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Foraging enrichment affects behaviour and enclosure utilisation in captive male gelada *Theropithecus gelada*

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Abstract

Enrichment devices are important tools to engage zoo-housed animals in species-specific natural behaviours, which is critical to ensure animal welfare. The gelada *Theropithecus gelada* has a unique graminivorous feeding ecology, yet there is minimal enrichment research on the species. A novel foraging enrichment device was evaluated in a bachelor group of captive geladas (n=6) at Wild Place Project, Bristol UK, with the aim of understanding both group and individual response. Particular focus was put on foraging behaviour, enclosure utilisation and nearest-neighbour relationships. Six identical cuboid plastic containers, with large holes on three of the sides and a frame containing grass on the fourth, were used. The devices held fruits, vegetables and hay. Observations were conducted under three conditions: baseline, experimental and a post-experimental baseline. The devices were introduced during the experimental phase. Time spent consuming provisioned food and foraging wild foliage was significantly greater during the experimental condition. The increase in foraging of wild foliage was attributed to appetitive foraging. The foraging activity budgets were considered similar to wild counterparts during the study period overall, but greater during device implementation. This trend was attributed to the captive geladas having more available time to forage than their wild counterparts. Enclosure utilisation was also significantly greater during device implementation. In summary, this enrichment device increased foraging and enclosure utilisation in a bachelor group of captive geladas and produced similar activity budgets to those of wild counterparts. Therefore, it can be considered effective in improving captive gelada welfare.

Introduction

The psychological and physical needs of captive wild animals are of great importance in maintaining animal welfare (Young 2003). The provision of enrichment aims to encourage natural behaviours seen in the wild, increase activity, decrease aggression and decrease abnormal behaviours (such as stereotypies), providing means to improve welfare of captive animals (Moberg and Mench 2000). Enrichment and training are used in partnership in modern zoo-housed animals to promote positive welfare and improve husbandry, where training can be used to encourage the use of a device and increase positive natural behaviours (Fernandez et al. 2019; Westlund 2014). Behavioural engineering is a historical approach to enrichment, whereby an animal's natural need for certain behaviours is restored using a device that can be operated to receive a reward, often food (Markowitz 1978; Young 2003). A more modern approach is environmental enrichment, whereby a species-specific environment is created to mimic natural habitat (Shepherdson et al. 1998). This encourages the animal to perform natural behaviours that are associated with positive welfare and discourage behaviours that are deemed negative, providing optimal physiological and psychological welfare (Swaisgood and Shepherdson 2005). For example, foraging enrichment devices were used for zoo-housed walruses *Odobenus rosmarus* to reduce stereotypies by encouraging complete foraging sequences to mimic naturalistic foraging behaviours (Fernandez and Timberlake 2019a). This study proved successful in reducing stereotypies using simple species-typical devices. Similar results have been observed in polar bears *Ursus maritimus* (Fernandez 2021).

Primate enrichment has been studied extensively and was initially researched to improve the welfare of laboratory primates (Beaver 1989; Bourgeois and Brent 2005; Markowitz 1978; O'Neill et al. 1991). One method of enrichment commonly used for primates, amongst others, is nutritional, which includes the method of food delivery as well as the type of food (Bloomsmith et al. 1991). Foraging devices are a form of nutritional enrichment that has been shown to encourage species-typical activity budgets similar to the time budgets of wild primates (Fekete et al. 2000; Wells and Irwin 2009; Williams et al. 2015). These devices can promote physical activity, cognitive challenges and multi-sensory stimulation (Bennett et al. 2014; Gronqvist et al. 2013). Wells and Irwin (2009) tested three different feeding devices on Javan gibbons *Hylobates moloch* and results indicate that the gibbons spent more time outside and in species-typical foraging when the devices were present. Gronqvist et al. (2013) expanded on this, testing a foraging device, a novel object and an olfactory enrichment device. All three devices significantly increased foraging behaviours and singing behaviour was increased by the presence of the novel object and foraging device. This shows that foraging devices can affect behaviours other than those related to foraging. Finally, a study on selection of high and low-preference food items in four species of lemur found that using higher-preferred food items in a simple foraging enrichment device created a greater response with regard to overall activity and enclosure use (Fernandez and Timberlake 2019b). When considering enrichment as a tool for welfare it should be noted that all behaviours typical of that species are important, so should be maximally maintained throughout captive generations. This will ensure that individuals of a species are in the best possible condition should they become involved in reintroductions (Reading et al. 2013).

The gelada is the only graminivorous (grass-feeding) primate and belongs to the genus *Theropithecus,* of which it is the only surviving species (Gippoliti and Hunter 2008). The gelada's closest relatives are in the baboon genus, *Papio* (Jablonski 1993). The most characteristic feature of the gelada is its sexual cue, a hairless red patch located on the chest (Snyder-Mackler et al. 2012). This is an adaptation in relation to the gelada's lifestyle, where it spends the majority of time sitting foraging grass in the rocky gorges, precipices and moorlands of Ethiopia (Gippoliti and Hunter 2008). In addition, gelada dentition, hand morphology and locomotion are specifically adapted for this feeding ecology. The habitat is threatened by climate change, agricultural practices and conversion of land for livestock grazing (Beehner et al. 2007; Dunbar 2002; Gippoliti and Hunter 2008). The exact constituents of the gelada's diet are dependent on region and time of year, but 55–82% of the diet is grass (Ejigu and Bekele 2014; Fashing et al. 2014; Mau et al. 2011; Woldegeorgis and Bekele 2015). A long-term study on gelada feeding ecology in an intact tall-grass Afroalpine ecosystem found that over a seven-year period geladas consumed >56 different plant species (Fashing et al. 2014). Graminoid parts were cumulatively the largest annual contributor to the geladas' diet, accounting for 56.8%. Forb parts contributed 37.8%, invertebrates 2.8% and the remainder was unidentified items. Wild geladas will spend 51–58% of their time grazing (Abie et al. 2017; Woldegeorgis and Bekele 2015). Therefore, enrichment in captivity should aim to include a method of delivering graminoid parts to geladas to ensure similar behaviours are expressed.

Geladas live in a multilevel society similar to that of hamadryas baboons *Papio hamadryas* (Snyder-Mackler et al. 2012). There are two basic groups: the uni-male unit and all-male groups (bachelor groups). Bachelor groups include 2–15 adult and sub-adult males that forage separately from uni-male groups. Males are considered to reach sexual maturity from six to nine years of age (Dunbar and Dunbar 1975, cited by Kawai et al. 1983; Kawai 1979).

Despite their unique taxonomic and ecological status, there is a shortage of studies on captive gelada, particularly related to enrichment. Miller (2004) showed that the provision of a naturalistic enclosure for geladas in captivity, with sufficient grazing opportunities, can result in expression of similar activity budgets to those of wild geladas. Previous research on the closely related hamadryas baboons examined foraging frequency in non-provisioned areas of the enclosure when the animals were excluded from a clumped, high quality, monopolisable food source (Jones and Pillay 2004). The results show that the introduction of a monopolisable foraging device, when one of the seven troop members was foraging from the device (usually the alpha male), caused a significant increase in group foraging levels in non-provisioned areas of the enclosure. For the non-monopolisable food source there was limited non-provisioned foraging, as feeding at the device precluded simultaneous foraging elsewhere. However, during this treatment, overt aggression occurred and the frequency of aggressive attacks was related to the number of animals at an enrichment device at one time.

The purpose of this research was to determine the impact of foraging-based enrichment in geladas, defining group- and individual-level responses of a zoo-housed bachelor group. The enrichment device is predicted to increase enclosure utilisation and time spent foraging and reduce aggression related to procurement of shared food resources. Specifically, it was hypothesised that the duration of time that the troop spent foraging in provisioned and non-provisioned areas of the enclosure could be altered; the introduction of an enrichment device could increase enclosure utilisation for the troop; and social relationships and use of enclosure space among individuals in the bachelor group could change. The findings would allow evidence-based enrichment to be implemented in zoo-housed gelada and specifically within a bachelor group.

Materials and methods

Study colony

A six-member troop of male geladas, housed at the Wild Place Project (WPP), Bristol, UK served as the subjects of this study. The group arrived from Zurich, Switzerland in August 2016. The troop was housed in an open-air enclosure, measuring approximately $2500m^2$ (W. Walker, personal communication 26 September 2017), containing three central artificial rock formations of varying heights and a diverse range of native British flora. The terrain produced a hill-like structure, behind which the geladas could retreat to be out of public sight if desired. There was also a ditch that ran along the front (south-west facing) edge of the enclosure enabling low fencing. The substrate consisted mostly of grass and a mixture of wild flowers, offering the opportunity for natural grazing within the enclosure. The night rooms opened directly into the open-air enclosure, which the troop could access freely day and night except during cleaning.

The troop were fed morning, mid-day and afternoon and cleaning was conducted during the morning feed. Their daily diet included a scatter feed of grass pellets; leaf-eater pellets; seed mix; grass/hay; various vegetables including celery, leek and carrot; and some fruits. Furthermore, on Mondays, Wednesdays and Fridays additional vegetables, fruits and invertebrates were provided (Supplement 1). Water was available in the night room and in small depressions in the artificial rocks.

During the study period, the troop was comprised of six adult male geladas, with ages ranging between 7 and 16 years. The group consisted of Hobbit, 16 years; Hector, 14 years; Herkules, 13

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years; Harshit, 9 years; Kidame, 7 years and Kito, 7 years. Hobbit, Hector and Herkules were all born at NaturZoo Rheine and are suspected to be related (W. Walker, personal communication 26 September 2017). Kito and Kidame are half-brothers, whilst Harshit is not thought to be related to any group member. The dominant male of the group, if there was one, was unknown at the time of study. Identifying features were discussed with the keepers and determined during the preliminary study period. Observations were conducted by one individual; therefore, geladas are presumed to have been identified consistently.

Enrichment device

Six identical devices were introduced at the beginning of each experimental study period. This number was chosen to ensure each gelada would have access to a device at the same time to reduce the occurrence of aggression over who monopolised the device (Jones and Pillay 2004). The device was a 25 L cuboid (48×30×23 cm) plastic liquid container with five 78 mm holes cut out of three sides and the final side had a wooden plywood frame attached to hold fresh turf in place (Figure 1). The container was loosely filled with hay and 2000–2800 g (approximately two-thirds of a bucket) of chopped fruits and vegetables, distributed evenly among the six devices. The fresh turf was replaced every two days and was held in place with a piece of wire mesh and four 60 mm bolts. All rough sides were filed down and the wire edges were covered to ensure safety. The grass was confirmed organic and safe for animal consumption by the suppliers (B&Q, UK). The turf contained 45% fine dwarf perennial ryegrass *Lolium perenne*, 35% slender creeping red fescue *Festuca rubra litoralis* and 20% strong creeping red fescue *Festuca rubra rubra* (Inturf 2017). Ethical approval was obtained from the University of the West of England Animal Welfare and Ethics Committee prior to the study (AWEC Ref: R40).

Sampling methods

The ethogram was adapted from one created to observe hamadryas baboons (Wood 2003). Descriptions and behaviours were added and altered to suit this study and species (Supplement 2).

Data were collected between July and September 2017. The total time spent observing the geladas was 96 hours. Observations started at 0900 or 1300 for four consecutive hours each day. Four days of observations were conducted each week and each condition had equal observation periods of eight days over a two-week period. The first condition was the baseline, where no treatment was added and the keepers continued with their normal routine husbandry. The second was the experimental treatment, when the enrichment device was introduced at the start of each session and the keepers continued again with their routine husbandry. Finally, a post-experimental baseline was conducted, where the baseline routine was followed.

The observer used instantaneous scan sampling to record the behaviours of all visible troop members every five minutes (Altmann 1974). Variables recorded for each visible gelada were behaviour,

Figure 1. The enrichment device used for the experimental treatment.

individual position in the enclosure (based on a grid system) and the nearest neighbour (closest individual). The visible side of the enclosure was divided into six zones using visible landmarks, such as the artificial rock formations and the edge of the gelada house, to define each zone (Figure 2). The dimensions of the zones were quantified as estimated percentages of the total visible enclosure size: B1=20%, B2=10%, B3=10%, F1=25%, F2=20%, F3=15%. If a gelada was in the house or in a non-visible area (i.e. behind the mound) it was classified as out of sight and no behaviours were recorded. Zones B1 and B2 contained the artificial rock placements and all three front zones included the ditch by the fence line. Zone B3 was the least biologically relevant zone due to the lack of grass and rock formation, both of which are key elements of gelada habitat. During the experimental treatment, the devices were placed in five out of six of the enclosure zones; two were usually placed in B2 (ground and artificial rock placement). B3 was excluded as the scrub was too dense. Nearest-neighbour identity was an instantaneous visual estimate of distance and individual, hence categories were used to ensure accurate distances were recorded (a=<1 m, b=1–5 m and c=>5 m).

Data analysis

Coding categories were created to analyse the percentage of time spent foraging. Provisioned foraging behaviours (PF) from the ethogram were categorised into feeding (FE), foraging in provisioned area (PFA), foraging content inside device (EFI), foraging contents of device (EFC) and foraging grass from device (EFG). Non-provisioned foraging behaviour was categorised as foraging in non-provisioned areas (NPF). The percentage of time spent on PF and NPF was determined for each individual during each day of observations. Foraging activity includes all PF and NPF behaviours. Mean values were generated for both provisioned and non-provisioned foraging for each gelada per research day (48 data points per condition). An activity budget of 'major activities' (Supplement 2) for each condition was determined by computing the mean percentages for each day of observations.

The nearest neighbour was determined by measuring the percentage of interactions that each gelada had with all others. All geladas were plotted on a sociogram and the nearest neighbour was defined as the gelada to which an individual was most often closest.

To determine effects on enclosure utilisation, a modified spread of participation index (SPI) was calculated for all three conditions (Plowman 2003). An SPI of one indicates unequal use of space (minimal enclosure utilisation) and an SPI of zero indicates equal use of space (maximum enclosure utilisation) (Dickens 1955; Plowman 2003). The index was calculated using the formula $SPI=(S|fo-fe|)/2(n-femin)$; where fo is the frequency with which an animal was observed in a zone, fe is the expected frequency for the zone (based on its respective size), femin is the expected frequency in the exhibit's smallest zone and n refers to the number of observations for the observation period.

IBM SPSS statistics 25.0 (IBM Corp 2017) was used to analyse all the data. Levene's and Shapiro-Wilk's tests were used for all statistical analysis to check for homogeneity of variances and normal distributions, respectively. Due to the small sample size, and some data not meeting the residual requirements, non-parametric statistical tests were used for most of the data. With regard to activity budget, Kruskal-Wallis tests were run for major activities with more than two data points per condition: antagonistic, foraging activities (including enrichment manipulation and feeding), grooming, inactivity and locomotion. If a significant P-value was obtained, the baseline and post-experimental baseline (control conditions) were compared using a Mann-Whitney test and subsequently grouped into a control if no significant difference was found. If a significant difference was present, the two conditions remained ungrouped and were compared separately. Mann-Whitney tests were used to determine between-condition differences. Play, appeasement and solicitation all had two or fewer data points per condition. For all statistical tests the level of rejection was set to $P<0.05$. A similar statistical strategy using Mann-Whitney tests was applied to determine if there was a difference in control foraging conditions and if experimental provisioned and non-provisioned foraging behaviours differed from the control. A Kruskal-Wallis test was used to determine whether there was a difference in individual

Figure 2. A front view of the enclosure, where the white dashed line indicates the boundaries for the zones in the grid system. The red X indicates the observer location. Observation area approximately measures 1250m^2.

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Table 1. Percentage of time wild geladas and Wild Place Project (WPP) geladas spend in the activities foraging, grooming, locomotion and inactivity. The wild gelada data was collated from Woldegeorgis and Bekele (2015) and Abie et al. (2017).

	Percentage (%) of time in activity				
	Wild geladas	WPP geladas			
Activity		Baseline	Experimental	Post-experimental baseline	Average
Foraging	51–58	54	74	51	60
Grooming	16–18	11	3	12	9
Locomotion	14–17	7	8	6	7
Inactivity	9–10	26	14	28	23

gelada response to the conditions (interaction effect). The mean modified SPI for each individual under each condition was analysed and produced results that met parametric assumptions. Therefore SPI was examined similarly but using independent sample t-tests.

Results

Activity budget

Across all conditions the geladas spent 59.98% of their time engaged in foraging activities (Table 1). For foraging, antagonistic, grooming behaviour and inactivity there was a significant difference between the three conditions (Kruskal-Wallis test: $X^2_{(1)}$=5.835, P=0.016; $X^2_{(1)}$=3.894, P=0.048; $X^2_{(1)}$=4.871, P=0.027; $X^2_{(1)}$=3.981, P=0.046). There was no significant difference between baseline and post-experimental baseline (Mann-Whitney test: U=32, n_B=n_{PEB}=8, P=1.00; U=32, n_B=n_{PEB}=8, P=1.00; U=26, n_B=n_{PEB}=8, P=0.574; U=30, n_B=n_{PEB}=8, P=0.878). Experimental treatment significantly increased foraging activity (Mann-Whitney test: U=108, n_C=16, n_E=8, P=0.006) and significantly reduced antagonistic behaviours (Mann-Whitney test: U=25, n_C=16, n_E=8, P=0.016), grooming (Mann-Whitney test: U=26, n_C=16, n_E=8, P=0.019) and inactivity (Mann-Whitney test: U=26, n_C=16, n_E=8, P=0.019) compared to the control. Locomotion did not significantly differ across the conditions (Kruskal-Wallis test: $X^2_{(1)}$=0.397, P=0.529) (Figure 3). During the experimental treatment, the average gelada-device interactions were as follows: 4.64% foraging inside the device (EFI), 5.59% foraging the contents of the device (EFC), 1.10% foraging grass from the device (EFG) and 0.43% non-foraging manipulation (EMA).

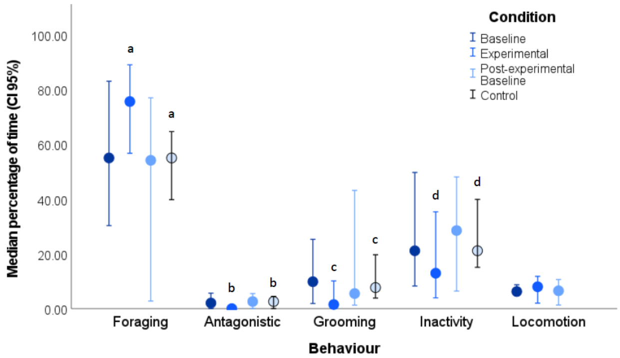

Figure 3. Median percentage of time (Confidence Interval 95%) the gelada troop spent in each activity for the conditions: Baseline, Experimental, Post-experimental baseline and Control (Baseline and Post-experimental baseline combined). Single letters indicate significance difference (P≤0.05).

Foraging behaviour

Provisioned foraging

There was no evidence to indicate an interaction effect between gelada and provisioned foraging behaviour among the baseline, experimental and post-experimental baseline (Kruskal-Wallis test: $X^2_{(5)}$=1.779, P=0.879; $X^2_{(5)}$=4.278, P=0.510; $X^2_{(5)}$=1.840, P=0.871 respectively), suggesting all geladas reacted similarly to the conditions. The percentage of time spent in provisioned foraging differed between the baseline and post-experimental baseline conditions (Mann-Whitney test: U=583, n_B=n_{PEB}=48, P<0.001) (Figure 4). The percentage of time spent in provisioned foraging for the experimental treatment was significantly greater than that in both the baseline (Mann-Whitney test: U=480, n_B=n_E=48, P<0.001) and post-experimental baseline (Mann-Whitney test: U=149, n_{PEB}=n_E=48, P<0.001).

Non-provisioned foraging

There was no evidence to indicate an interaction effect between gelada and non-provisioned foraging behaviour among the baseline, experimental and post-experimental baseline (Kruskal-Wallis test: $X^2_{(5)}$=4.271, P=0.511; $X^2_{(5)}$=7.620, P=0.178; $X^2_{(5)}$=5.824, P=0.324 respectively), suggesting all geladas reacted similarly to the conditions. The percentage of time spent in non-provisioned foraging was similar for the control conditions (Mann-Whitney test: U=994, n_B=n_{PEB}=48, P=0.245) (Figure 4). The percentage of time spent in non-provisioned foraging was significantly greater during the experimental condition compared to the control (Mann-Whitney test: U=−1841, n_C=96, n_E=48, P=0.050).

Nearest neighbour

The nearest-neighbour analysis presented two clear groupings, with three geladas in each. Hobbit, Herkules and Hector were one group and Harshit, Kidame and Kito were the second. During the entire observation period, on average, Hobbit and Herkules were closest to each other and Hector spent most of his time nearest Herkules. Kidame and Harshit were closest to each other and Kito spent most of his time nearest to Kidame (Table 2). The two groups were distinct throughout all three conditions (Figure 5). For both groups, the maximum time that an individual from one group was nearest neighbour to a member of the opposite group was 8% for the baseline, 13% for the experimental treatment and 13% for the post-experimental baseline.

Enclosure utilisation

The gelada troop utilised the enclosure similarly among the three conditions, but with greater utilisation of the front sections during the experimental treatment (Table 3). The average modified SPI was found to be similar for both control conditions ($t_{(10)}$=−1.344, P=0.209). The modified SPI was significantly lower for the experimental treatment compared to the control ($t_{(16)}$=2.724, P=0.15), showing that the experimental treatment increased enclosure utilisation (Figure 6). Individual gelada SPI indicates that during the experimental treatment, Hobbit (0.44), Hector (0.33) and Harshit (0.40) remained within a small area of their enclosure, whereas Herkules (0.29), Kito (0.19) and Kidame (0.26) utilised the enclosure more widely. Both groups of three appeared to dominate certain enclosure zones (Table 3).

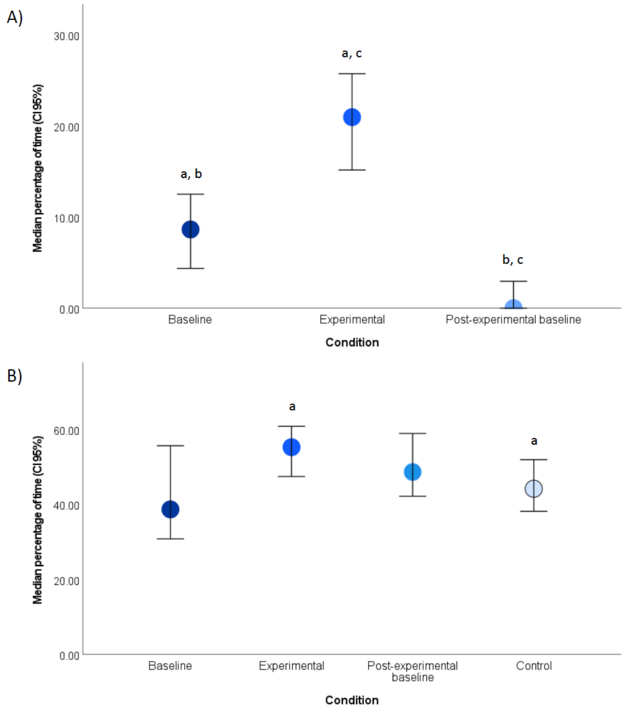

Figure 4. Median percentage of time (Confidence Interval 95%) the gelada troop spent provisioned foraging (A) and non-provisioned foraging (B) for the conditions: Baseline, Experimental, Post-experimental baseline and Control (where relevant). Single letters indicate significance difference (P≤0.05).

Discussion

Wild versus captive

Previous research has shown that wild geladas spend the majority of their time partaking in foraging activities (Abie et al. 2017; Fashing et al. 2014; Woldegeorgis and Bekele 2015). This study of captive gelada found a similar result across all three conditions, where foraging during the control conditions fell within the range of that of wild geladas and was greater during the experimental condition. All three conditions presented higher percentages (54, 74 and 51%, respectively) than that of a previous study of captive gelada (44%) (Filipčík et al. 2014). Similar captive and wild foraging levels are vital to ensure preservation of natural behaviours and can be a useful metric to assess welfare conditions.

The findings also show that during the control periods WPP geladas spent approximately 11–12% of their time in grooming activities, which was less than wild geladas (16–18%; Abie et al. 2017; Woldegeorgis and Bekele 2015). The presence of the enrichment device reduced grooming activities to 3%. Woldegeorgis and Bekele (2015) found that geladas in the wild participated in greater percentages of grooming and resting activities in the first few hours of observation (0700–1000). The data collection period for the captive troop started at 0900, consequently earlier key hours of grooming behaviour could have been missed. Conversely, wild geladas, much like other primates, engage in grooming as a social cue related to sexual and social status. The social integrity of a uni-male group is maintained by the strength of the social relationships, not by aggressive herding from males (Dunbar and Dunbar 1975, cited by Mancini and

Table 2. The nearest-neighbour percentage matrix, showing the percentage of time each gelada over the entire observation period was the nearest-neighbour of each individual.

	Nearest-neighbour identity					
Focal individual	Hobbit	Hector	Herkules	Harshit	Kidame	Kito
Hobbit	-	37.35	45.53	4.67	3.89	8.56
Hector	40.91	-	55.10	1.38	1.24	1.38
Herkules	50.62	46.51	-	1.37	0.55	0.96
Harshit	5.06	2.83	1.62	-	57.89	32.59
Kidame	3.35	1.18	0.79	53.06	-	41.62
Kito	11.05	4.99	3.39	34.58	45.99	-

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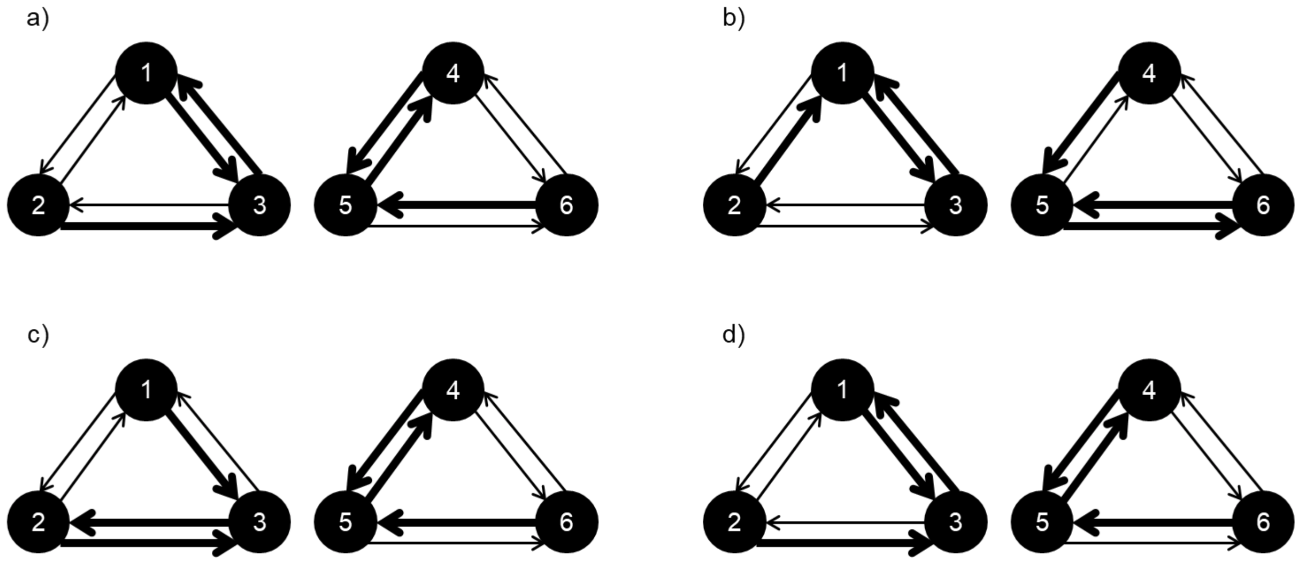

Figure 5. The nearest-neighbour relationship of individual geladas within the gelada troop; where the thicker line represents the gelada that the individual spent the highest percentage of time nearest (nearest-neighbour), the thinner line represents an individual's second nearest-neighbour. Graph: a) average of complete study period; b) average for Baseline; c) average for Experimental treatment; d) average for Post-experimental baseline. Numbers 1-6 represent a gelada: 1 Hobbit, 2 Hector 3 Herkules, 4 Harshit, 5 Kidame, and 6 Kito.

Palagi 2009). A study of hamadyras baboons found that grooming between a female-male pair is most common, in comparison to male-male and female-female pairs (Chalyan et al. 2012). The greatest occurrence of male-male grooming interactions was in young males aged 4–7 years. As this is an all-male group of predominantly mature status, it is likely that high levels of grooming are not necessary to maintain the bachelor group's social relationships, reflecting the results seen in the current study. The increase in foraging behaviour could account for the reduction in grooming when the enrichment device was present. As stated, a greater percentage of grooming could occur in the earlier hours when no enrichment was present in the enclosure. In addition, the reduction in grooming could be linked to the reduced aggression observed in the experimental period.

A comparison of wild and WPP gelada showed that the captive group displayed a lower percentage of locomotive behaviour

Table 3. The percentage of time each gelada spent in each zone of the enclosure during the Baseline (B), Experimental (E) and Post-experimental baseline (PB) periods.

	Enclosure Zone																		
		F1			F2			F3			B1			B2			B3		
Nearest neighour group	Focal gelada	B	E	PB	B	E	PB	B	E	PB	B	E	PB	B	E	PB	B	E	PB
Group 1	Hobbit	11.9	14.9	11.2	6.9	8.9	3.6	21.1	6.7	10.0	30.3	48.7	39.8	29.1	20.8	33.7	0.8	0.0	1.6
	Hector	10.0	29.1	18.2	5.4	8.2	6.7	12.5	6.6	7.5	49.4	40.6	44.3	21.6	14.8	22.9	1.2	0.8	0.4
	Herkules	22.9	19.3	14.2	7.2	8.6	9.9	14.9	15.0	9.9	23.3	31.3	34.8	31.7	24.5	30.8	0.0	1.3	0.4
	Average	14.9	21.1	14.5	6.5	8.6	6.7	16.2	9.4	9.1	34.3	40.2	39.6	27.5	20.0	29.1	0.7	0.7	0.8
Group 2	Harshit	4.7	13.0	5.0	8.1	10.1	3.3	15.7	8.2	12.5	32.6	22.1	31.7	37.2	43.8	41.7	1.7	2.9	5.8
	Kidame	9.5	16.6	4.8	8.9	17.1	12.4	14.0	10.7	9.7	25.7	24.6	32.4	36.9	28.9	39.3	5.0	2.1	1.4
	Kito	10.8	26.9	18.1	6.7	18.4	11.6	13.9	6.7	5.8	42.2	28.3	48.6	24.7	16.6	15.2	1.8	3.1	0.7
	Average	8.3	18.8	9.3	7.9	15.2	9.1	14.5	8.5	9.3	33.5	25.0	37.6	32.9	29.8	32.1	2.8	2.7	2.6
Average		11.6	20.0	11.9	7.2	11.9	7.9	15.4	9.0	9.2	33.9	32.6	38.6	30.2	24.9	30.6	1.8	1.7	1.7

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and higher inactivity during the control conditions (Abie et al. 2017; Woldegeorgis and Bekele 2015). However, inactivity was reduced by almost half (14% versus 27%) during the experimental treatment, yet was still slightly greater than in wild counterparts. Locomotion did not significantly change. Groups that exceed an ecologically tolerable size show signs of ecological stress, i.e. spending less time resting and socialising. Therefore, as captive geladas' resources are more readily available in a smaller spatial area, they will have more available time to spend resting. However, this reduction in inactivity is a positive step for this zoo-housed group of geladas and allows their activity budget to match more closely to that of their wild counterparts. Increased inactivity has been linked to overweight body condition (Bauer et al. 2012), therefore reduction in this behaviour can increase positive welfare of the individuals.

Provisioned and non-provisioned foraging behaviour

The species-typical device provided the opportunity for the geladas to engage in naturalistic foraging behaviour. The gelada enclosure had high grass coverage, but overgrazing means that the grass needs replacing frequently, which is difficult. Consequently, the provision of a replaceable source could prevent overgrazing and also allow expression of the need to forage in a more manageable and sustainable manner. The enrichment device worked to increase provisioned foraging. There was a significant increase in time spent foraging in provisioned areas of the enclosure when the device was introduced. In addition to provisioned foraging, the enrichment device also increased non-provisioned foraging behaviour, suggesting that it encouraged a more wide-ranging pattern of foraging that was not restricted to the device itself. Much like Jones and Pillay (2004) found, foraging using the device may have further stimulated the need for geladas to partake in natural foraging behaviours such as appetitive foraging of graminoids. The device's grass element was designed to stimulate this part of their natural behaviour, yet there was limited interaction with that component.

The presence of the enrichment device appears to have increased the time the geladas spent obtaining their captive measured diet, suggesting increased effort and energy expenditure, therefore showing a positive response to the feeding device. The ability for each individual gelada to access one device would appear to have been important in the increase of provisioned foraging. Jones and Pillay (2004) noted how the introduction of a monopolisable enrichment device that was being foraged by one individual encouraged other individuals in the group to independently forage non-provisioned areas (appetitive behaviours). Therefore, the use of six non-monopolisable devices has enabled each gelada to forage from their diet independently and gain greater equal access to the provisioned feeding resource. In turn it can be noted that a reduction in antagonistic behaviours was observed when the enrichment was present. This is corroborated by a study on domestic pigs *Sus scrofa*, where the individuals had to work for their food via cognitive enrichment which was shown to reduce reactivity and aggression among individuals (Puppe et al. 2007).

Evidence shows that during the observation period Harshit spent the most time in provisioned foraging behaviour compared to the rest of the group, suggesting that Harshit dominated the provisioned food source and could be the dominant male of the group (King et al. 2008). However, as Pappano (2013) states, in bachelor groups some geladas can be consistently higher ranking, but there is a lack of clearly defined dominance relationships and bachelors are unable to be ranked in a linear and transitive dominance hierarchy. Furthermore, as all of the geladas had access to their own device during the experimental period, this is an unlikely result. It is more likely that Harshit preferred the challenge of consuming food from the device.

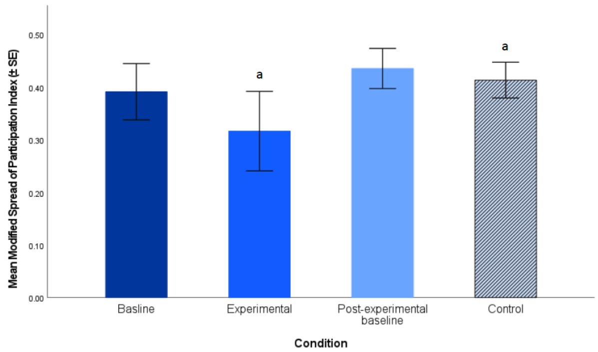

Figure 6. The Modified Spread of Participation Index (SPI) for all six geladas for the conditions: Baseline, Experimental, Post-experimental baseline and Control (Baseline and Post-experimental baseline combined).

Group relationships

All four nearest-neighbour tests showed that there were two distinct foraging groups, both consisting of three individuals. Hobbit, Herkules and Hector were one group and Harshit, Kidame and Kito were the second. Harshit and Kidame were in each other's company most often, suggesting that they had the strongest relationship. Kito and Hobbit separately appeared to have the lowest percentages of time spent near their corresponding nearest-neighbour, suggesting that they had not developed as strong bonds with their counterparts. In the wild, relatedness is more common within all-male groups than between all-male groups (Pappano 2013). Overall, most bachelors are unrelated, only some pairs are distinct kin and a few are close kin. Hobbit, Hector and Herkules are assumed to be related and Kidame and Kito are known to share the same sire. Therefore, the two larger groups that have formed are what would be expected if solely looking at kin relatedness.

Enclosure use

Introduction of the enrichment device presented a significant increase in enclosure utilisation, attributed to placement of enrichment devices in five out of six of the zones. By encouraging greater use of space, the effective size of the enclosure can be increased, potentially making the animals more visible to public view (Schultz and Young 2019). The ability to spread the enrichment devices out across the enclosure can aid in preventing an individual from monopolising multiple devices, which in turn would reduce the chance of aggression (Jones and Pillay 2004). The placement of enrichment can also increase the functionality of a zone. Therefore, an increase in enclosure utilisation through the use of enrichment can assist in improvement of welfare.

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Conclusion

Enrichment is a well-utilised tool in zoos, used to increase welfare and maintain natural behaviours of species. This study has shown that the use of nutritional foraging enrichment can encourage stimulation of similar activity budgets in captive geladas to those of their wild counterparts. The introduction of six monopolisable enrichment devices to a bachelor group of six geladas is shown to increase the group's provisioned foraging and can ensure that the geladas gain equal access to their provisioned diets. An increase in non-provisioned foraging in the troop was observed, therefore in agreement with previous research that states that an enrichment device can encourage appetitive foraging. However, unlike previous studies, all the individual animals could access a device at the same time, suggesting that the introduction of any enrichment device can increase appetitive foraging and reduce inactivity. The results also show that an enrichment device can be used to encourage geladas to utilise their enclosure to a more equal extent. Therefore, this study has shown that the use of a low-cost enrichment device is an effective way of stimulating zoo-housed geladas and providing positive welfare benefits. Similar devices should be considered for bachelor groups in other collections.

The results were limited as the full enclosure was not visible from one single point due to the central hill structure. Further research could compare how the geladas respond to being on public view and how the enclosure is utilised fully considering the off-show half. The activity budget was also restricted due to the constraints of observation time blocks. Camera traps could be used to gauge a full 24-hour activity budget for the gelada. This could dramatically change the grooming and inactivity results. Future research could also be conducted on how foraging behaviour changes throughout the year in captivity, how a breeding group of geladas would react to an enrichment device such as this and the best method of forage delivery to ensure that the welfare needs of this uniquely graminivorous primate are fully met.

Conflicts of interest

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The authors declare no conflict of interest.

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