, parrots are known for contra-freeloading behaviour, in which they prefer to work for their food (James et al. 2021; Mellor et al. 2015) and this feeding method may stimulate problem-solving that promotes this type of behaviour. The macaws also had access to a pellet diet, thus, despite a reduction in feeding behaviour, they may still obtain all their nutritional requirements. Produce in captive parrots is primarily intended to be used as food enrichment to stimulate foraging behaviours rather than for its nutritional content (Brightsmith 2012). This strategy has been seen to work on Lear's macaws as they foraged more on food enrichment than their regular diet when both were given at the same time (Azevedo et al. 2016). Therefore, placing produce as food enrichment may stimulate parrots to work harder for the more interesting food pieces. This may have been a factor influencing a potential decrease in pellet consumption. Pellet consumption was not assessed in this study but it would be a valuable aspect of future studies.

The effect of whole food on food manipulation differed from previous studies, as macaws performed significantly less beak manipulation behaviour with whole food. However, no significant change was observed in podomanipulation. Whole food was provided in large pieces, thus making this type of presentation more of a challenge for the macaws to eat (James et al. 2021). This may have pushed macaws to use a mixture of beak and podomanipulation with whole food pieces, in contrast with chopped food pieces. Such dexterity has been observed to be beneficial in parrots (Rozek et al. 2010). Nonetheless, further research is needed to fully understand food manipulation preference in psittacines. It is important that parrots are provided with a variety of opportunities to use different manipulation skills during foraging and feeding as these are innate behaviours in most parrots. If this behaviour is suppressed, welfare may be jeopardised (Yeates 2018). However, when the whole food feeding practice cannot be implemented due to diet restrictions or other recommendations, dispersed chopped food may become a valuable alternative to increase foraging and reduce aggression and dominance as observed in white-naped mangabeys *Cercocebus lunulatus* (Waasdorp et al. 2021).

In this study, frequency of intra- or inter-specific aggressions was either not significant between food presentations or was overall very low. Similar findings were observed in James et al. (2021). It is important to note that their study was on an individual pair with one feeding site, where competition for food is less than in large groups. When large pieces of food were offered in dispersed sites to a large group of rhesus macaques, increased aggression and monopolisation of food sites was observed, potentially due to limited food availability for the entire group (Mathy and Isbell 2002). Conversely, a study on three ring-tailed coatis found that dispersing whole food resulted in less aggression (Shora et al. 2018). This highlights the importance of accounting for the number of animals within an enclosure when implementing a dispersed whole food approach.

Effect of diet presentation on behaviour: Curassows

This study revealed interesting dynamics between macaws and curassows in relation to food acquisition that reflected similarities to their feeding ecology in the wild. Curassows were observed feeding from macaws' food under both food presentations. Data from the heat map suggests that when whole food was provided, curassows retrieved less food directly from the feeding sites but instead retrieved the produce fallen on the ground. Thus, this feeding method encouraged a more innate feeding behaviour for these birds (Srbek-Araujo et al. 2012). Curassows also showed a tendency to feed more and were observed to manipulate the food significantly longer with chopped food in a bowl, given they ate directly from the bowl. This may indicate that presenting chopped food in a bowl led them to monopolise the feeding site more

often. Given the curassows' territorial nature in the wild (Bertsche 2006; Lafleur et al. 2014), this behaviour may pose a risk for the macaws, potentially leading to a loss of feeding opportunities.

In terms of activity, providing dispersed whole food resulted in the curassows walking significantly more and resting less. This could be attributed to the absence of direct visual cues from the macaws' feeding sites, encouraging the curassows to explore many areas of the enclosure. Overall, the conclusions mentioned above concerning behaviour changes with food presentation need to be taken with caution, as they may not be representative for both species due to the small sample size.

Effects of food presentation in mixed exhibits

So far, there is limited research available on mixed exhibits in zoos. Results from this study may help to further implement and improve existing recommendations for their successful maintenance. The findings suggest that chopped food presented in a bowl did not function as a species-specific feeding site, as data shows that curassows were able to exploit the macaws' food. This is an important factor to consider when placing food in mixed exhibits to allow for all species to thrive (Kaandorp 2012). Restricting food sites to one location in a mixed exhibit may lead to elevated stress levels due to food competition among the species sharing the space (AZA Ape Taxon Advisory Group 2017). Although aggression rate with chopped food was overall low, curassows were able to reach the feeding site and manipulate chopped food, indicating an ability to claim this macaw food site. Differences in species size can also lead to conflicts in a mixed exhibit, such as the establishment of a dominant species, which can affect aggression rate and animal welfare (Daoudi et al. 2017; Green et al. 2022; Leonardi et al. 2010, Probst and Matschei 2008). Based on this, the curassows should be seen as the dominant species in this exhibit, given their greater body size and ability to acquire macaws' food. Macaws likely showed more feeding behaviour with chopped food due to limited space and time at the feeding station, influenced by the presence of curassows. The curassows' dominant position over the chopped food feeding site may intimidate the macaws and stimulate them to overeat in shorter periods of time. This leaves less time for explorative feeding behaviours and more inactive periods as observed when presenting chopped food. By placing dispersed whole food in higher areas, the likelihood of macaws rather than curassows acquiring the food increased, encouraging more feeding behaviours. Thus, this food presentation seemed to benefit both species. The macaws exhibited an increased interaction with their food, while the curassows were more engaged with explorative feeding behaviours.

Food consumption

In this study, no significant difference in the amount of food eaten was observed between diet presentations, as also reported by James et al. (2021) for blue and gold macaws. However, as monitoring food consumption in mixed exhibits poses many challenges, it is difficult to draw a conclusion. A limitation of this study is that it was only possible to record the total amount of food consumed by both species. Therefore, findings on whether food presentation had an impact on macaw food consumption should be taken with caution. In fact, curassows consumed produce meant for the macaws, suggesting that species in mixed exhibits can directly affect food consumption of allospecifics.

Food preparation time

Whole food presentation appears to have clear advantages for zookeepers. It significantly reduced preparation time, saving on average two minutes per day. Although minimal, these time savings may result in a total of 12 hours of staff-work saved per year in this aviary. Implementing whole food in other frugivore exhibits would have an exponential effect, substantially reducing the workload in one year.

Future directions

Mixed exhibits require more attention from zookeepers and researchers, particularly when space is limited (Kaplan 2022). This study calls for expansion of food presentation research and feeding husbandry practices in mixed-species enclosures. Another area of interest may be species compatibility through ecological niches and furniture distribution in mixed exhibits (Green et al. 2022). As previously mentioned, a limitation of this study was the difficulty in differentiating species-specific food intake. Applying artificial intelligence to automate ethogram analysis may be an interesting approach to overcome this challenge.

Conclusions

Dispersed whole food benefited both Mexican military macaws and red-billed curassows, increasing activity levels and promoting natural behaviours. Dispersed whole food reduced monopolisation of feeding sites by curassows, allowing macaws to forage more on produce. Macaws' food consumption in both conditions was affected by interference of curassows as intake per species was not distinguishable. Whole food preparation saved zookeepers' time and reduced their workload. Further research is needed to expand food presentation studies, especially in mixed exhibits, to gain a deeper understanding of the effects of food placement, ecological niches and species compatibility.

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