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Behavioural and Glucocorticoid Responses of a Captive Group of Spider Monkeys to Short-Term Variation in Food Presentation

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Key Words
Ateles · Captivity · Feeding behaviour · Food competition · Food monopolization · Physiological stress

Abstract

The presentation of food may affect feeding competition and the well-being of captive social species. We hypothesized that feeding competition in a captive group of 5 black-handed spider monkeys *(Ateles geoffroyi)* should increase in response to certain food presentations in terms of size, distribution and quality of food, and that higher feeding competition should lead to an increase in agonism and physiological stress (measured by faecal glucocorticoid metabolites, FGCM) as well as to a decrease in affiliation, proximity among individuals and feeding activity. We used 5 experimental treatments representing different combinations of size, distribution and quality of food. We observed social interactions for 100 h, collected 6,500 proximity and feeding activity records, and gathered 226 faecal samples. When food was clumped, individuals spent less time feeding, and there was also significant individual variation in feeding activity within treatments. FGCM levels were higher when food was clumped. These results are probably linked to an increase in feeding competition when food is concentrated. At least in small groups of spider monkeys, dispersing food in two feeding stations may be sufficient to decrease differences among individuals in priority of access to food resources, hence reducing physiological stress and interindividual differences in feeding activity.

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Introduction

Feeding competition is an inevitable consequence of group living and one of the main evolutionary forces influencing the social organization of many animals [Alexander, 1974; Krause and Ruxton, 2002]. When food is distributed so that it can be monopolized or defended, differential access to resources among group members may develop, leading to direct contests over access to food in the form of aggression, displacement or avoidance [Wrangham, 1980; Blanckenhorn et al., 1998; Grant et al., 2000]. In the wild, individuals can decide whether to engage in direct competition with conspecifics or not, and it has been demonstrated that many animals display conflict management strategies to cope with feeding competition [Aureli and de Waal, 2000]. In contrast, the presence of visitors, spatial restrictions and human management may limit the ability of captive individuals to display their natural behavioural patterns [Hosey, 2005; Mason, 2010], which could lead to increased feeding competition.

In the wild, the availability of food resources typically follows highly complex patterns. Food resources vary in space in terms of size, density, distribution and quality [Chapman and Chapman, 2000], and they also vary over time [van Schaik et al., 1993]. The interaction between the spatial and the temporal availability of food resources will determine the possibility of monopolizing food patches [Goss-Custard et al., 1984; Grenier et al., 1999; Weir and Grant, 2004]. For instance, when food occurs in discrete patches, spatial clumping and temporal dispersion of patches may promote resource monopolization, whereas spatial dispersal and high abundance of food reduces the defensibility of food patches [Goldberg et al., 2001; Mathy and Isbell, 2001]. When food monopolization occurs, within-group feeding competition may emerge, either directly, through the expression of ritualized or aggressive behaviours, or indirectly, through dominance relationships [Goss-Custard et al., 1984; Grenier et al., 1999; Mathy and Isbell, 2001; Weir and Grant, 2004]. In addition to its influence on the establishment and maintenance of social relationships among group members, feeding competition represents a stressor to many animal species, as attested by changes in the secretion of glucocorticoids (e.g. primates [Abbott et al., 2003]) or heart rate (e.g. pigs, *Sus scrofa* [de Jong et al., 2000]) in individuals that compete for food. Therefore, when food resources can be monopolized, feeding competition may emerge and affect the behaviour and stress physiology of individuals.

Although many efforts have been dedicated in the last few decades to making the social and physical environments of captive animals more complex and naturalistic [Shyne, 2006; Whitham and Wielebnowski, 2013], the spatial and temporal variation in food availability in captivity usually differs dramatically from that observed in the wild. At the temporal level, captive animals are regularly supplied food at predictable fixed schedules, and do not need to spend time finding it [Swaisgood and Shepherdson, 2005; Morgan and Tromborg, 2007]. Furthermore, food is commonly presented in a ready-processed form, which further reduces the need to forage [Morgan and Tromborg, 2007]. As a consequence, captive animals spend less time foraging and feeding than their wild counterparts [Britt, 1998; Lukas, 1999; Höhn et al., 2000; Kerridge, 2005]. At the spatial level, although the benefits of scattering food in the substrate have been recognized for several decades, food is often delivered in predictable locations in containers that represent discrete monopolizable food clumps [Anderson and Chamove, 1984; Forthman et al., 1992; Swaisgood and Shepherdson, 2005].

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Therefore, captive animals often face reduced spatial and temporal variation in food availability, which could facilitate resource monopolization and, as a consequence, increase feeding competition. Although no studies have directly compared feeding competition between wild and captive individuals of a species, there is evidence that the frequency of aggressive interactions is higher among captive than among wild individuals (e.g. Somali wild asses, *Equus africanus somalicus* [Asa et al., 2012]; eastern grey kangaroos, *Macropus giganteus* [Höhn et al., 2000]). In this context, decisions concerning the presentation of food will affect feeding competition and may be critical for the well-being of social species maintained in captivity [Young, 1997; Kawata, 2008].

Spider monkeys are Neotropical primates that live in communities of 15–56 individuals [Shimooka et al., 2008], which occupy home ranges of up to 963 ha [Di Fiore and Campbell, 2007]. Spider monkey communities are characterized by a high degree of fission-fusion dynamics [Aureli et al., 2008], with individuals forming small subgroups or parties that vary in size and membership frequently throughout the day [Symington, 1990; Chapman et al., 1995]. Fission-fusion represents a strategy to cope with the contrasting pressures of avoiding predators (which favours large subgroups) and minimizing feeding competition (which favours small subgroups) when there is temporal or spatial fluctuation in predation pressure and food availability [Boesch and Boesch-Achermann, 2000; Aureli et al., 2008]. Social interactions within groups are mostly affiliative, with infrequent aggression [Fedigan and Baxter, 1984; Symington, 1987; van Roosmalen and Klein, 1988; Slater et al., 2009]. Although spider monkeys are common in zoos [International Species Identification System, 2015], captive populations have seldom been studied. The available data indicate that female-female affiliative interactions are more frequent in captivity [van Roosmalen and Klein, 1988], that male-male aggression is more frequent in captivity than in the wild and a disproportionate amount of the aggression involves lethal or serious aggression between males [Davis et al., 2009]. This difference in the patterning of social interactions between wild and captive spider monkeys has been interpreted as a possible consequence of several factors, including housing familiar females together, housing unfamiliar males together or the reduced opportunities for fissioning offered by small enclosures [Pastor-Nieto, 2001; Davis et al., 2009].

Because the captive environment can affect spider monkeys' well-being through increases in aggression, it is important to investigate which factors in that environment affect the social behaviour and physiological stress responses of individuals. Therefore, the aim of the present study was to address for the first time the impact of variation in food presentation on feeding competition in spider monkeys, and to this end, we focused on a captive group of black-handed spider monkeys *(Ateles geoffroyi)*. Based on the patterning of feeding competition reported by previous studies in primates [Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997], and specifically on studies of captive primates that indicate that the clumping of food leads to increases in feeding competition [Gil-Burmann et al., 1998; Stahl and Kaumanns, 2003], our working hypothesis was that feeding competition should increase in response to certain food presentations in terms of size, distribution and quality of food patches. Higher feeding competition should lead to the following behavioural and physiological responses: increase in agonism, decrease in affiliation, decrease in proximity among individuals, decrease in feeding activity and increase in physiological stress (measured through concentrations of faecal glucocorticoid metabolites, FGCM hereafter). We specifically hypothesized that: (1) if the size of food patches is the main attribute determining feeding competition, feeding competition should increase when food is distributed in small patches; (2) if the quality of food patches is the main attribute determining feeding competition, feeding competition should increase when food patches vary in quality and high-quality foods are clumped; (3) if the distribution of food patches is the main attribute determining feeding competition, feeding competition should increase when food is clumped.

Methods

Ethics Statement

Our research complied with the ethic and administrative requirements of the Mexican law (approved by permit SEMARNAT SGPARN.03.VS.3644/11) and with the Guidelines for the Treatment of Animals in Behavioural Research and Teaching from the Animal Behaviour Society.

Housing, Subjects and Husbandry

The study was conducted with a captive group of spider monkeys that lives in the Unidad de Manejo Hilda Ávila de O'Farrill (locally known as Pipiapan), near the town of Catemaco, in the state of Veracruz, Mexico (18°28′–18°26′ N, 95°03′–95°01′ W). Pipiapan is a natural preserve with approximately 400 ha that belong to the Universidad Veracruzana. It includes areas of natural tropical evergreen forest as well as facilities for housing native Mexican primates confiscated from the illegal pet trade and their descendants. Study subjects were housed under seminatural conditions in a 1,800-m^2 outdoor enclosure of trees surrounded by an electric fence and were thus exposed to natural environmental conditions concerning ambient temperature, relative humidity and light. The group comprised 5 individuals: 1 adult male, 2 adult females, 1 juvenile male and 1 female infant. One adult female and all immature individuals were born in Pipiapan and were the offspring of the other adult female and the adult male.

Each day at 9:30 h, the group received the following foods: 6 red tomatoes, half a beetroot, 6 celery stems with leaves, 3 chard leaves, half a cantaloupe melon, half a papaya, 1 avocado, 3 carrots, half a broccoli, 30 bananas, half a pineapple, half a cucumber and 6 apples. All food items were chopped before serving and offered to the individuals in a stainless-steel food tray (50 cm length × 30 cm width × 15 cm height), which was raised with a rope and sheave up a tree (to approx. 8 m).

Pilot Observations

From February to March 2012, we habituated the group to the presence of 3 researchers (30 days, approx. 150 observation hours). Although individuals were already fully habituated to the presence of humans in areas surrounding their enclosure, human presence inside the enclosure usually occurred only during feeding. Therefore, because the collection of faecal samples required the frequent entry of people into the enclosure, we performed this habituation to minimize the probability that researchers represented a potential stressor for spider monkeys. On each observation day, 2 researchers entered the enclosure when one of the subjects defecated and performed the faecal sample collection procedure described below. All faecal samples collected during pilot observations were excluded from analyses.

During pilot observations we determined which foods were selected preferentially by individuals by recording ad libitum which items were first consumed upon the presentation of food, and by recording which foods were entirely consumed (i.e. no leftovers in the food tray or on the ground). Based on these observations, we classified avocado, bananas, cucumber, melons, papayas, pineapples and tomato as preferred foods, and beetroot, celery, chard, carrots, broccoli, and apples as non-preferred foods. Also, these observations allowed us to determine that feeding activity usually decreased dramatically 1 h after provisioning. After this period individuals would

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Table 1. Experimental treatments

Treatment	Characteristics of food patches				Description
	size		preference	distribution	
LC	large		preferred and non-preferred	clumped	large tray with all food types
SC	small		preferred and non-preferred	clumped	small tray with all food types
VDFM	variable		preferred and non-preferred	dispersed	one large and one small tray with all food types
VDPL	variable	large small	preferred non-preferred	dispersed	one large tray with preferred foods and one small tray with non-preferred foods
VDPS	variable	large small	non-preferred preferred	dispersed	one large tray with non-preferred foods and one small tray with preferred foods

LC = Large clumped; SC = small clumped; VDFM = variable dispersed with food in mixed presentation; VDPL = variable dispersed with preferred food in large tray; VDPS = variable dispersed with preferred food in small tray.

forage sporadically on the food that remained and occasionally foraged on the natural vegetation in their enclosure.

Experimental Set-Up

We used 5 experimental treatments and 1 neutral condition for food presentation. Each treatment represented a particular combination of size, distribution and quality (defined as preference, as described above) of food (table 1). Food trays were positioned so that researchers could observe the subjects during food provisioning without visual barriers. The size of food patches was manipulated by presenting food in two differently sized stainless-steel food trays, one large tray (80 × 40 × 15 cm) and one small tray (40 × 30 × 15 cm). Food distribution was manipulated by presenting food in a single tray (clumped condition) or in two trays (dispersed condition) separated by 10 m. Food quality was manipulated by presenting all food items in one or two trays, or by presenting high-quality foods in a different tray from low-quality foods. The neutral condition was presented between treatments to increase the independence of behavioural and hormonal data between treatments. In the neutral condition, food was presented to subjects as before the start of the study.

Each treatment was replicated twice. We randomly decided the order of treatments by assigning each treatment a different number and then consulting a random number table until all numbers appeared twice. The resulting sequence was: VDFM, LC, VDPL, VDPS, SC, VDPL, SC, VDPS, VDFM, LC (abbreviations as described in table 1). With this set-up we minimized the probabilities that individuals responded to a particular sequence of treatments rather than to variation in food patch characteristics, and were able to test for within-treatment consistency in behavioural and hormonal results. Each treatment was presented to the group for 10 consecutive days, followed by 4 days in the neutral condition.

Behavioural Observations

All subjects were identified on the basis of their natural anatomical and physiognomic characteristics, such as body size and proportions or genital morphology and pigmentation. From March to July 2012, we performed behavioural observations. Behavioural sampling began when food was presented to the spider monkeys and finished 1 h after. To study social interactions occurring in the feeding context, we sampled all occurrences of affiliative and agonistic behaviours with continuous recording [Altmann, 1974] (online suppl. table 1; for all online suppl. material, see www.karger.com/doi/10.1159/000441059). When a social interaction occurred, we noted its type and the identity of both actor and recipient. To study proximity patterns of individuals in the feeding context, we used scan sampling with instantaneous recording [Altmann, 1974]. Every 5 min we noted whether each individual had other group members in close proximity (defined as <5 m). Simultaneously, to study feeding activity, during scan sampling, we recorded whether subjects were feeding. We collected a total of 100 h of social interaction data and 6,500 instantaneous recordings of proximity and feeding activity (1,300 recordings per individual).

Faecal Sample Collection, Processing and Analysis

Faecal samples were collected opportunistically throughout the day whenever they could be matched with individuals. Fresh samples uncontaminated by urine were collected from the floor and deposited in polyethylene bags labelled with the identity of each individual. We collected a total of 226 faecal samples, with a mean (±SD) number of 44.8 ± 1.3 samples per individual. A mean of 45.2 ± 5.4 samples was collected per treatment. We collected faecal samples from all individuals in all treatments.

Faecal samples were kept in a cooler with frozen gel packs while in the field and stored at the end of the day in a freezer at −20°C until extraction was performed. Samples were stored at constant temperature (−20°C) for a maximum of 12 months until the extractions were conducted. The freezing procedure used for storing the samples has had little effect on faecal hormone metabolites in other primate species [Khan et al., 2002].

Steroid metabolites were extracted following a modification of the method described in Wasser et al. [2000]. Briefly, 0.6 g of homogenized, lyophilized and pulverized faeces was shaken for 24 h in 6.0 ml of analytical-grade methanol. Extracts were then centrifuged (460 *g* for 30 min at −4°C), and the supernatant containing the steroids was recovered. After complete evaporation (at 60°C) of the solvent, pellets were reconstituted with 3 ml albumin buffer and used for the FGCM analysis. FGCM assays were conducted at the Instituto de Ciencias Médicas y Nutrición Salvador Zubirán, in Mexico City. FGCM levels in all samples were measured using a commercial radioimmunoassay ^{125}I cortisol kit (Izotop, Institute of Isotopes Ltd., Budapest, Hungary; sensitivity = 2.9 nmol/l; calibration range = 0–1,600 nmol/l) and a gamma counter (Cobra Model E5005, Packard Inc., Downers Grove, Ill., USA). The manufacturer reports low cross-reactivity with corticosterone (4.3%). Spider monkeys' pooled faecal extracts, when added to the standard curve points, exhibited an accuracy of $R^2 = 0.98$ ($n = 4$, $p < 0.001$). Serial dilutions of faecal extracts gave displacement curves parallel to those obtained with the cortisol standard ($t = 1.01$, $p = 0.152$). Intra- and interassay coefficients of variation of high- and low-quality controls were 7.5% (high, n = 12) and 8.2% (low, n = 12), and 6.3% (high, n = 25) and 12.1% (low, n = 25), respectively. Hormone concentrations are reported as nanograms per gram of dry faeces.

As a biological validation of our assay, we determined the short-term effect of capture (an acute stressor) and anaesthesia (ketamine) on the faecal glucocorticoid excretion profile of 2 adult spider monkeys (1 male and 1 female) that were housed separately from our study group. These animals were captured for veterinary management, which provided a unique opportunity to perform the biological validation. We collected all faecal samples (n = 15) from 48 h before to 48 h after capture, and compared precapture levels with postcapture concentrations with a Mann-Whitney test. FGCM levels peaked at a mean (±SD) of 18 ± 2.3 h after capture. After this result, to assess the effects of treatments on FGCM levels, we used faecal samples collected between the second day of any particular treatment and the first day in the neutral condition following each treatment.

Postcapture FGCM levels (mean ± SD = 161.3 ± 130.5 ng/g) were significantly higher than precapture levels (19.5 ± 16.7 ng/g; $Z = 3.18$, precapture $n = 6$, postcapture $n = 9$, $p < 0.001$), indicating that our FGCM assays measured adrenal responses of spider monkeys to stressors.

We found no differences in FGCM levels between samples collected in the morning (9:00–12:00 h) and in the afternoon (12:00–17:00 h; Mann-Whitney test $Z = 1.15$, morning $n = 90$, afternoon $n = 158$, $p = 0.257$). We therefore analysed all faecal samples irrespectively of time of collection.

Statistical Analyses

We calculated the total frequency of affiliative and agonistic social interactions in each treatment for each actor. Proximity and feeding were analysed as the mean proportion of instanta-

Table 2. Descriptive statistics (means ± SD) for each response variable

Treatment	Affiliation	Agonism	Proximity	Feeding	FGCM, ng/g
LC	1.8±1.3 (0.8)	1.2±0.9 (0.3)	0.6±0.2 (0.01)	0.4±0.3 (0.04)	67.8±24.5 (1.8)
SC	1.6±0.8 (0.8)	2.5±1.6 (0.4)	0.5±0.2 (0.07)	0.3±0.3 (0.02)	85.5±17.5 (9.7)
VDFM	1.6±0.9 (0.6)	1.1±0.9 (0.1)	0.5±0.3 (0.05)	0.6±0.2 (0.06)	25.4±20.3 (10.6)
VDPL	1.6±0.9 (0.0)	0.9±0.8 (0.4)	0.5±0.2 (0.06)	0.6±0.1 (0.01)	29.7±23.1 (4.0)
VDPS	1.1±0.9 (0.9)	1.3±0.9 (0.4)	0.5±0.1 (0.07)	0.7±0.2 (0.06)	33.1±27.5 (14.6)

LC = Large clumped food; SC = small clumped food; VDFM = variable dispersed with food in mixed presentation; VDPL = variable dispersed with preferred food in large tray; VDPS = variable dispersed with preferred food in small tray. Affiliation and agonism were calculated as mean frequencies per focal period (i.e. 1-hour samples). Proximity and feeding were analysed as the mean proportion of instantaneous samples per hour per individual in which each individual had other group members in close proximity or fed, averaged for each treatment. Standard deviations calculated between replicates are presented in parentheses.

neous samples per hour per individual in which each individual had other group members in close proximity or fed and averaged them for each treatment. We calculated mean FGCM levels per individual per treatment to obtain a measure that reflected individual hormonal activity in response to food presentation.

To assess the effects of food presentation on the behaviour and FGCM of spider monkeys, we used generalized linear mixed models (GLMMs [Rabe-Hesketh et al., 2005]). We ran one model for each response variable (frequency of agonism, frequency of affiliation, proximity, feeding activity and FGCM levels). We used multinomial logistic models (and identity link functions) to analyse social interactions, as the individual frequencies of both affiliative and agonistic interactions were low (affiliation range = 0–4 interactions per individual per treatment; agonism range = 0–5). We square root transformed FGCM levels and used the arcsine transformation for both proximity and feeding activity to achieve normal distributions. We checked that the assumptions of normally distributed and homogeneous residuals were fulfilled. Individual identity was used as a random factor in all models. In all models we also included replicate nested within treatment and subject nested within treatment as categorical predictors to account for variation between replicates in response variables recorded in each turn, and variation among subjects in response variables in each treatment. When treatment had a significant effect on a response variable, we performed pairwise post hoc comparisons between treatments with GLMM (n = 20 cases). In these tests, treatment was included as a fixed factor and individual identity was used as a random factor.

All analyses were performed with SPSS 22.0 (IBM Corp., Armonk, N.Y., USA). The statistical threshold was set at $p \leq 0.05$.

Results

Descriptive statistics for response variables are presented in table 2. The frequencies of affiliative and agonistic social interactions, as well as the proportions of instantaneous recordings in which individuals had other group members in proximity were unaffected by treatment (table 3). In contrast, both feeding activity and FGCM levels varied significantly as a function of treatment. Spider monkeys spent a lower propor-

Table 3. GLMM results

	F	d.f.	p
Affiliation (null model)	0.57	29, 17	0.908
Treatment	0.43	4, 17	0.788
Replicate (treatment)	1.65	5, 17	0.200
Subject (treatment)	0.36	20, 17	0.986
Agonism	0.47	29, 16	0.961
Treatment	1.45	4, 16	0.265
Replicate (treatment)	0.24	5, 16	0.938
Subject (treatment)	0.352	20, 16	0.985
Proximity	1.46	29, 20	0.193
Treatment	0.49	4, 20	0.743
Replicate (treatment)	1.28	5, 20	0.311
Subject (treatment)	1.69	20, 20	0.124
Feeding	10.59	29, 20	<0.001
Treatment	17.99	4, 20	<0.001
Replicate (treatment)	1.31	5, 20	0.300
Subject (treatment)	11.43	20, 20	<0.001
FGCM	2.81	29, 20	0.010
Treatment	14.72	4, 20	<0.001
Replicate (treatment)	0.89	5, 20	0.505
Subject (treatment)	0.91	20, 20	0.583

tion of time feeding in treatment SC than in treatments VDFM, VDPL and VDPS, and in treatment LC than in treatments VDPL and VDPS (all post hoc GLMM tests $p < 0.05$; table 2). In this model there was also significant variation among individuals in feeding time within treatments (LC: $F_{4, 20} = 18.05$, $p < 0.001$; SC: $F_{4, 20} = 17.11$, $p < 0.001$; VDFM: $F_{4, 20} = 9.51$, $p < 0.001$; VDPL: $F_{4, 20} = 5.57$, $p = 0.005$; VDPS: $F_{4, 20} = 6.91$, $p = 0.002$; table 3). FGCM levels in treatments LC and SC were significantly higher than in treatments VDFM, VDPL and VDPS (all post hoc GLMM tests $p < 0.05$; table 2).

Discussion

We examined for the first time how feeding competition in captive black-handed spider monkeys was affected by short-term variation in food presentation. In particular, we expected that both behaviour and glucocorticoid levels varied as a function of changes in the size, distribution and quality of food patches. Whereas social interactions and proximity patterns were unaffected by variation in food presentation, when food was clumped time spent feeding decreased and glucocorticoids increased, as compared with treatments in which food was dispersed. Time spent feeding also varied significantly among individuals within food presentations. Therefore, our study suggests that food presentation, and specifically food distribution, can be an important factor determining the behaviour and physiological stress response of captive spider monkeys.

Although some studies report aggressive interactions and agonistic displacements among wild spider monkeys in feeding contexts [Symington, 1987; Chapman, 1990], aggression is overall infrequent [Asensio et al., 2008; Aureli and Schaffner, 2008; Slater et al., 2009]. Furthermore, there is little evidence for the existence of dominance relationships (i.e. consistency in the outcomes of dyadic agonistic conflicts) in both wild and captive populations [Aureli and Schaffner, 2008]. The frequency of social interactions and proximity among individuals were unaffected by food presentation, even when resources were clumped. Still, spider monkeys changed their behaviour under clumped conditions: overall feeding time decreased; variation in feeding time among individuals within treatments was significant for all food presentations, but was more marked when food was clumped. Although no changes were recorded in interference competition (i.e. behavioural interactions between competitors [Miller, 1967]) throughout the study, it is possible that differences among group members in priority of access to food allowed some individuals to maintain their feeding times but not others. For instance, the adult female that had an infant showed low variation in feeding time through the study, whereas the juvenile male had low feeding times when food was clumped compared to when food was dispersed. Such differences in priority of access to food could be explained by deference of some individuals during feeding, as has been reported in other primates (e.g. ring-tailed lemurs, *Lemur catta* [Kappeler, 1990]). However, the decrease in the proportion of time spent feeding on clumped food was associated with overall higher FGCM levels, suggesting that this food presentation represented a stressful situation for all individuals. Thus, differences among individuals in priority of access to food, even if not accompanied by aggressive behaviour, could reflect higher feeding competition. For individuals with priority of access to food, higher FGCM levels could reflect the effects of physical challenges associated with changes in behaviour aimed at defending food resources (e.g. vigilance), and for all individuals the perceived risk of having to evict or being evicted from food trays may have represented a significant psychosocial stressor [Creel, 2001; Abbott et al., 2003]. Additionally, for a species that copes with food competition by adjusting subgroup size to food abundance [Asensio et al., 2008], it might be particularly challenging to deal with clumped food resources when individuals cannot employ their normal subgrouping strategies. Therefore, in species that do not compete aggressively for food, such as spider monkeys, the clumping of food resources may lead to the emergence of interindividual differences in feeding activity and result in physiological stress.

Although this was a short-term study, spider monkeys presented very immediate physiological responses to changes in their environment. Changes in FGCM were documented from the first treatment, as demonstrated by the significant difference between treatments VDFM (dispersed distribution) and LC (clumped distribution). These changes were also highly consistent throughout the study, because variation in hormone levels between replicates in each treatment and among individuals in each treatment were not significant. The observed variation in FGCM levels during the study suggests that individuals were able to display salutary glucocorticoid responses to the challenges imposed by our experimental set-up, but also that food presentation is perhaps not such a strong stressor as to elicit chronic stress [Wingfield et al., 1998; Sapolsky et al., 2000] in captive spider monkeys. The modulation of glucocorticoids is part of the adaptive physiological stress response, and these hormones are involved in diverse actions [Sapolsky et al., 2000]. Before the start of our study, food had been

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offered to the group in a clumped presentation for many years. If that presentation represented a sufficiently strong and prolonged stressor as to induce a chronic stress response, we would not expect individuals to present variation in FGCM levels in response to our experimental set-up, or such variation should not be consistent throughout the study (e.g. individuals responding to changes in food presentation rather than to variation in food patch characteristics). A better understanding of these results will inevitably depend on the long-term monitoring of the stress responses of captive individuals to their environment, with particular emphasis on the physiological and behavioural impact of different husbandry regimes.

There are several implications of our results for the husbandry of captive spider monkeys. First, in contrast with most zoos, at Pipiapan spider monkeys: (1) are never exposed to large numbers of people who are unfamiliar to them; (2) may avoid contact with humans due to the size of the enclosure and the vegetation present in it; (3) are not captured for routine veterinary procedures; (4) are exposed to natural environmental conditions concerning ambient temperature, relative humidity and light. In zoos, these attributes of the captive environment have a positive effect on the well-being of individuals [Hosey, 2005; Morgan and Tromborg, 2007; Mason, 2010]. The fact that individuals presented significant changes in their behaviour and physiological stress in response to variation in food presentation suggests that naturalistic captive environments and low-intensity management practices are not sufficient to assure the well-being of spider monkeys. Second, aggressive behaviour among group members was not affected by variation in food presentation, even when food was clumped. Therefore, our study agrees with a previous analysis of aggressive behaviour among captive spider monkeys by discarding feeding competition as an important factor associated with the emergence of agonism that may result in the injury or death of individuals [Davis et al., 2009]. Finally, we experimentally manipulated the spatial availability of food resources when no temporal variation existed in food presentation. Although it remains for future research to determine whether the behaviour and physiological stress response of captive spider monkeys are also affected by temporal variation in food presentation, our results indicate that when food is presented only once during the day, dispersing food may be sufficient to limit the emergence of feeding competition. In this sense, we emphasize that adding a second tray/feeding station, when only one is present, may not represent a significant increase in husbandry effort but will improve the well-being of individuals.

Conclusion

A family group of captive black-handed spider monkeys responded to the clumping of food by reducing feeding time and increasing FGCM levels. These responses are probably linked to an increase in feeding competition when food is concentrated, which highlights the importance of providing suitable housing and husbandry practices for spider monkeys. Although our study was conducted with a single, small group, our results suggest that it is possible that dispersing food items inside enclosures may be a sufficient practice to decrease differences among individuals in priority of access to food resources, hence reducing interindividual differences in feeding activity and physiological stress.

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