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# Chopped and dispersed food enhances foraging and reduces stress-related behaviours in captive white-naped mangabeys (*Cercocebus lunulatus*)

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ABSTRACT

The white-naped mangabey is an endangered and rare zoo species, yet little is known concerning their welfare in captivity. The assessment of welfare should incorporate a net balance of negative and positive welfare behavioural indicators. These behaviours, and thus welfare, can be affected by the way food is presented based on its distribution, clumped or dispersed, and its size, chopped or whole. This study investigated the effect of food presentation on time-budget behaviours (i.e. forage, activity, inactivity, allogroom, self-groom, play) and stress-related measures (i.e., diarrhoea, aggression, self-directed behaviours), in four crossed-over test conditions of food distribution. The group-living mangabeys of Rotterdam Zoo were provided with vegetables that differed in distribution and size: clumped-chopped, dispersed-whole, dispersed-chopped, and clumped-whole. Mangabeys spent least time being inactive and subordinates and juveniles spent most time foraging during the dispersed-chopped condition, while the reversed was found during the clumped-whole condition. In addition, mangabeys stole food more often and engaged in less self-directed behaviours during dispersed-chopped, compared with dispersed-whole. In contrast, food distribution and size did not affect aggression, play, activity, self-grooming and diarrhoea. Consistent with most of the literature, chopped, dispersed items appeared to be the best, whereas presenting whole food items appeared to be the worst for welfare. In conclusion, presenting food in a distributed and chopped instead of whole manner is suggested to improve welfare of zoo-housed mangabeys.

## 1. Introduction

The white-naped mangabey (*Cercocebus lunulatus*) is an endangered (Dempsey et al., 2020) and rare zoo species (15 holding institutions in Europe, Abelló et al., 2018). For endangered species, the captive zoo population plays an important role in raising awareness and funding for conservation efforts in their native habitat. There is little literature concerning white-naped mangabeys' welfare in captivity (Singh and Kaumanns, 2005). Assessments of welfare of captive animals should incorporate a net balance of negative and positive welfare indicators (Yeates and Main, 2008). Common measures of negative welfare include diarrhoea, excessive aggression and self-directed behaviours (Maestripieri et al., 1992; Honess et al., 2004). Positive welfare indicators concern species-typical socio-positive behaviours, e.g. social play and the lack of abnormal idiosyncratic behaviours (Boissy et al., 2007; Held and Špinka, 2011). In addition, a time budget similar to wild conspecifics is considered optimal (e.g. increased foraging and decreased inactivity) (Melfi and Feistner, 2002; Yamanashi and Hayashi, 2011). The effect of husbandry on these negative and positive welfare indicators can be measured.

The behaviours related to negative and positive welfare can be affected by the way food is presented: based on its distribution, i.e. clumped or dispersed, and its size, i.e. chopped or whole. Distributing food items clumped rather than dispersed increases frequency of aggression, duration of allogrooming and social cohesion, while duration of play behaviour and foraging time is decreased (bonnet macaques

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(*Macaca radiata*): Boccia et al., 1988; Japanese macaques (*Macaca fuscata*): Saito et al., 1998; rhesus macaques (*Macaca mulatta*): de Waal, 1984; Southwick et al., 1976; rhesus macaques and hamadryas baboon (*Papio hamadryas*): Gore, 1993;). An explanation for this could be that clumped foods are easier to monopolise than dispersed foods; dispersed foods at an inter-food distance of 5 m may even be impossible to monopolise (Mathy and Isbell, 2001). Variable effects of food size have been reported. A study on rhesus macaques (Mathy and Isbell, 2001) found that chopped foods decreased aggression and increased foraging duration. Furthermore, chopped diets require increased food preparation time for zookeepers (Plowman et al., 2009) and are more prone to desiccation and contamination (Rico et al., 2007). Also, food for wild animals is unlikely to be presented in bitesize chunks, and many species possess specific food handling behaviours (Mathy and Isbell, 2001). Thus, presenting animals with whole foods is more similar to the natural setting. Moreover, food distribution and food size can affect behaviour in different ways. A study on rhesus macaques found that food size was a better predictor of aggression, whereas food distribution was a better predictor of the ability to monopolise foods (Mathy and Isbell, 2001). However, aside from these effects of food distribution and size on monopolisation, aggression, foraging times, and social play, no study investigated the effect of food dispersal and food size on self-directed behaviours and allogrooming.

This study investigated the effect of the food distribution and size on time-budget behaviours (foraging, activity, inactivity, allogrooming, self-grooming, play) and stress-related measures (diarrhoea, aggression, self-directed behaviours (SDBs)) of a captive group of white-naped mangabeys. The following four crossed-over test conditions of food distribution and size were used: clumped-chopped, dispersed-whole, dispersed-chopped, and clumped-whole. Clumped-whole was expected to be the “worst” condition, as whole foods are easiest to monopolise for the higher-ranking individuals. During clumped-whole, increased stress-related behaviours and allogrooming durations and decreased foraging durations were expected. Dispersed-chopped was expected to be the “best” condition, since smaller food items take longer to find (increased foraging times) and are less easily monopolised by the higher-ranking individuals. During dispersed-chopped, the least stress-related behaviours, shortest durations of allogrooming and the longest foraging durations were expected.

## 2. Methods

### 2.1. Welfare statement

This study was non-invasive and permission from Rotterdam Zoo for diet manipulation was obtained as it fell within the normal range of variation in the mangabey feeding regime. No permission from the Animal Ethics Committee was needed.

### 2.2. Subjects and housing

Observational data were collected from November 2019 to January 2020 at Rotterdam Zoo (also known as Blijdorp Zoo), The Netherlands. A captive group of nine white-naped mangabeys was studied. Data were collected on six females and two males, but not on the infant. All individuals were born in captivity, parent-reared and ranged in age from 10 months to 24 years old (mean age 7.1 years) at the start of this study. The three oldest individuals were born in other zoos and the group with the current composition has been established since October 2011 (Table 1). The group was permanently housed in an indoor-outdoor enclosure (inside: 55 $m^2$, outside: 250 $m^2$) (Fig. 1) and had fulltime access to both enclosures. The enrichment regime consisted of browse (e.g. willow branches) four days a week and seeds and/or nuts three days a week. The outside enclosure had a height of 6 m of wired mesh, which functioned as vertical enrichment. Both the inside and outside enclosure contained multiple branches and platforms at different heights. The inside enclosure had a concrete floor and the outside enclosure had a grass floor with several stones and a rivulet. The average temperature of the inside enclosure was artificially kept at 21 °C and contained an infra-red light during the night.

### 2.3. Nutrition and care

The mangabeys were fed a balanced diet (Supplementary 1), following EAZA guidelines (Abelló et al., 2018), three times a day: 07:30–08:30 h, 11:00–14:00 h, and 15:30–16:30 h. During the normal feeding regime, husbandry practices concerning food distribution and size varied per caretaker. Vegetable distribution varied between clumped in one place, evenly distributed among the individuals either through the mesh or directly (by hand), and dispersed. In addition, the vegetables were either chopped or provided whole. The inside and outside area were cleaned daily before or after the morning or midday feeding. All mangabeys were familiar with the husbandry staff. Water was available ad libitum.

### 2.4. Study design

Food distribution and size were systematically modified over four weeks, providing four test conditions that were administered in the following order: clumped-chopped (CC), dispersed-whole (DW), dispersed-chopped (DC), clumped-whole (CW). Each condition was conducted once and per condition, 18 h of data were collected (72 h of data in total). At the end of each condition, another began. When clumped, food items were provided on one area of 2 × 2 m, and when

**Table 1**
White-naped mangabey individuals (n = 9) at Rotterdam Zoo as recorded in the studbook, ordered by dominance rank (1=highest in rank (alfa male), 8=lowest in rank) which was calculated using MatMan (Han de Vries, 1993). Age and dominance category are indicated.

| Name | Sex | Age (years)[a] | Age category | Dominance rank | Dominance category | Date of arrival | Birth mother | Birth location |
|---|---|---|---|---|---|---|---|---|
| Ignazio (IG) | M | 24 | Adult | 1 | Dominant | 10-6-2009 | | Italy[b] |
| Esperanza (ES) | F | 18 | Adult | 2 | Dominant | 24-3-2009 | | Spain[c] |
| Eline (EL) | F | 3 | Juvenile | 3 | Dominant | | ES | Netherlands[e] |
| Casper (CA) | F | 12 | Adult | 4 | Dominant | 21-10-2011 | | France[d] |
| NB | F | 2 | Juvenile | 5 | Subordinate | | ES | Netherlands[e] |
| Quinn (QU) | F | 0 | Juvenile | 6 | Subordinate | | ES | Netherlands[e] |
| Boldi (BO) | F | 2 | Juvenile | 7 | Subordinate | | CA | Netherlands[e] |
| C | M | 3 | Juvenile | 8 | Subordinate | | CA | Netherlands[e] |
| Infant[f] | F | 0 | | | | | CA | Netherlands[e] |

[a] Age determined at the start of this study (1st of November 2019).
[b] Fondazione Bioparco di Roma.
[c] ZooBotánico de Jerez.
[d] Menagerie du Jardin des Plantes.
[e] Rotterdam Zoo (Diergaarde Blijdorp).
[f] Infant was not observed during this study.

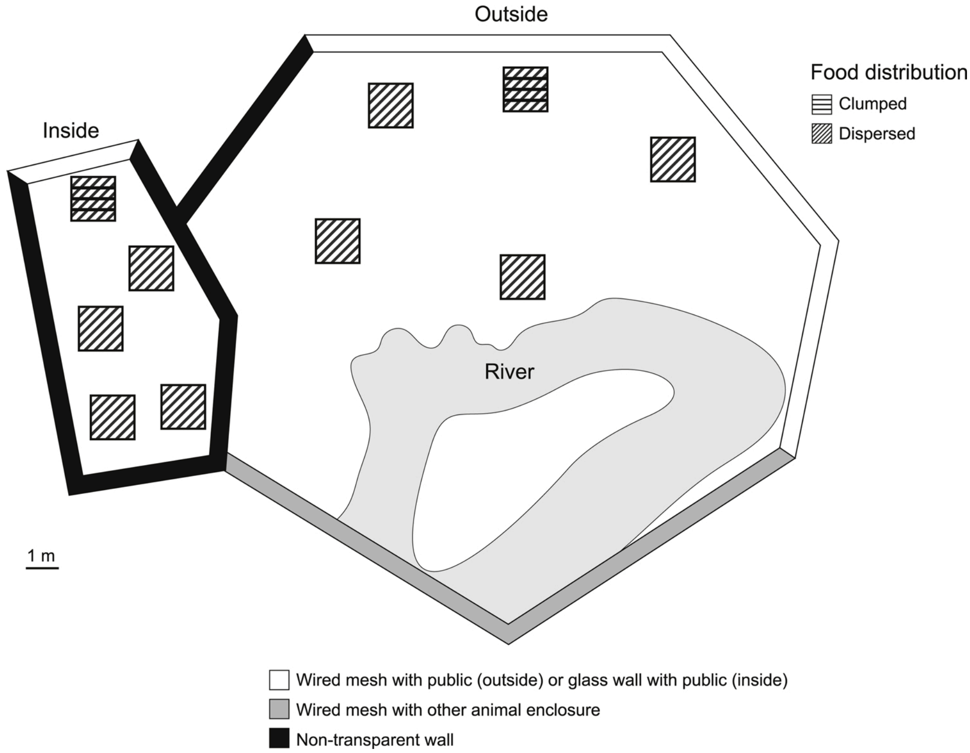


**Fig. 1.** Food was presented either in the inside or in the outside enclosure. In both the inside and outside enclosure five feeding areas were available, both food platforms and on the ground. During the clumped conditions, food was presented in one area of 2 × 2 m (horizontal lines). During the dispersed condition, the food was scattered across five areas (diagonal lines).

dispersed, food items were distributed throughout the enclosure within five areas (e.g. food platforms and on the ground) either indoors or outside (Fig. 1). Additionally, chopped foods were presented in pieces of approximately 5 × 5 cm and whole food items were intact.

## 2.5. Data collection and measures

Observational data were collected using focal-animal sampling and all-occurrence sampling (Altmann, 1974). All data were collected by two observers (SW and JT).

### 2.5.1. Focal-animal sampling

Each individual was observed two times 15 min on four days and 15 min on one day per condition, resulting in 9 h of data per individual in total. The observation order was balanced to ensure that all individuals were observed at each time of the day. Observations took place between 07:30 h and 13:45 h, to ensure that both morning and midday feeding (which were manipulated) were included in the observations.

When the focal animal was out of sight for more than 5 min, either before or during the sampling period, the observation was stopped and repeated at another time of the day, maintaining a balanced observation schedule. During focal animal sampling, the application Animal Behaviour Pro version 1.2 (Newton-Fisher, 2012) on an iPad model: A1822, 5th generation, 2017 and an iPad mini 2 model: A1489, 2014 was used.

We used an ethogram (Supplementary 2) adapted from those used by Gottlieb et al. (2013) and Abelló et al. (2018). We focussed on time-budget duration behaviours: time foraging, time being active, time being inactive, time allogrooming, time self-grooming and time playing. Play was only recorded for juveniles ($n = 5$), as adults showed no play. Recorded behavioural events were the number of aggressive interactions and the number of self-directed behaviours (SDB) (summed counts of scratching, self-sucking, and self-injurious behaviours (SIBs; e.g. self-biting, and hair pulling)). Observation times were equal for all individuals, so data were expressed in total durations (in seconds) and number of events per two hours per condition (behaviour rate). In the result section, we differentiate between number of individuals (referred to as n) and total sample size (e.g. datapoints as N).

### 2.5.2. All occurrence sampling

In addition to focal-animal sampling, all occurrences of defecation and aggression were recorded. Using the same definitions for both sampling methods (Supplementary 2). Aggression included the subcategory ‘stealing food’.

For defecations, the type of faeces produced was recorded, i.e. diarrhoea (e.g. faeces were soft without shape or liquid), normal (e.g. faeces were firm, or soft with shape), or unknown (when it was not possible to see, e.g. when the faeces dropped outside in the high grass). To compare faecal consistency across individuals, diarrhoea proportions were calculated as: number of instances of diarrhoea / total number of defecations.

### 2.5.3. Dominance ranks

Dominance ranks were determined with a linearity test using h’ index and were based on the number of aggressive interactions between the actors and receivers (Supplementary 3), with a linearity index (h’) of 0.73 (corrected for unknown relationships) and $p = 0.02$ (de Vries et al., 1993). Dominance ranks ranged from 1, for the most dominant individual, to 8, for the least dominant individual.

### 2.5.4. Inter-observer reliability

Behaviours were recorded by two observers. Inter-observer reliability was calculated using a Pearson (when data were normally distributed) or Spearman (when data were not normally distributed) correlation coefficient. As correlation coefficients were strong and positive ($R > 0.90$, $p < 0.05$, $n = 8$, $N = 24$), data collected by both observers were merged and analysed together.

### 2.6. Statistical analysis

Data were entered in Excel and exported to R version 3.4.3 (R Foundation for Statistical Computing, Vienna, Austria) for statistical analysis. To determine the effect of food presentation (distribution and size) on the subjects' behaviours and diarrhoea proportion, linear mixed models (lmm) were used. The stress-related behaviours (diarrhoea, aggression, and SDBs) were used as dependent variables and test conditions (CC, DW, DC, CW) were used as independent variables. Interactions between test condition and dominance rank were determined. Individuals were categorised as dominant or subordinate (Table 1). Note that dominance rank and age were correlated (Spearman; R=−0.73, p = 2.7e-9) (Supplementary 4). Therefore, interactions between test condition and age were also investigated and subjects were categorised as adult or juvenile (Table 1). Individuals were considered to have a random effect and indicated with (1 | Ind.) in each model, to control for repeated measures on the same individual. A Tukey post hoc test was used to adjust p-values (Supplementary 5).

## 3. Results

Only significant ($p \leq 0.05$) and non-significant trends ($p > 0.05$ but $< 0.10$) are presented in this section.

### 3.1. Effects of food distribution and food size on negative welfare indicators

Mangabeys expressed significantly more potentially stress-indicating self-directed behaviours (SDBs) during dispersed-whole compared with dispersed-chopped condition (lmm: n = 8, N = 36; DC-DW p = 6.5e-3, DW-CW p = 0.06, DW−CC p = 0.07) (Fig. 2a). The rate of SDBs was significantly higher in dominant than subordinate individuals during dispersed-chopped and clumped-whole (lmm: n = 8, N = 36; p = 3.4e-2 resp. p = 4.9e-2).

Stealing food, a subcategory of aggression, occurred significantly less during dispersed-whole compared with dispersed-chopped (lmm; n = 8, N = 36; p = 4.6e-2) (Fig. 2b). For stealing food, a significant interaction between test condition and age (lmm: n = 8, N = 36; p = 4.1e-3) was found: juveniles stole significantly more food during both clumped conditions (lmm: n = 8, N = 36; p = 1.0-e4 resp. p = 2.0e-4) and during the dispersed-chopped (lmm: n = 8, N = 36; p = 0.01) compared with adults.

Moreover, mangabeys were significantly more often inactive together during clumped-whole compared with dispersed-chopped (lmm: n = 8, N = 36; p = 0.03) (Fig. 2c). During dispersed-chopped, adults were significantly more inactive together than juveniles (lmm: n = 8, N = 36; p = 0.02). During DC, DW, and CW, adults spent more time inactive alone compared with juveniles (lmm: n = 8, N = 36; DC p = 0.01; DW p = 0.01; CW p = 8.6e-3) (Fig. S1c).

Altogether, the negative welfare indicators self-grooming, aggression, inactive alone, and diarrhoea proportion were not affected by the four test conditions, while SDBs, stealing food, and inactive together were affected by the test conditions.

### 3.2. Effect of food distribution and food size on positive welfare indicators

A non-significant trend suggested that the mangabeys spent more time foraging during dispersed-chopped compared with clumped-whole (lmm: n = 8, N = 36; p = 0.08) (Fig. 3a). During dispersed-chopped subordinates and juveniles spent significantly more time foraging than dominant and adult individuals (lmm: n = 8, N = 36; p = 0.03 resp. p = 1.6e-3). Similarly, during clumped-chopped, juveniles also spent more time foraging than adults (lmm: p = 1.8e-3). In contrast, significantly more time was spent allogrooming during clumped-whole compared with dispersed-chopped and clumped-chopped (lmm: n = 8, N = 36; DC-CW p = 1.3e-3, CC-CW p = 0.03) (Fig. 3b). During dispersed-chopped dominants spent significantly more time allogrooming than subordinates (lmm: n = 8, N = 36; p = 0.01), but there was no significant interaction with age (lmm: n = 8, N = 36; p = 0.73).

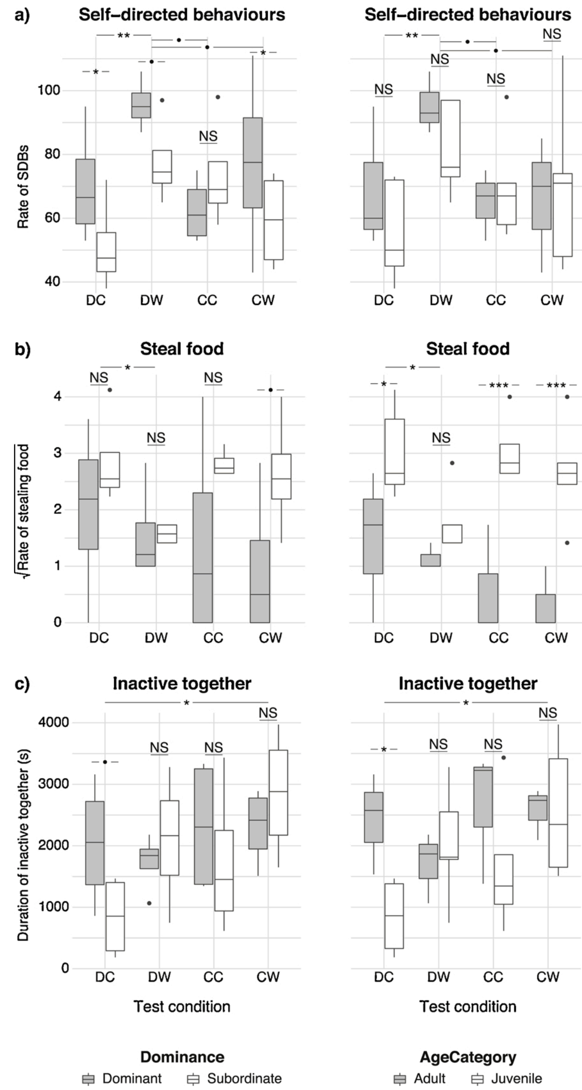


**Fig. 2.** The effect of the four test conditions (dispersed-chopped, dispersed-whole, clumped-chopped, clumped-whole) and the interaction with dominance (dominant versus subordinate) and age (adult versus juvenile) on the negative welfare indicators of white-naped mangabeys (n = 8, N = 36), using linear mixed models.

There was a significant interaction between the conditions and dominance for play (lmm: n = 8, N = 36; p = 0.04) (Fig. S2b), subordinates tended to play more during dispersed-chopped than dominant individuals (lmm: n = 8, N = 36; p = 0.09), while subordinates tended to play less than dominant individuals during clumped-whole (lmm: n = 8, N = 36; p = 0.06). For activity, there were significant interactions with both dominance and age (lmm: n = 8, N = 36; p = 0.02 resp. p = 0.01), where subordinates and juveniles spent more time being active than dominant and adults during dispersed-chopped (lmm: n = 8, N = 36; p = 0.03 resp. p = 0.03). Also, during clumped-whole juveniles spent more time being active than adults (lmm: n = 8, N = 36; p = 0.04).

Altogether, white-naped mangabeys spent least time allogrooming and subardinates and juveniles spent most time foraging during dispersed-chopped compared with clumped-whole, while the duration of social play and activity did not differ between the test conditions.

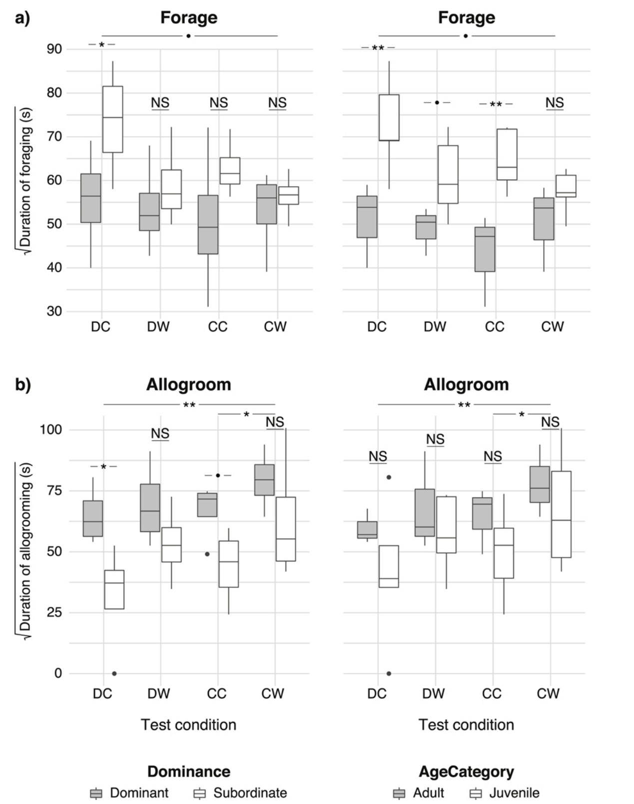


**Fig. 3.** The effect of the four test conditions (dispersed-chopped, dispersed-whole, clumped-chopped, clumped-whole) and the interaction with dominance (dominant versus subordinate) and age (adult versus juvenile) on positive welfare indicators of white-naped mangabeys (n = 8, N = 36), using linear mixed models.

## 4. Discussion

In this study, food distribution and food size were manipulated systematically to investigate possible food presentation effects on negative and positive behavioural welfare indicators in a group of captive white-naped mangabeys. The results partially fit the expectations, with clumped-whole as the "worst" condition and dispersed-chopped as the "best" condition. Potential indicators of stress were most evident in the dispersed-whole condition, although more food was stolen in chopped compared with whole conditions. The components of the time budget showed an interdependent pattern: in dispersed-chopped foraging was high, while inactive together and allogrooming were low, while in clumped-whole the reverse was found; foraging was low, while inactive together and allogrooming were high. Overall, presenting dispersed and chopped food seems preferable, since the subordinate and juvenile mangabeys foraged longer and all individuals expressed less signs of stress.

The different food presentations had contrasting effects on components of the time budget. As expected, mangabeys spent the most time being inactive together during clumped-whole compared with dispersed-chopped and subordinates and juveniles spent most time foraging during dispersed-chopped compared with clumped-whole. Lower durations of being inactive together were also found in captive rhesus macaques when multiple small apple pieces were provided compared with one larger apple piece (de Waal, 1984), and increased foraging times during chopped conditions compared with whole were also found in ring-tailed coatis (Shora et al., 2018). However, lion-tailed macaques that were accustomed to receiving a chopped diet, foraged longer when whole foods were provided (Smith et al., 1989). Since the lion-tailed macaques were not familiar with whole foods, novelty may explain why foraging durations were longer instead of shorter. Moreover, against our expectation, mangabeys allogroomed less during dispersed-chopped condition than the clumped-whole condition. Possibly, more time foraging meant less time to spend on allogrooming and being inactive together. In rhesus macaques decreased durations of allogrooming were also found when smaller food items were provided compared with larger foods (de Waal, 1984). So, it is suggested that dispersed-chopped is the best condition when the goal is to enhance the positive welfare indicator foraging and reduce the negative welfare indicator inactive behaviour.

In contrast with the prediction that most SDBs would be found in the clumped-whole condition, mangabeys expressed most stress behaviour during dispersed-whole, and this appeared especially so for dominant mangabeys, while in clumped conditions no social rank effect on stress behaviour was found. Additionally, no effects of age were found. This indicates that dispersed conditions were more stressful for high-ranking individuals, in particular the dispersed-whole condition, when dominants and adults tended to express more aggression. More SDBs might result from the fact that whole, dispersed foods are less easy to monopolise by higher-ranking individuals (Mathy and Isbell, 2001). Physical demands of frequent aggressive actions produce the greatest physiological indices of stress on dominant or adult individuals (Cavigelli, 1999). So, feeding dispersed, chopped foods are suggested to decrease the negative welfare indictor SDBs, while dispersed, whole foods are suggested to increase SDBs. This indicates that food distribution and size cannot be treated independently from each other when targeting SDBs.

Although total aggression was not affected by the distribution and size of food, a subcategory of aggression, stealing food, was higher when food was chopped. Potentially, whole foods are easier to monopolise and take possession of, thus single large foods are harder to steal than chopped foods. Moreover, for a dominant mangabey it is costlier when a whole food is stolen than when one of multiple pieces of chopped food is stolen. During chopped but not whole conditions, the victim of theft was left with some food items. The distribution of food, either dispersed or clumped, did not much affect stealing behaviour. Similarly, in rhesus macaques (Mathy and Isbell, 2001) food size was a better predictor for aggression than was food distribution. However, stealing food did not lead to greater stress (e.g. SDBs). During three test conditions stealing food was more prevalent in juveniles than adults, suggesting that juveniles stole more food than adults. As we did not analyse from whom food was stolen, stealing food may have actually represented a form of tolerated theft. These outcomes indicate the importance of studying the effects of both dominance and age when studying food presentation.

Against our expectations, aggression, inactive alone, diarrhoea proportion, and play were not affected by food distribution and size. Similarly, in rhesus macaques play did not differ between chopped and whole food conditions (de Waal, 1984) and being inactive was not affected by food distribution or food size in ring-tailed coatis (Shora et al., 2018). This is contradictory to the findings of two other studies; rhesus macaques expressed more aggression when they were fed with larger food items compared with small foods and when foods were clumped rather than dispersed (Mathy and Isbell, 2001) and in bonnet macaques less play was observed during clumped compared to dispersed conditions (Boccia et al., 1988). These contrasting outcomes may result from interspecific differences in tolerance or in coping, which can extend to differences in the display of aggression. For example, rhesus and stump-tailed macaques differ in aggressiveness (de Waal and Johanowicz, 1993). Differences in group composition may also explain the different outcomes: groups with relatively more males may be more aggressive than groups with relative more females (Mathy and Isbell, 2001). In addition, the lack of effect of food distribution and size on aggression, inactive alone, diarrhoea proportion, and play may also reflect greater importance of social than environmental factors in regulating these behaviours. However, it should be noted that the relationship between food presentation, behaviours, and potential stress indicators can be more complex. Given the small sample size of this study (eight white-naped mangabeys), replication studies at more holding institutes would be beneficial.

These outcomes indicate that for mangabey welfare, providing vegetables dispersed- chopped is the best way to present food. Yet a potential disadvantage of chopping foods is that this type of provisioning is more prone to desiccation and contamination (Rico et al., 2007). However, Rico et al. (2007) study investigated foods for human consumption and was based on a large time difference between food processing and consuming. The vegetables of the mangabeys were processed right before the moment of feeding, so there was less chance of contamination. In addition, vegetables can be presented on platforms., reducing the risk of contamination. Moreover, because of a strictly weighed diet (Supplementary 1), food was usually quickly consumed and there were little to no vegetables left over.

## 5. Conclusion

In conclusion, our results suggest that offering food dispersed-whole should be avoided as it incites the most stress behaviour. By contrast, offering food dispersed-chopped results in the least amount of stress behaviour and inactivity while promoting foraging behaviour (an overall trend and significant for subordinates and juveniles), and is our recommended method of food provision. Diarrhoea and other stress-related behaviours (aggression and self-grooming) were not affected by food presentation. Food stealing, in particular by juveniles, did not result in increased stress behaviour and may actually be largely tolerated. Thus, in mangabeys a husbandry practice that combines both the dispersal and chopping of food enhances positive welfare indicators and reduces negative welfare indicators.

## Declaration of Competing Interest

The authors report no declarations of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.applanim.2021.105392.

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