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A survey of captive hylobatid diets and their association with gastrointestinal distress

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Abstract

Despite their ubiquity in captivity, specific dietary recommendations are few for captive hylobatid apes. In the wild, these small apes consume a diverse array of food materials, with a predominance of fibrous plant matter. In captivity, however, animals are more likely to be fed commercial diets and locally available fruits and vegetables. For optimal health, animal diets must contain appropriate amounts of macromolecules, nutrients and minerals, and dietary imbalances can contribute to poor health and animal welfare. Captive hylobatids, in particular, commonly suffer from gastrointestinal distress (GID), typically manifest as chronic diarrhoea (CD), but little documentation exists of the extent of, causes of, or treatments for this often-chronic condition in small apes. In this study, an anonymous survey of 10 questions pertaining to small ape diet and faecal characteristics was made available globally to institutions housing small apes. A total of 53 different institutions completed the survey, providing dietary and faecal characteristics data for 248 individuals representing eight of the 17 recognised small ape species. Little standardisation of hylobatid diet exists, with some institutions feeding nearly all fruit and/or vegetable matter and others feeding only processed meals. A total of 26 of the 53 responding institutions reported animals with CD, in 51 out of the 248 subjects represented. CD was evenly distributed across the subjects in the sample, having no specific association with subject species, gender or age. Captive populations that included subjects with CD (CD+) and without CD (CD-) received diets containing similar amounts of citrus fruits, plant-based matter and protein. However, CD+ populations received non-citrus fruits at higher average levels than CD- populations, and also received food-based enrichments, on average, more often than CD- groups. These data confirm that (i) captive hylobatid diets vary widely among institutions, (ii) vegetables and fruits comprise the bulk of most captive diets, with substantial protein but little citrus included, (iii) CD is a common aspect of captive small ape health, (iv) the occurrence of CD is not specifically associated with any identified captive small ape subpopulation, and (v) higher amounts of dietary fruits and food-based enrichments are associated with the occurrence of CD in captive small apes. More work is needed to determine if specific food types within these general categories are typical causative agents of CD in captive small apes.

Introduction

Maintaining the physical and mental health of animals housed in captivity is essential for animal welfare and conservation efforts (Association of Zoos and Aquariums 2010), and the zoological community is justly committed to striving for the best housing conditions for captive animals. Despite best efforts, however, zoological housing can generate high levels of physiological stress in captive animals (Prongay et al. 2013; Clayton et al. 2014; Kottwitz and Ortiz 2016; Reppert 2015), whether due to space, social or environmental factors, or other causes. While physiological stresses manifest in a variety of ways, gastrointestinal distress (GID) is a common indicator of compromised health in captive mammals (Bockus 1969; Chen et al. 2018). Mammal GID can stem from many causes (including changes in gut microbiota, poor diet, social stress; Lloyd et al. 1986; Dierenfeld 1997; Nijboer et al. 2006; Clayton et al. 2014; Caravaggi et al. 2018; Chen et al. 2018), and may present as impaired stool formation related to chronic diarrhoea (CD), irritable bowel syndrome (IBS), or colitis (Fenoglio-Preiser et al. 1999; Lankester et al. 2008; Wilk et al. 2008; Aron-Wisnewsky and Clement 2016; Vandeputte et al. 2016; Thompson 2018).

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Table 1. The survey questions used for data collection. In addition to the basic numerical responses, survey respondents provided a variety of open-ended, textual descriptions of their subjects, their diets and their stool characteristics.

Number	Question
1	*How many gibbon(s) are housed at your current institution?*
2	*Please list the age, sex, and species of all the gibbon(s) you are including in this survey.*
	What percentage (from scale of 0%-100%) of the gibbon(s) diet at your institution is made up of:
3	*non-citrus fruits (ex. apples, blueberries, bananas)?*
4	*citrus fruits (ex. oranges, grapefruit, lemons)?*
5	*vegetables (ex. spinach, romaine, kale, celery)?*
6	*high protein items (ex. beans, monkey biscuits, hard-boiled eggs)?*
7	*How often do your institution's gibbon(s) receive food-based enrichment(s)?*
8	*Do any of your institution's gibbon(s) have chronic diarrhea?*
	Using the Bristol Stool Chart, what is the
9	*most common type of stool you see the gibbon(s) produce?*
10	*most common type of abnormal stool you see the gibbon(s) produce?*

Small apes (Hylobatidae; including the gibbons and siamang) are common in captivity, popular for their relatively small size, aerial acrobatics and engaging behaviours. They present a number of housing challenges, including the attempt to match their natural Southeast Asian diet of (primarily) plant matter. Hylobatid diets in the wild generally consist of fruits, leaves, flowers and insects, with ripe fruit making up >50% of the diet in some species (Ripley 1984; Smith 1984; Chivers 2000; Rowe and Jacobs 2016). However, diet is not uniform among these small apes; siamangs *Symphalangus syndactylus* and crested gibbons *Nomascus* spp. are known to consume more foliage than other gibbons (Chivers 1974; Palombit 1997), and the specific dietary components of any particular species vary by geography (Elder 2009; Ni et al. 2014). Ideally, captive diets should, of course, mirror natural diets as much as possible (Chivers and Raemaekers 1986; Dierenfeld 1997; Campbell 2008; Caravaggi et al. 2018). Collectively, small apes generally thrive on captive diets containing local fruits and plant matter, but GID is commonly reported (Keeling and McClure 1972).

While general guidelines for the captive feeding of frugivorous/folivorous primates do exist (Edwards 1997), community-wide guidance for hylobatid diets is lacking. At present, there is no 'universal' set of diet protocols for small ape species available through the Association of Zoos and Aquariums (AZA), the European Association of Zoos and Aquaria (EAZA), the United States Department of Agriculture (USDA), Gibbon Species Survival Plan (SSP), or the Ape Taxonomic Advisory Group (Ape TAG). This lack of standardised hylobatid dietary protocols has led to a wide diversity of small ape dietary practices (examples in Campbell 2008; Miller 2010), with hylobatid dietary and enrichment practices varying considerably from institution to institution.

If captive hylobatid diets are being structured more through habit and convenience than through the collective wisdom of the zoological community, the risk of dietary imbalances increases, with the concomitant potential to contribute to animal stress, perhaps especially including gastrointestinal stress. Sub-optimal diets are known to cause intestinal hypermobility, leading to the production of loose, watery stool (Keeling and McClure 1972). While acute diarrhoea is not uncommon in captive nonhuman primates (Anderson et al. 1993; Prongay et al. 2013; Clayton et al. 2014; Reppert 2015), chronic CD appears to impact hylobatids frequently, and often without resolution. At most institutions, resource limitations are likely to preclude exhaustive evaluation of CD, and efforts to combat it appear to involve trial-and-error dietary modifications, primarily (personal observation).

This landscape of diverse hylobatid dietary practices and the commonality of captive gibbon CD supports the belief that dietary GID contributes to CD in captive small apes. The goal of this study was to evaluate this association through examination of specific dietary components and practices, relative to the distribution of CD in captive subjects. Specifically, the study sought to (i) survey an array of institutions for the captive gibbon dietary practices employed, including the diversity, amounts and presentation of foods included, to (ii) examine how CD is distributed within and among institutions housing gibbons, and to (iii) evaluate associations between the diets reported and the occurrence of CD. In doing so, the intention is to stimulate discussion of dietary standards for captive hylobatids, with a concomitant goal of reducing dietary stresses and the risk of CD in captive subjects.

Methods

Survey and data collection

A custom, online "Gibbon/Siamang Diet Survey" was created using SurveyMonkey (http://www.surveymonkey.com). The survey (Table 1) evaluated (i) the size and make-up of the small ape population held at an institution, (ii) the dietary practices and foodstuffs used in their care, and (iii) the occurrence of CD and the general stool characteristics (including Bristol stool score; Lewis and Heaton 1997) which typified the subjects. Respondents were asked to estimate dietary make-up by food class (non-citrus and citrus fruits, vegetables), to identify the percentage of high-protein foods in use, and also to identify the frequency and type of dietary enrichments used. The amount of dietary protein provided was a key point of interest, as protein is potentially limiting in the natural diet of wild primates (Ganzhorn et al. 2017). Likewise,

Table 2. A tally of specific food items regularly included as part of respondents hylobatid diets, have been nominally categorised as fruits, vegetables, protein sources and enrichment: n=1 institution unless specified by number in brackets. Enrichment food items were also included as part of the regular diet, by other insitutions; all enrichments were offered less regularly than other dietary components (see Results).

Fruits	Vegetables	Protein sources	Enrichment
“non-citrus fruits” *	“greens” (11)*	“biscuits” (15)*	"cereal"
apple	lettuce (2)	Mazuri Primate Browse	"dry forage"
banana	spinach (2)	Mazuri Browser Breeder	"insects"
honeydew		Mazuri Leafeater (8)	"nuts" (2)
	“root vegetables” (7)*	Mazuri Old World (2)	"seeds/grains" (4)
“citrus fruits” (5)*	carrot (4)	Mazuri Primate Growth & Reprod.	apple juice
orange (3)	swede	Mazuri Maintenance	applesauce
pineapple	sweet potato (3)		cranberries (dried)
tomato	yam	egg (13)*	egg
			grape
	“cruciferous vegetables” (5)*	“legumes/beans” (8)*	Hi-maize resistant starch
	broccoli (2)	green beans (2)	ice cubes
	cabbage	kidney beans	Jello
	cauliflower	peanuts (2)	melon
	kale (2)		oatmeal
		“canned diet” (2)	popcorn
	(other)*	Zupreem	raisins
	aubergine		timothy
	celery	poultry meat (cooked) (2)*	yogurt
	cucumber (2)	chicken (2)	
	green pepper	turkey	
	leeks		
	sweet corn	(other)*	
	zucchini (2)	“chow cake”	
		rice (white, cooked)	
		seeds	
		Trio Munch	

*General food groups
‘‘non-specific identifiers used by respondents in describing their subject diets

protein is normally carefully controlled in captive animal diets in order to prevent over-feeding as well as to limit the effects on stool solidity (Nijboer et al. 2006). Respondents also were asked to delimit their uses of citrus versus non-citrus fruits, as hylobatids in the wild make very limited use of citrus fruits, which are more readily available and less seasonal in captivity.

Respondents also were asked to rate typical and extreme subject stool scores, as a way to estimate the frequency and severity of CD in their hylobatid subjects. Subjects’ responses were not bounded, allowing respondents to provide additional textual description of their numerical responses if they chose.

The survey was made available electronically in 2017 to gibbon/siamang studbook keepers and through online “primate keeper” social media groups. Responses were anonymised to the extent that respondents wished them to be (e.g., no identifying information was requested or required).

Data summarisation and analysis

All data were tabulated in Microsoft Excel (Microsoft Corp.; Redmond, WA). Data analyses were performed in both Microsoft Excel and SPSS (Version 25; IBM Corp; Armonk, NY). Dietary characteristics and food-based enrichments were summarised at the institution level, as respondents most commonly reported a single diet for all subjects at their location. The occurrence and severity of CD first was assessed across the entire data set at the institutional level as well, as only a subset of respondents reported having any subjects with CD at their facility. The occurrence of CD was also characterised at the individual level within a subset of the data, as multiple respondents specifically described the breakdown between individuals who were, or were not, afflicted with CD at their institution.

Statistical analyses focused upon (i) assessments of the distributions of dietary components (identity of foods within

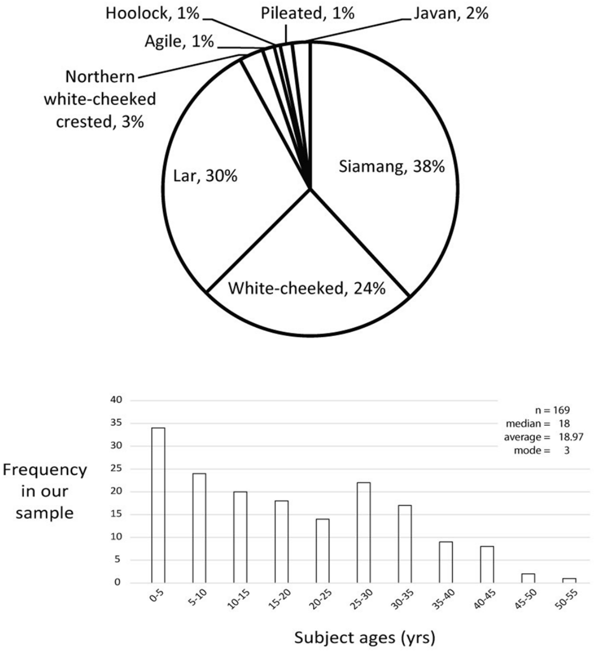

Figure 1. Of the 248 small apes described in survey responses, 152 small apes were identified by species. In the sample, the most common subjects were siamang, lar, and white-cheeked gibbons, which together comprised 92% of the identified subjects (top panel). An additional 96 subjects (39% of the total number of subjects represented in our sample) were not identified by species. Subjects ranged from 0.5 to 52 years of age (bottom panel), with all age groups <45 years (9 of 11 age groups) represented by ≥8 subjects in the sample.

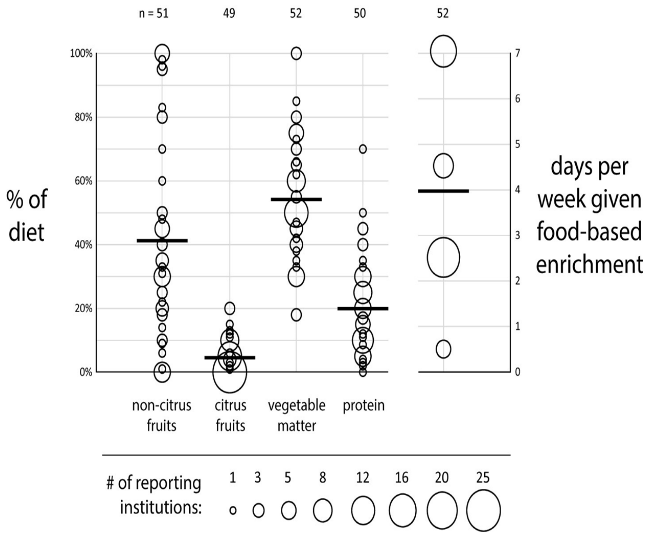

Figure 2. Survey respondent estimates of hylobatid dietary make-up and enrichment frequency at their institutions. Plotted here are dietary estimates (as percentages of total diet) for non-citrus fruits, citrus fruits, vegetables, and high-protein items in subject diets, relative to the axis at figure left. Symbol size indicates the number of data points at any one location on the graph, relative to the symbol size scale at figure bottom. Data means for each column are indicated by horizontal bars. Also plotted is the frequency of dietary enrichment at institutions, relative to the scale at figure right. The total sample size (# of reporting institutions) represented in each data column is depicted at figure top. Because "high-protein" content is not a food group *per se*, dietary component percentages total >100%. The survey reveals that captive hylobatid diets are highly variable among institutions, and are, on average, structured with a predominance of vegetable matter and fruits, with protein supplementation.

each category, ranges and average of dietary percentages, frequencies of dietary enrichment), (ii) dietary differences among subject populations characterised as having CD versus not (via t-test; t statistic reported), and (iii) associations between subject characteristics and the presence of CD (via Chi-square tests; X^2 values reported). Where appropriate, samples were tested for equality of variances (F tests) and normality (Shapiro-Wilk tests) before analysis; comparisons between samples of unequal variances are identified below. All statistical tests were one-tailed.

Results

Respondents and described subjects

A total of 53 separate institutions responded to the survey with information about their small apes, their diets and stool characteristics, and the occurrence of CD. Respondent identity and location were not requested as part of the survey; any information that suggested either respondent identity or location was removed before data summarisation in order to preserve respondent anonymity. Due to partial responses from some respondents, sample sizes in individual analyses vary and are specified below.

Captive hylobatid population characteristics

Survey responses described a total of 248 small apes, with an average of 4.8 small apes per institution (range: 1–42). A total of 152 small apes (n=248; 61%) were identified by species, while 96 (39%) were unidentified. Identified subjects were distributed very unevenly (Chi square test: X^2=205.47, df=7, P<0.001) across eight small ape species. Siamang *S. syndactylus* (n=58), Lar *Hylobates lar* (n=45), and white-cheeked gibbons *N. leucogenys* (n=37) were the most common in the sample, while agile *Hylobates agilis* (n=2), pileated *Hylobates pileatus* (n=2) and hoolock *Hoolock* spp. (n=1) gibbons were the least common (Figure 1, upper panel). Subjects in the sample averaged 19 years of age (range: 0.5–52 years old; Figure 1, lower panel). Subjects were relatively evenly distributed in age, rather than normally distributed (Shapiro-Wilk test for normality of subject ages: S-W statistic=0.948, df=169, P<0.001).

Captive gibbon diet characteristics

Gibbons in the sample received a very broad mixture of food materials. Vegetable matter (51% of diets, on average) and non-citrus fruits (40% of diets, on average) comprised the bulk of the foods reported, with relatively much smaller amounts of citrus fruits (Figure 2). Still, within these general categories, there was

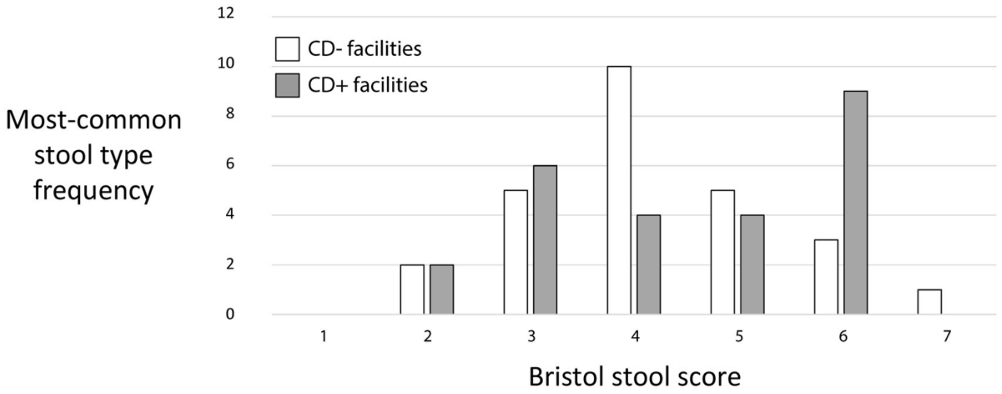

Figure 3. Small ape subjects at institutions that did not report the presence of CD (CD- facilities) tended to have stools that commonly scored at moderate levels (3–5) on the Bristol stool scale (open bars), with relatively fewer stools of high Bristol score. In contrast, individuals at institutions at which CD was reported (CD+ facilities; shaded bars) most commonly had stools of Bristol score 6, with relatively fewer stools of moderate Bristol score.

much variation among institutions, with some reporting 100% of the diet as non-citrus fruit, while other institutions offered a diet that was 0% fruit and 100% vegetable in make-up. Five of the 53 responding institutions (10%) fed 100% fruit-free diets, while 20 institutions (38%) fed diets that lacked citrus fruits of any kind. Most institutions used relatively little citrus fruit (averaging only 5% of the diet), and most diets contained a moderate amount (20%, on average) of high-protein items (including high-protein plant material, commercial primate "biscuits" and egg).

Respondent open-ended comments on dietary make-up (Supplementary Table 1) suggest relatively fixed diets at some locations and relatively more relaxed diets at others. The comments also revealed the striking diversity of dietary items used. Only a small number of institutions voluntarily identified the specific food items they used in their diets (Table 2), with oranges being the most-commonly identified fruit given (but typically in small amounts). Vegetables comprised the largest average portion of the diets reported (Figure 2), with leafy green vegetables being identified most frequently (Table 2), followed by root and cruciferous vegetables. A total of 17 specific vegetables were mentioned as being used in subject diets (Table 2). Fruits and vegetables were reported by multiple facilities to be on a rotational basis (either by design or due to local availability).

Commercial primate "biscuits", of a variety of types, were the most commonly identified high-protein dietary items, closely followed by eggs (typically identified as hard-boiled; Table 2). Care staff also used high-protein plant matter (including legumes) in subject diets, and less commonly reported uses of poultry meat or canned diets (each at two locations only). A total of 19 different foods were identified as enrichment items (Table 2), with dietary enrichment frequencies ranging from daily to weekly (Figure 2). A dietary enrichment frequency of 2–3 times per week was most common (23 out of 52 facilities). Multiple respondents reported that enrichment foods were either taken from or replaced typical diet items, reflecting a general theme of caloric conservation and maintenance of subject body masses.

Institutional occurrence of chronic diarrhoea

CD, interpreted here as a sign of intestinal distress, was frequently reported. A total of 26 institutions reported that one or more of their small apes had CD, while 27 respondents reported not having small ape CD at their institution.

Stool characteristics

That CD was reported at half of respondent institutions allowed a comparison of populations at facilities at which CD was reported (CD+ populations) with subjects at facilities at which CD did not occur (CD- populations). These comparisons are conservative, as not all subjects at CD+ institutions themselves were CD+. Still, CD+ and CD- populations differed markedly in their general stool characteristics. CD- subjects had lower typical Bristol stool scores for their most common stool type than did CD+ populations (modal Bristol stool scores of 4 vs 6), reflecting more-firm and better-formed stool in CD- populations. Overall, common stool scores differed markedly between CD- and CD+ populations (X^2=13.42, df=4, P<0.02; Figure 3), as CD+ populations produced more stools of higher Bristol stool score. The distribution of stool scores at CD+ institutions was bimodal (Figure 3), reflecting the fact that not all individuals at a CD+ facility were themselves afflicted with CD: individuals of normal health produced firmer stools of scores 2–4, while individuals with CD commonly produced stools of Bristol scores 5–6.

Dietary contributions to the presence of chronic diarrhoea

In order to evaluate the ability of dietary make-up to contribute to CD, the study assessed whether diets at CD+ and CD- institutions differed. Institutions that reported the presence of CD gave their animals more non-citrus fruits (47.3 ±7.5% of total diet) than did institutions that did not report the presence of CD (35.3 ±5.6%); a difference that was marginally distinct statistically (two-sample t-test: t=1.34, df=49, P=0.092; Figure 4). In contrast, neither the percent of citrus fruit (4% vs 5%) nor the percent of plant matter (54% vs 55%) in small ape diets differed between CD+ and CD-institutions. CD+ institutions provided more variable amounts of dietary protein than did those without CD (two-sample test for equivalence of variances: $F_{25,23}$=0.47, P<0.05), although the mean amounts of dietary protein did not differ between CD- and CD+ populations (18.5 ±2.2% vs 21.6 ±3.5%; t=0.76, NS; Figure 4). However, institutions reporting small ape CD gave food-based enrichment items a greater number of days per week (on average) than did institutions without small ape CD (4.6 ±0.5 vs 3.3 ±0.4 days per week), a difference that was highly statistically significant (t=2.14, df=50, P=0.015; Figure 4).

Non-dietary predictors of chronic diarrhoea

Apart from institutional-level analyses of the occurrence of CD, this study also sought to examine individual subject characteristics for associations with CD. Some survey respondents provided enough individual subject detail that it was possible to compare CD+ and CD- subject characteristics across identified individuals. These comparisons did not yield any specific subject associations with CD. The overall sample included eight identified small ape species, and the occurrence of CD was not associated with any particular species (X^2=10.19, df=8, NS). Siamang (38%), lar (30%), and white-cheeked gibbons (24%) made up the majority of the sample pool, and they constituted similar percentages of the CD+ sub-sample (31%, 29% and 27%, respectively). Likewise, the occurrence of CD was equally distributed among male and female subjects (X^2=0.06, df=1, NS), as females comprised 46% of the sample and 47% of observed CD+ subjects.

The global sample pool included individuals from 0.5 to 52 years of age. However, there was no apparent age structure to the occurrence of CD, as the age distributions of subjects with CD (mean: 21 years) and without CD (mean: 18 years) were equivalent (t=1.67, df=125, NS). Thus, the occurrence of CD in the captive small apes represented here appears to have an extrinsic (e.g., environmental) basis, rather than stemming from an intrinsic characteristic of one or more subpopulations of captive small apes.

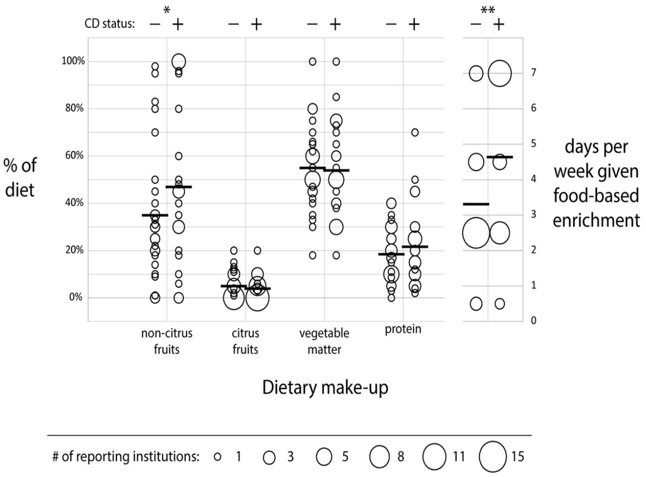

Figure 4. In order to assess the ability of diet to contribute to CD, the study evaluated captive hylobatid dietary make-up independently for those institutions reporting the absence (-), or presence (+), of chronic diarrhoea (CD) in their small apes. Non-citrus fruits, citrus fruits, plant-based matter and protein were evaluated in terms of their overall contribution to diet (in percent; figure left axis), while food-based enrichment was assessed in terms of the average number of offerings per week (figure right axis). The CD status of each data column is indicated at figure top; significant differences between CD- and CD+ institutions for individual dietary elements are denoted by asterisks (* for P<0.1, ** for P<0.02). Bubble size indicates the number of institutions represented at each point in the graph, relative to the scale at figure bottom. Due to incomplete survey responses, sample size in figure data columns ranges from 24–27 reporting institutions within each column. Solid bars indicate population means within each data column. The amount of citrus fruit, plant-based matter and overall protein in captive small ape diets did not differ between institutions reporting the presence or absence of CD. However, institutions at which CD was reported gave higher amounts of non-citrus fruits, and offered food-based enrichments more frequently, than did institutions whose small apes do not experience CD.

Discussion

The data and analyses presented here provide several clear findings relative to the diets used in support of captive hylobatids as well as the frequency of chronic diarrhoea (CD) and how diets may contribute to its occurrence in captive small apes, including:

I. On average, captive hylobatids are fed diets that are roughly half vegetable in make-up, with slightly lesser amounts of fruit (mostly non-citrus), with substantial protein supplementation and frequent/diverse enrichment. Individual institutions, however, vary widely in their relative uses of these categories of foods.

II. The specific fruits and vegetables used in captive hylobatid diets varies widely among institutions, and is likely to be driven by local availability. Many specific food items were reported as being in use at only a small number of institutions. That captive hylobatids generally thrive on such an array of foods is likely to reflect some combination of their ability to tolerate a natural diversity of foodstuffs, combined with individual subject abilities to choose from among the food items presented.

III. CD is common in captive small apes, with half of all respondents reporting gibbon CD at their institution. At any one institution, typically only a subset of subjects experienced CD, with others being unaffected.

IV. Captive small ape CD is unrelated to subject species, age or sex, suggesting that the occurrence of CD is related to environmental variables, rather than intrinsic factors.

V. While the relatively low level of detail in subject responses precludes fine-grained analyses, the occurrence of CD in captive small apes is significantly related to diet, with greater amounts of non-citrus fruits and greater frequencies of food-based enrichments being significant predictors of CD in captive hylobatids.

Survey respondents successfully used a diverse array of fruits and vegetables in their hylobatid diets, and the relative percentages of dietary fruits (from 0–100%) and vegetables (from 18–100%) varied widely among institutions. The survey did not evaluate the relative success with which these different food items or groups were consumed, but the data do suggest that captive hylobatids can thrive on a wide variety of natural plant materials. Hylobatids naturally eat an array of plant products in the wild, including fruits, shoots, buds and leaves (Ripley 1984; Palombit 1997; Rowe and Jacobs 2016), and their generalist dietary tendencies do not appear to be constrained in captivity. A small number of institutions used diets which were entirely fruit or entirely vegetable (Figure 2), a practice which seems likely to risk insufficient provisioning of dietary protein. Captive subjects have little access to natural sources of protein, and protein supplementation was very common in the present survey (with commercial diets and eggs as the most-frequently used items). In the wild, hylobatids are known to include insects, seeds/grains and flowers in their diets, but these were represented very infrequently here (voluntarily reported by 1, 5 and 0 institutions, respectively). As expected, citrus fruits made up a relatively small proportion of diets overall (mean of 5%; Figure 2), but comprised 10–20% of the diets at a quarter of respondent institutions (12 of 49 reporting institutions).

The survey also confirms that CD is common among captive hylobatids and that it typically strikes only a subset of animals at any one location. This latter finding suggests that an infectious basis for CD is less likely than some other causative agent. While the study found no specific subject characteristics associated with the occurrence of CD (such as species, gender or age), it did find two significant dietary predictors of CD. Higher levels of non-citrus fruits and higher rates of dietary enrichment were both associated with the occurrence of CD (Figure 4). How these could lead to CD in some subjects is unknown, although alterations of the gut microbiome are an obvious candidate. It is tempting to assume that a diverse diet is generally associated with a diverse intestinal bacterial flora (Heiman and Greenway 2016), but this effect is not uniform in the human and animal studies to date (e.g., Bolnick et al. 2014). It is also true that temporary introductions of atypical food items (e.g., enrichment of diet with novel foods) may cause significant and unexpected alterations in gut bacterial diversity (Xu and Knight 2014; Singh et al. 2017), which themselves can trigger significant changes in gut regulation and function (Guarner and Malagelada 2003; Barbara et al. 2005; Bercik et al. 2012). There is much about the relationships between animal and human diets, intestinal microflora and physiological health that is yet to be discovered, and appreciation for the complexity of their interactions is growing (Conlon and Bird 2015). Investigations of these relationships in captive hylobatids is underway.

Dietary recommendations

While dietary preferences and needs are expected to differ among hylobatid species and among individuals of differing age class or reproductive condition, these data lend themselves to some general suggestions regarding diets for captive hylobatids, in concert with the general recommendations available for frugivorous/folivorous primates (Edwards 1997). Assuming that the diets reported here have been shaped by local experience and found to be generally effective at their institution, these data suggest that captive hylobatid diets should be comprised predominantly of vegetable matter (primarily leafy greens), with non-citrus fruits making up the next largest dietary component. Proteins can be included through the use of legumes, although plant-based protein sources alone appear to be generally insufficient in their ability to provide enough protein, given the widespread use of non-plant-based protein supplements. Eggs are a widely accepted choice of supplemental protein, and one that is easily used as enrichment. Commercial diets, specifically manufactured to include protein and fibre, are advantageous in that they are available with an array of nutrient content, allowing specific use to support growing or lactating individuals, or to support weight loss/management. Citrus fruits are best used only at very low levels (no more than 5% of the overall diet), and enrichment of atypical dietary items should be relatively infrequent (<2x per week), with concomitant reductions in other daily rations. It is also suggested that significant attention be paid to the selection of food choices by individual subjects, as non-optimal food selection among dietary items may contribute to individually compromised subject health.

Limitations of current study design and suggestions for further research

While this survey has provided clear evidence of the diversity of captive hylobatid diets and the associations between diet and the incidence of CD in captive small apes, additional details of subject dietary components is required to determine if particular types of fruits or food-based enrichments are causal for the occurrence of CD. For example, the survey reveals that high-fruit diets alone are not sufficient to cause small ape CD, as some CD- subjects received diets that were nearly all fruit. This suggests that the choice of particular fruit types, or their preparation/handling, is crucial. In addition, respondents identified (by percentages) the primary components of their subjects' given diets but did not evaluate subject free choice among dietary elements. Individual subjects are likely to have consumed parts of their diets at very different rates/amounts (authors' observations), which could explain why only a subset of individuals at any one institution could be reported to have CD.

It is intended that this survey and these results will stimulate the development of a more standardised dietary plans for captive small ape species, including the identification of diets that can be used to prevent or manage the occurrence of CD. Because captive primate CD may arise from a number of hypothesised causes, the development and use of standardised dietary protocols will be necessary to eliminate diet as one of the contributing factors to this unhealthy and troublesome condition often seen in small apes.

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References

Anderson K.F., Kiehlbauch J.A., Anderson D.C., McClure H.M., Wachsmuth I.K. (1993) Arcobacter (Campylobacter) butzleri-associated diarrheal illness in a nonhuman primate population. *Infection and Immunity* 61(5): 2220–2223.

Association of Zoos and Aquariums (2010) "Ape Taxon Advisory Group", from http://www.apetag.org.

Aron-Wisnewsky J., Clement K. (2016) The gut microbiome, diet, and links to cardiometabolic and chronic disorders. *Nature Reviews Nephrology* 12(3): 169–181.

Barbara G., Stanghellini V., Brandi G., Cremon C., Di Nardo G., De Giorgio R., Corinaldesi R. (2005) Interactions between commensal bacteria and gut sensorimotor function in health and disease. A*merican Journal of Gastroenterology* 100(11): 2560–2568.

Bercik P., Collins S.M., Verdu E.F. (2012) Microbes and the gut-brain axis. *Neurogastroenterology & Motility* 24(5): 405–413.

Bockus H.L. (1969) Reflections on functional-structural interrelationships in digestive tract disorders. *Canadian Medical Association Journal* 100(10): 476–480.

Bolnick D.I., Snowberg L.K., Hirsch P.E., Lauber C.L., Knight R., Caporaso J.G., Svanbäck R. (2014) Individuals' diet diversity influences gut microbial diversity in two freshwater fish (threespine stickleback and Eurasian perch). *Ecology Letters* 17(8): 979–987.

Campbell C. (2008) Husbandry manual for the Javan gibbon (*Hylobates moloch*) (revised). Perth, Western Australia, Perth Zoo.

Caravaggi A., Plowman A., Wright D.J., Bishop C. (2018) The composition of ruffed lemur (*Varecia* spp.) diets in six UK zoological collections, with reference to the problems of obesity and iron storage disease. *Journal of Zoo & Aquarium Research* 6(2): 41–49.

Chen X., Li Q.Y., Li G.D., Xu F.J., Han L., Jiang Y., Huang X.S., Jiang C.L. (2018) The distal gut bacterial community of some primates and carnivora. *Current Microbiology* 75(2): 213–222.

Chivers D.J. (1974) The siamang in Malaya. A field study of a primate in tropical rain forest. *Contributions in Primatology* 4: 1–335.

Chivers D.J. (2000) The swinging singing apes: fighting for food and family in far-east forests. *The apes: Challenges for the 21st century,* Brookfield, IL, Chicago Zoological Society.

Chivers D. J., Raemaekers J.J. (1986) Natural and synthetic diets of Malayan gibbons. *Primate ecology and conservation.* J.G. Else & P.C. Lee, Cambridge, UK, Cambridge University Press: 39–56.

Clayton J.B., Danzeisen J.L., Trent A.M., Murphy T., Johnson T.J. (2014) Longitudinal characterization of *Escherichia coli* in healthy captive non-human primates. *Frontiers in Veterinary Science* 1(24).

Conlon M.A., Bird A.R. (2015) The impact of diet and lifestyle on gut microbiota and human health. *Nutrients* 7(1): 17–44.

Dierenfeld E.S. (1997) Captive wild animal nutrition: a historical perspective. *Proceedings of the Nutrition Society* 56(3): 989–999.

Edwards M.S. (1997) Leaf-eating primates: nutrition and dietary husbandry. *Nutrition Advisory Group Handbook*, American Zoological Association.

Elder A.A. (2009) Hylobatid diets revisited: the importance of body mass, fruit availability, and interspecific competition. *The gibbons. Developments in primatology: Progress and prospects.* D.L. Whittaker, S. New York, NY, Springer: 133–159.

Fenoglio-Preiser C.M., Noffsinger A.E., Stemmermann G.N., Lantz P.E., Isaacson P.G. (1999) *Gastrointestinal pathology: An atlas and text.* Philadelphia, PA, Lippincott-Raven.

Ganzhorn J.U., Arrigo-Nelson S.J., Carrai V., Chalise M.K., Donati G., Droescher I., Eppley T.M., Irwin M.T., Koch F., Koenig A., Kowalewski M.M., Mowry C.B., Patel E.R., Pichon C., Ralison J., Reisdorff C., Simmen B., Stalenberg E., Starrs D., Terboven J., Wright P.C., Foley W.J. (2017) The importance of protein in leaf selection of folivorous primates. *American Journal of Primatology* 79(4): e22550.

Guarner F., Malagelada J.R. (2003) Gut flora in health and disease. *The Lancet* 361(9356): 512–519.

Heiman M.L., Greenway F.L. (2016) A healthy gastrointestinal microbiome is dependent on dietary diversity. *Molecular Metabolism* 5(5): 317–320.

Keeling M.E., McClure H.M. (1972) *Clinical management, diseases, and pathology of the gibbon and siamang*. Gibbon and Siamang. D.M. Rumbaugh. Basel, Karger. 1: 207–249.

Kottwitz J.J., Ortiz M. (2015) Bovine viral diarrhea virus in zoos: A perspective from the veterinary team. *Frontiers in Microbiology* 2016: 1–5.

Lankester F., Matz-Rensing K., Kiyang J., Jensen S.A., Weiss S., Leendertz F.H. (2008) Fatal ulcerative colitis in a western lowland gorilla (*Gorilla gorilla gorilla*). *Journal of Medical Primatology* 37(6): 297–302.

Lloyd J.M., Peet R.L., Gaynor W.T., Bamford V. (1986) Colitis in a gibbon associated with *Shigella flexneri* type 3. *Journal of Zoo Animal Medicine* 17(3): 83–86.

Miller S. (2010) *Husbandry manual for white-handed gibbon Hylobates lar (Mammalia - Hylobatidae)*. Richmond, Western Sydney Institute of TAFE.

Ni Q.Y., Huang B., Liang Z.L., Wang W.W., Jiang X.L. (2014) Dietary variability in the western black crested gibbon (*Nomascus concolor*) inhabiting an isolated and disturbed forest fragment in Southern Yunnan, China. *American Journal of Primatology* 76(3): 217–229.

Nijboer J., Clauss M., Everts H., Beynen A.C. (2006) *Effect of dietary fibre on the faeces score in colobine monkeys at Dutch zoos*. Zoo Animal Nutrition. A. Fidgett, M. Clauss, K. Eulenberger, J.-M. Hatt, I. Hume, G.P.J. Jules, J. Nijboer. Filander Verlag, Fürth. Volume III: 145–155.

Nijboer J., Clauss M., Olsthoorn M., Noordermeer W., Huisman T.R., Verheyen C., van der Kuilen J., Jurgen W.S., Beynen A.C. (2006) Effect of diet on the feces quality in Javan langur (*Trachypithecus auratus auratus*). *Journal of Zoo and Wildlife Medicine* 37(3): 366–372.

Palombit R.A. (1997) Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia Primatologica* 68(6): 321–337.

Prongay K., Park B., Murphy S.J. (2013) Risk factor analysis may provide clues to diarrhea prevention in outdoor-housed rhesus macaques (*Macaca mulatta*). *American Journal of Primatology* 75(8): 872–882.

Reppert A. (2015) *Medical Nutrition Therapy for Human Gastrointestinal Disorders and Application to Captive Non-Human Primates*. Eleventh conference on zoo and wildlife nutrition, Portland, OR, AZA Nutrition Advisory Group.

Ripley S. (1984) *Environmental grain, niche diversification and feeding behaviour in primates*. Food acquisition and processing in primates. D.J. Chivers, B.A. Wood, A. Bilsborough, Boston, MA, Springer: 33–72.

Rowe N., Jacobs R. (2016) Gibbons and siamangs (Hylobatidae). All the world's primates. N.M. Rowe, M. Charlestown, RI, Pogonias Press: 632–661.

Singh R.K., Chang H.-W., Yan D., Lee K.M., Ucmak D., Wong K., Abrouk M., Farahnik B., Nakamura M., Zhu T.H., Bhutani T., Liao W. (2017) Influence of diet on the gut microbiome and implications for human health. *Journal of Translational Medicine* 15(1): 73–73.

Smith R.J. (1984) *Comparative functional morphology of maximum mandibular opening (gape) in primates*. Food acquisition and processing in primates. D.J. Chivers, B.A. Wood, A. Bilsborough, Boston, MA, Springer: 231–255.

Thompson J. (2018) Improving outcomes for patients with irritable bowel syndrome in primary care, with specific focus on diet. *Primary Health Care* 28(4) 43–48.

Vandeputte D., Falony G., Vieira-Silva S., Tito R.Y., Joossens M., Raes J. (2016) Stool consistency is strongly associated with gut microbiota richness and composition, enterotypes and bacterial growth rates. *Gut* 65(1): 57–62.

Wilk J.L., Maginnis G.M., Coleman K., Lewis A., Ogden B. (2008) Evaluation of the use of coconut to treat chronic diarrhea in rhesus macaques (*Macaca mulatta*). *Journal of Medical Primatology* 37(6): 271–276.

Xu, Z., Knight R. (2014) Dietary effects on human gut microbiome diversity. *British Journal of Nutrition* 113(1): 1–5.