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Aggression and self-directed behaviour of captive lemurs (*Lemur catta, Varecia variegata, V. rubra* and *Eulemur coronatus*) is reduced by feeding fruit-free diets

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Abstract

Primate diets in captivity often differ considerably in their nutrient composition to those eaten by wild conspecifics. In particular, captive diets often contain much higher levels of sugar and other readily-digestible non-structural carbohydrates and much lower levels of fibre. This has been shown to have negative effects on captive primate physical health but to date there is little evidence of any effects on behaviour. In line with ongoing dietary improvements the diets of four species of lemur housed at Newquay Zoo and Paignton Zoo were changed to completely remove all fruit, resulting in a lower concentration of non-structural carbohydrate and increased fibre, to better reflect the composition of their wild diet. The effects of this diet change on behaviour of the lemurs were monitored, paying particular attention to possible welfare indicators: aggression, auto-grooming, foraging and self-directed behaviour. When fed the fruit-free diet both aggression ($p < 0.001$) and self-directed behaviour ($p < 0.001$) were significantly lower than when fed the original diet in all four lemur species. There was no significant effect of diet on foraging and auto-grooming. These results suggest that feeding a fruit-free diet for these lemur species has a positive effect on their psychological welfare in a zoo setting.

Introduction

Lemurs are a common sight in zoos, but in the wild are forest-dwelling primates endemic to the island of Madagascar (Mowry and Campbell 2001). Lemurs are frugivorous and folivorous (MacLeod et al. 2003) and display evidence of a varied seasonal diet (Sbeglia et al. 2010). Diet varies between lemur species, but most select various leaves and fruits (Godfrey et al. 2004) with a wild lemur expected to consume over 125 different plant species annually (Milton 1999). Flowers, sap, tree bark and buds (Dierenfeld and McCann 1999; Mowry and Campbell 2001; Curtis 2004) are also common components of a wild diet, with items such as roots, fungi and soil also ingested (MacLeod et al. 2003); there have even been sightings of lemurs eating chameleons and invertebrates such as caterpillars and grasshoppers (Sussman 1977).

Analysis of wild lemur diets show that they contain only small quantities of non-structural carbohydrates and high levels of neutral detergent fibre, but captive lemur diets often have much greater concentrations of non-structural carbohydrate, especially sugar, and lower fibre levels than in the wild (Dempsey et al. 2002; Dierenfeld and McCann 1999). Over 75% of captive primate diets consist of at least 50% fruit and vegetables (Kaummans et al. 2000) with the vegetable component frequently including a large portion of starchy vegetables such as turnips and sweet potato, and fruits such as apples, bananas and grapes (Mowry and Campbell 2001). Fruits available in the captive setting have been selectively grown for humans so tend to have high non-structural carbohydrate and low fibre content and are very sweet, unlike those available in the wild (Milton 1999), which have a much lower energy content (Goodchild and Schwitzer 2008). Schmidt et al. (2005) found that fructan constitutes an average of 4.9% of orchard-grown fruit, much higher than that found in vegetables (1.45%) and leafy greens (0.6%). Fruits grown for human consumption were also found to be higher in starch (24.3%) than vegetables (22.5%) and leafy greens (14.0%) such as kale, alfalfa and lettuce.

Inappropriate nutrition, especially high levels of non-structural carbohydrate, is known to be a contributory factor in many physical health problems in captive primates, including obesity, heart disease, diabetes and gastro-intestinal disorders (e.g. Kuhar et al. 2013). There have also been anecdotal reports of links between high levels of non-structural carbohydrate and an increased prevalence of undesirable behaviours, but little research has focused on this aspect. In humans, adverse nutrition, especially high sugar levels, is closely associated with several behavioural disorders (Bellisle 2004). The human body is heavily dependent on digestible carbohydrates as a major source of energy in the form of glucose, but high levels have been found to negatively affect cognition (Bellisle 2004; Stephen et al. 2012). The effect of sugar on human behaviour has caused widespread concern (Nicol et al. 2005) due to associations with aggression (Prinz et al. 1980), hyperactivity (Dykman and Dykman 1998; Bellisle 2004; Kim and Chang 2011), anti-social behaviour, increased crime rates and greater levels of violence (Benton 2007). In addition, diet manipulation trials have shown that withdrawal of sucrose from the diet caused an improvement in behaviour, but reintroduction saw a decline (Crook 1974), indicating a positive diet change can result in behavioural improvements (Bellisle 2004; Lien et al. 2006).

The effect on behaviour of high levels of non-structural carbohydrate in non-human primate diets has received much less attention. As non-human primates have many similarities to humans, excess dietary sugar may have similar consequences. Thus, captive primates receiving diets higher in sugar might be predicted to have increased incidences of aggression and self-directed behaviours (SDBs) (Roberts et al. 2001). SDBs, behaviours directed at an animal's own body such as shaking (Hosey et al. 2009), over-grooming and scratching, have been shown to be associated with stress and anxiety in non-human primates (e.g. Baker and Aureli 1997). Some aggression in primate groups should be expected as this is a method employed to establish a dominance hierarchy and maintain social dynamics (Britt 1998), but high levels can increase anxiety levels which are then often displayed through SDBs and in extreme cases self-mutilation.

In common with other captive primates, captive lemurs are reported to exhibit physical problems, such as obesity (Schwitzer and Kaummans 2001; Goodchild and Schwitzer 2008), and in some cases worrying levels of aggression (Hosey 2005). This study investigated the effect of removing fruit from the diets of zoo-housed lemurs on nutrient levels in the diet and on the behaviour of the animals, particularly aggression, SDBs and self-grooming, but also foraging, which is commonly considered to be a desirable behaviour to encourage in captivity (e.g. Reinhardt 1993).

Table 1. Individual lemurs at two zoos included in behavioural observations before and after fruit was removed from their diets.

Species	Sex	Date of birth	Location
Varecia variegata	Male	21 February 2003	Newquay Zoo
Varecia variegata	Female	21 April 2007	Newquay Zoo
Varecia rubra	Male	13 May 2005	Paignton Zoo
Varecia rubra	Female	18 April 2002	Paignton Zoo
Lemur catta	Male	26 February 2003	Newquay Zoo
Lemur catta	Male	03 March 2010	Newquay Zoo
Lemur catta	Male	22 March 2012	Newquay Zoo
Lemur catta	Female	12 April 2002	Newquay Zoo
Lemur catta	Female	16 March 2004	Newquay Zoo
Lemur catta	Female	21 February 2011	Newquay Zoo
Lemur catta	Male	31 March 2009	Paignton Zoo
Lemur catta	Male	08 April 2010	Paignton Zoo
Lemur catta	Male	05 July 2010	Paignton Zoo
Lemur catta	Male	05 July 2010	Paignton Zoo
Eulemur coronatus	Male	01 June 2005	Newquay Zoo
Eulemur coronatus	Female	22 May 1997	Newquay Zoo
Eulemur coronatus	Female	24 May 2012	Newquay Zoo

Methods

Subjects, housing and husbandry

The study subjects were 17 individual lemurs (Table 1), aged 1–16 years, of four species: black and white ruffed (*Varecia variegata*), red ruffed (*V. rubra*), ring-tailed (*Lemur catta*) and crowned lemur (*Eulemur coronatus*). They were housed at Paignton Zoo Environmental Park or Newquay Zoo, both in the UK, and observed during May–July 2012 (Paignton) or May–July 2013 (Newquay). Throughout the study all species were housed in their normal enclosures with their usual husbandry routine. At Paignton *L. catta* and *V. rubra* were each housed in a separate indoor house and adjoining small outdoor area with 24 hour access to both, but from 1000 to 1600 each day both species also had access to a very large, shared outdoor enclosure through which the public were allowed to walk. Throughout the study the daily diet was provided in two feeds, dry feed scattered in the indoor house before 1000 and produce scattered in the indoor enclosure at approximately 1600.

At Newquay *L. catta* and *V. variegata* were both housed on separate moated island enclosures with 24-hour access to both an outdoor area and indoor house. The *E. coronatus* were housed in a mixed-species exhibit with a pair of narrow-striped mongoose (*Mungotictis decemlineata*) in an enclosure which had a small indoor area and larger outdoor area with solid sides, acrylic viewing panes for the public and a mesh roof. Throughout the study all lemurs at Newquay Zoo were fed three times a day: dry feed in bowls in the indoor houses at approximately 0830, and produce scattered in the outdoor enclosures at approximately 1230 and 1530. No naturally growing browse was available to the Newquay lemurs.

Diets and nutrient analysis

The original diets of all lemurs consisted of various dry pelleted feeds and fruit and vegetables (Table 2). New fruit-free diets (Table 2) were formulated using Zootrition software to remove all fruit, reduce the number of different dry feeds used and increase the amount of vegetables. Much of the original diet was uneaten so the required energy of the new diet was estimated from the amount of food actually eaten by each species, since the animals were judged to be an appropriate weight. Differences in estimated energy requirements, presumably as a result of different ambient temperatures and activity levels, resulted in slightly different fruit-free diets for *L. catta* at the two zoos. The new diets were introduced gradually over a week and no other changes were made to feeding times, methods or locations. The nutrient content of the diets was analysed using standard published values for dietary

Table 2. Components of the original and newly formulated fruit-free diets provided to four species of lemur at two zoos. [1] Manufactured by Mazuri Zoo Foods, Witham, Essex, UK; [2] Winalot Shapes, manufactured by Purina, Horley, Sussex, UK; *soaked in cranberry juice.

	Amount provided per animal per day (g)									
	Varecia variegata		*Varecia rubra*		*Lemur catta* (Newquay)		*Lemur catta* (Paignton)		*Eulemur coronatus*	
Ingredient	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free
Trio Munch[1]	60*	-	40	-	40*	-	28	-	30*	-
Leaf Eater Primate[1]	-	50	40	33	-	30	28	33	-	30
Dog biscuits[2]	-	-	40	-	-	-	28	-	-	-
Egg	-	-	27	-	-	-	27	-	-	-
Fruit	100	-	489	-	25	-	266	-	25	-
Vegetables	500	260	406	297	175	200	422	220	175	200

items using Zootrition software. Non-structural carbohydrate was estimated as the non-fibre carbohydrate fraction, calculated as total dry matter minus crude protein, crude fat, ash and neutral detergent fibre.

Behavioural data collection and analysis

Each lemur was observed for 15 (Paignton Zoo) or 30 (Newquay Zoo) sessions of 20 minutes in each of two observation periods, first prior to any change in diets and secondly after the diets had been completely changed. Although more sessions were conducted at Newquay Zoo the total length of observation periods across both zoos was similar (approximately 35 days in each period). Diet changes were implemented gradually, usually taking a week to slowly reduce or increase the amounts of relevant ingredients. No observations were conducted during the diet change period and the second observation period did not begin until at least one week after the diet change was fully implemented. In both periods sessions were spread throughout the day from 0900 to 1800, but avoiding the times immediately after food provision. During each session continuous focal sampling was used to record time spent performing state behaviours (Table 3), and event behaviours were counted. A new occurrence of an event behaviour was only counted if at least three seconds had passed since the previous occurrence.

State behaviours were converted to percentage of total observation time spent in that behaviour and event behaviours were calculated as rate per minute. For statistical analysis aggression and submission were pooled to give an indication of total aggressive incidents (Aggression) and scratch, yawn, lick and stretch were pooled to give a total Self-Directed Behaviour rate (SDB). Thus four behaviours of interest, Aggression, SDB, Auto-grooming and Foraging, were analysed. All data were non-normally distributed so were analysed using General Linear Mixed Models (GLMM) specifying an inverse-Gaussian distribution. Models were created with main effects of diet, species, individual (nested within species) and all possible pairwise interactions with diet. Lemur age and zoo were entered as covariates.

Table 3. Ethogram used to record behaviour of lemurs at two zoos before and after a diet change to remove all fruit from the diet (S = state behaviour, E = event behaviour).

Behaviour	Description
Locomotion (S)	All forms of motion, e.g. walking, climbing, running
Auto-grooming (S)	The act of preening or cleaning one's own body
Allo-grooming (S)	The act of preening or cleaning a conspecifics body
Feeding (S)	Consumption of keeper provided food items or water
Foraging (S)	The browsing and consumption of food items not provided by keepers
Aggression (S)	All forms of agonistic behaviour, e.g. chasing, biting, pouncing
Submission (S)	Response to aggression, e.g. rapid retreat, avoidance, flinching
Rest (S)	Not moving. Recorded either as Alert (eyes open, interest shown towards surrounding noise and movements) or Not alert (eyes closed no response to surrounding noise or movements)
Out of sight (S)	Animal cannot be seen by observer
Scratch (E)	Animal uses limbs to scratch/rub the body
Yawn (E)	Mouth is opened and extended, tongue often also extended
Lick (E)	Tongue is extended beyond snout repeatedly for no grooming purposes and includes licking of animal's surroundings
Stretch (E)	Fully extending body part(s) for no apparent purpose
Vocalisation (E)	Expression of audible sound

Results

Diets

Nutrient analysis of the diets showed that all fruit-free diets contained 80–150% more NDF and 21–30% less non-structural carbohydrate than the original diets (Table 4). Crude protein and ash were also higher in the fruit-free diets by 6–38% and 15–26% respectively (Table 4). The energy provided by the fruit-free diets was considerably less than the original; this was intentional as much of the food was not consumed on the original diets, and actual energy intake was considered to be similar between the two diets.

Behaviour

Both Aggression (Wald's $\chi^2_{[1]} = 89.12$, $p < 0.001$) and SDBs (Wald's $\chi^2_{[1]} = 91.64$, $p < 0.001$) were performed significantly less when the lemurs were fed the fruit-free diet (Table 5, Fig. 1). This effect was similar across all species although there were significant interactions between diet and species (Table 5); for Aggression the effect was not so great for *L. catta* as for the other species, whereas for SDBs it was not so great for *V. rubra* as for the other species (Fig. 1).

The overall effects of diet were clearly evident despite significant differences between species (SDB only) and individuals

Table 4. Nutritional analysis of original and newly formulated fruit-free diets for four species of lemur at two zoos. Dietary content presented as % of dry matter. Non-structural carbohydrate estimated as the non-fibre carbohydrate fraction calculated by deduction. *Metabolisable energy (primate).

	Varecia variegata		*Varecia rubra*		*Lemur catta* (Newquay)		*Lemur catta* (Paignton)		*Eulemur coronatus*	
Nutrient	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free	Original	Fruit-free
Energy* (kJ/day)	2506	1318	3833	1172	1113	808	2883	954	971	925
Crude protein	17.7	20.7	14.8	20.4	19.5	21.4	16.1	21.1	18.9	20.1
Crude fat	3.4	3.8	4.6	3.6	3.9	3.9	4.7	3.8	3.7	3.6
Ash	4.9	6.2	4.9	6.0	5.4	6.4	5.1	6.2	5.2	6.0
NDF	11.9	22.2	11.4	21.6	9.0	22.6	12.2	22.0	10.3	21.7
Non-structural carbohydrate	62.1	47.1	69.2	48.4	62.2	45.7	61.9	46.9	61.9	48.6
Ca	0.6	0.7	0.6	0.7	0.7	0.7	0.6	0.8	0.7	0.7
P	0.6	0.5	0.4	0.5	0.7	0.5	0.4	0.6	0.6	0.5

(both Aggression and SDB, Table 5). Diet did not have a significant effect on Auto-grooming (Wald's $\chi^2_{[1]} = 0.25$, p = 0.62) or Foraging (Wald's $\chi^2_{[1]} = 0.30$, p = 0.58) (Table 5, Fig. 1) and there was no significant interaction between diet and species, although there were significant differences between species and individuals in these behaviours (Table 5). Other general state behaviour was not substantially affected by the diet change (Fig. 2).

Table 5. GLMM results showing the effects of diet (original or fruit-free), species and individual (nested within species) on behaviour of four species of lemurs at two zoos.

Behaviour	Main effects	Wald's χ^2	df	P
Aggression	Diet	89.12	1	<0.001***
	Species	4.56	3	0.27
	Individual (Species)	85.05	13	<0.001***
	Diet x Species	7.84	3	0.007**
	Diet x Individual (Species)	47.52	13	<0.001***
SDB	Diet	91.64	1	<0.001***
	Species	54.49	3	<0.001***
	Individual (Species)	95.38	13	<0.001***
	Diet x Species	32.05	3	<0.001***
	Diet x Individual (Species)	75.72	13	<0.001***
Auto-grooming	Diet	0.25	1	0.62
	Species	20.22	3	<0.001***
	Individual (Species)	24.75	13	0.03*
	Diet x Species	3.35	3	0.34
	Diet x Individual (Species)	5.45	13	0.96
Foraging	Diet	0.30	1	0.58
	Species	46.71	3	<0.001***
	Individual (Species)	41.03	13	<0.001***
	Diet x Species	0.91	3	0.82
	Diet x Individual (Species)	22.28	13	0.05*

Discussion

This study found remarkably consistent effects of fruit-free diets on aggression and SDB rates in both zoos and all five groups of lemur of four species and varying group sizes and social composition, including male/female pairs (*V. variegata* and *V. rubra*), family groups (*L. catta* and *E. coronatus*) and an all-male group (*L. catta*). This suggests that significantly reduced aggression and SDB rates are a consistent result of removing fruit from captive lemur diets. It is even more remarkable that such significant and consistent effects of diet were found given that there were significant differences between species and individuals which could have masked the overall trend across all subjects in the study.

Although rates of aggression and SDBs in all groups were low and not of concern to zoo staff prior to the diet change, a reduction in these behaviours can still be regarded as beneficial. SDBs are commonly used as indicators of social stress and anxiety in primates (e.g. Reamer et al. 2010; Molesti and Majolo 2013) and a high incidence rate can indicate poor welfare (Beisner and Isbell 2009). Aggression is also a normal part of primate social behaviour (McCowan et al. 2008), but can become severe in captivity where individuals may have less opportunity to avoid each other or escape aggressors (Beisner and Isbell 2009). Therefore captive primate managers should aim to keep aggression and SDB rates as low as possible. Excessive grooming is also thought to indicate stress in primates and in extreme cases can lead to hair loss (Beisner and Isbell 2009). Grooming rates in this study were not excessive and were not significantly affected by the diet change. Foraging, which occupies much of the day in free-living primates but is often much less prevalent in captive primates, was also unaffected by the diet change.

Nutrient analysis showed that the main difference between the two diets is an average 25% reduction in non-structural carbohydrate content and a corresponding increase in fibre when fruit was removed. There is little information on the effects of dietary carbohydrate content on non-human primate behaviour, although in humans there are reports of negative behavioural impacts of high sugar levels (e.g. Nicol et al. 2005), including increased aggression, violence and criminal behaviour (Prinz et al. 1980; Benton 2007). However, the effects observed in this study could also be a result of increased fibre concentration, which prolongs the feeling of satiety for longer periods in the day; for example, this has been shown to reduce aggression and stereotypy

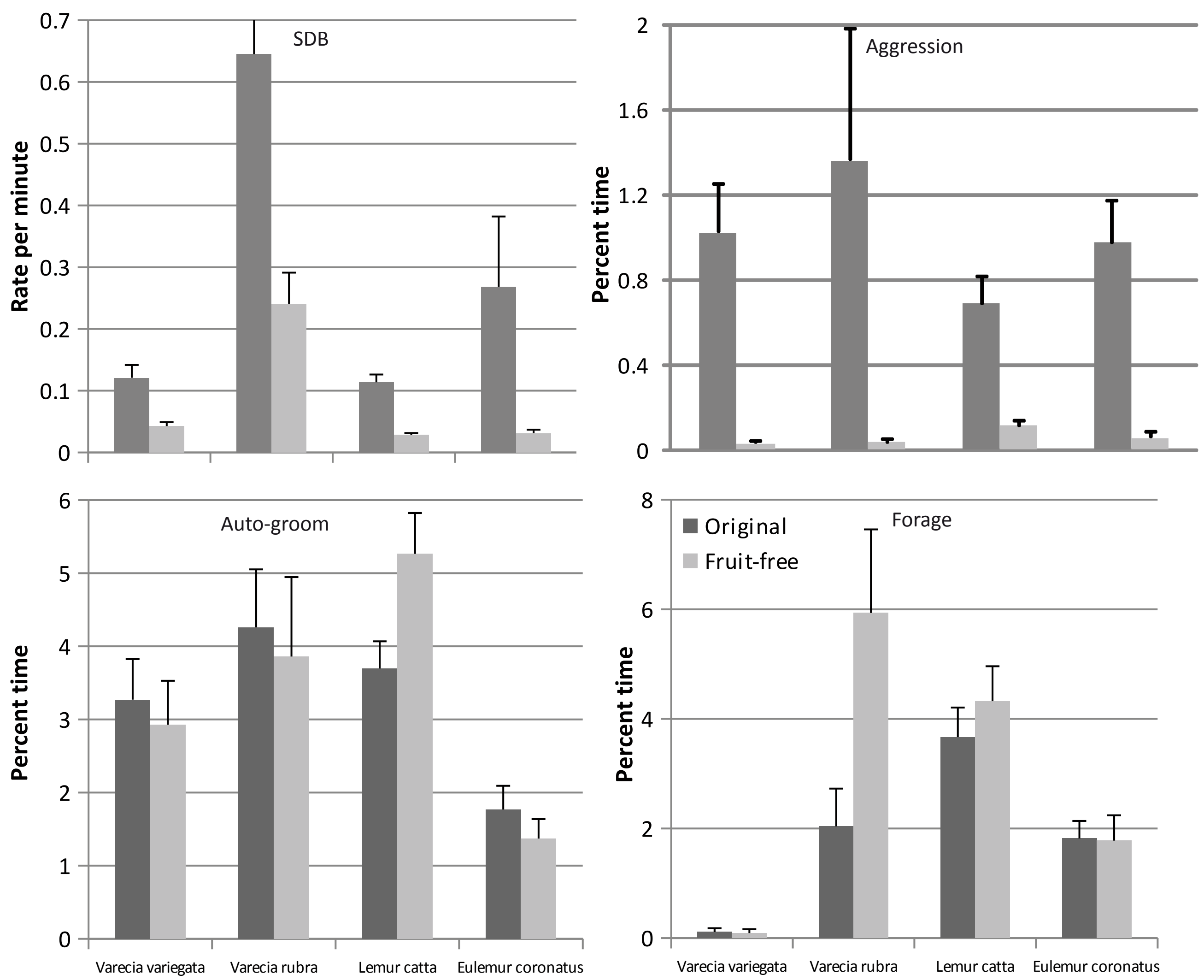

Figure 1. Mean rate (± standard error) of self-directed behaviour (SDB) per minute, and mean (± SE) percentage of time spent performing aggression, auto-grooming and foraging by four species of lemur when fed their original diet (dark bars) and a newly formulated fruit-free diet (light bars).

in pigs (e.g. Danielsen and Verstergaard 2001). Given the large increase in fibre concentration in the fruit-free diets this is a real possibility and could be investigated further by investigating rates of aggression and SDB relative to meal times.

Increased protein levels in the fruit-free diets may also have contributed to the effects on behaviour since many amino acids are precursors of neurotransmitters. In particular, increased dietary intake of tryptophan, a precursor of serotonin, has been shown to reduce levels of aggression, stress and/or other problem behaviour in vervet monkeys (Chamberlain et al. 1987), rhesus macaques (Weld et al. 1998) and several other mammalian species including humans (Bosch et al. 2007). However, although tryptophan is present in most dietary protein, it occurs at lower concentrations than other large neutral amino acids (LNAAs). These other LNAAs inhibit serotonin synthesis at high blood concentrations so an increase in total protein in the diet is more likely to cause the opposite effect of simply increasing tryptophan alone (Bosch et al. 2007). Low levels of n-3 polyunsaturated fatty acids (PUFAs) have also been shown to have negative impacts on behaviour in a range of species. However, it is unlikely that changes in n-3 PUFA concentration were responsible for the effects in this study since n-3 PUFAs are only found in appreciable levels in a very limited range of available dietary items (e.g. linseed oil, oily fish), none of which were included in either diet.

It is also possible that diet nutrient content *per se* was not the cause of the effects observed in this study. There is no doubt that fruit is a strongly preferred food of captive lemurs (Schwitzer and Kaumanns 2000), therefore, in the absence of this highly desirable resource, it could be that there is less motivation for aggressive or dominance behaviour and therefore also less social anxiety overall.

Although not the case in the groups included in this study, aggression in captive primate groups can be very severe and result in serious physical and/or psychological damage (McCowan et al. 2008). Whilst a certain level of aggression is to be expected for the maintenance and development of group social dynamics (McCowan et al. 2008), it can often become more problematic in captivity than in the wild. Excessive aggression in captive breeding groups is of particular concern as it has been found to negatively impact upon female reproductive success (Ha et al. 2011). This could have implications for endangered species reliant upon captive breeding for genetic improvement and increased population sizes. Finding

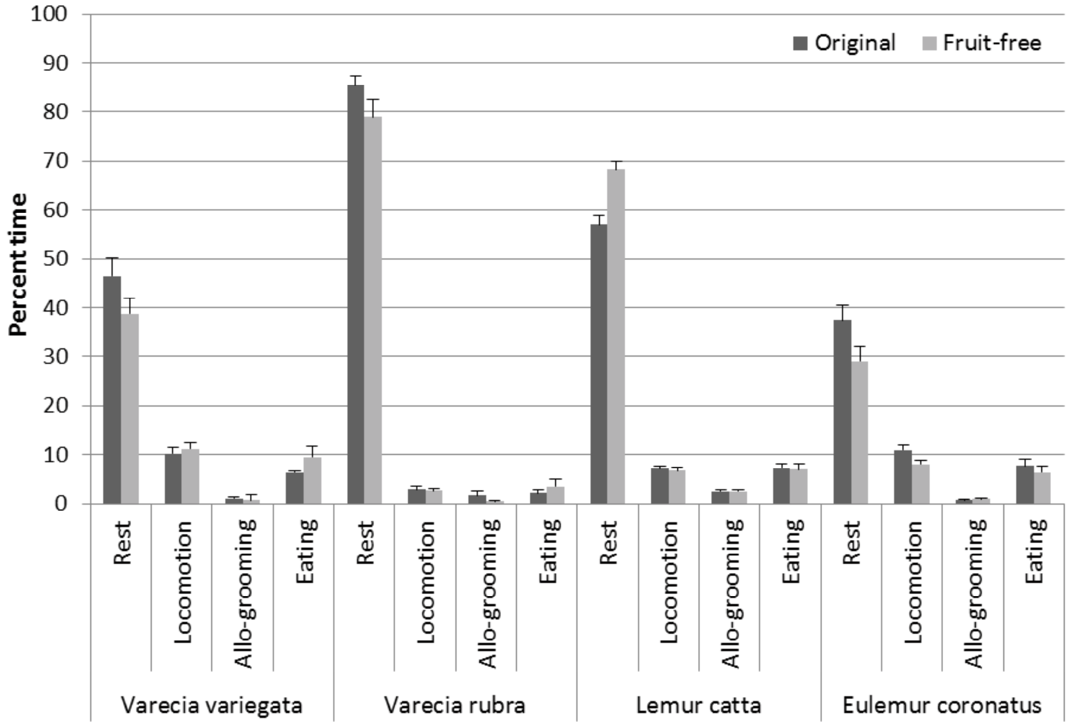

Figure 2. Mean (± standard error) percent time spent performing main state behaviours by four species of lemur at two zoos when fed their original diet and a newly formulated fruit-free diet.

methods to reduce aggression can be difficult but is a priority for captive primate managers (Daneault 2012). To our knowledge diet manipulation has rarely been considered, and much more rarely tested, as a behavioural modifier for zoo-housed primates (see Daneault 2012). These results suggest that simple dietary changes can have significant behavioural effects and diet should be considered, alongside other husbandry measures, when dealing with problem behaviour in captive primates.

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