

A survey of the attitudes of stakeholders in the zoo industry towards the husbandry requirements of captive Great Apes

AC Fernie^{†‡}, A Tribe^{†‡}, PJ Murray[†], A Lisle[§] and CJC Phillips^{*‡}

[†] School of Animal Studies, University of Queensland, Queensland, Australia

[‡] Centre for Animal Welfare and Ethics, School of Veterinary Sciences, The University of Queensland, Gatton Campus, Gatton 4343, Queensland, Australia

[§] School of Land, Crop and Food Sciences, The University of Queensland, Australia

* Contact for correspondence and requests for reprints: c.phillips@uq.edu.au

Abstract

The attitudes of experts towards the husbandry of captive Great Apes was sought in order to gain a greater understanding of the potential importance of different features of the captive environment that may be critical in maintaining a high standard of welfare. Following initial consultation with the convener of the Primate Taxon Advisory Group of the Australasian Regional Association of Zoological Parks and Aquaria, 17 husbandry attributes, such as social structure of the group, enclosure size and staff qualifications, each with two to four levels (ie husbandry scenarios) of possible provision in an enclosure were identified and described. An online survey using Adaptive Conjoint Analysis was distributed internationally to relevant stakeholders: zoo management staff, keepers and education staff, research colony personnel, veterinarians, animal welfare organisation representatives and scientists. A total of 359 respondents completed the survey, and the average importance values for the attributes, and rank order of importance for each of their levels were calculated. Great Ape social structure, enclosure appearance, group size, avoidance provision and enclosure furnishings were considered the most important attributes of captive Great Ape husbandry, whereas feeding interval, staff qualifications, the inclusion of plants within the enclosure, enrichment rotation, and the amount of time an animal spent in an outdoor enclosure were considered of low importance. The order in which these issues were ranked was influenced by the Great Ape species, with physical attributes of the enclosure being rated as more important for orangutans (*Pongo pygmaeus*) and group social attributes more important for the other species. Stakeholder group had little influence on the ranking of issues. It is concluded that experts provided a consensus view on the importance of husbandry attributes of the different Great Ape species that can be used to evaluate their welfare.

Keywords: animal welfare, Great Ape, husbandry, stakeholder, survey, zoo

Introduction

For a captive zoo animal to experience a high level of welfare a variety of environmental and social needs must be met. Currently, husbandry standards for captive Great Apes are influenced primarily by minimum levels of resources advised by regional zoological associations, such as the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) and the Association of Zoos and Aquariums (AZA) in their published guidelines and Animal Care Manuals. These are based generally on the opinion of stakeholders from affiliated institutions housing the species that were consulted during their preparation, rather than a systematic review of the importance of a variety of husbandry resources attributed by experts with different types of involvement with captive Great Apes. To assess the influence of different husbandry scenarios on Great Ape behaviour and welfare, a husbandry assessment is needed that can be

used globally, with the objective of highlighting the aspects most important for captive Great Apes. Fraser (1995) asserts that an evaluation of the 'most important' factors affecting the ability of an individual to cope with its environment is essential in the assessment of its welfare; this has been done, for instance, in the Austrian livestock industry with the development of the 'Animal Needs Index' (Bartussek 1999). The first step towards making this type of assessment a reality is to determine what the most important husbandry factors are. This is achieved commonly by interviewing relevant stakeholders and reviewing the literature (Zubkovic & Kaleta 2005), before comparing the findings with quantitative physiological values. We began this process for captive Great Apes by asking the opinions of relevant experts.

Some studies have attempted to identify and list important physical or social aspects of the environment for captive Great Apes. Woolverton *et al* (1989) suggested that the key factors

affecting the quality of the habitat for primates include its social environment, available area and variety of furnishings. A USDA report (USDA-APHIS-AC 1999) identified five general elements critical to the psychological well-being of non-human primates. These included social groupings, social needs of infants, structure and substrate, foraging opportunities and the provision of objects to manipulate (USDA-APHIS-AC 1999). It is particularly important to provide Great Apes with conspecifics of appropriate age and gender in order to meet their social, reproductive or psychological needs (Price & Stoinski 2007), although flexibility in group size and structure is warranted in solitary species such as orangutans (*Pongo pygmaeus*) (Zucker *et al* 1978).

Enclosure furnishings have been demonstrated by several researchers (Carlsted *et al* 1993; Hebert & Bard 2000; Caws *et al* 2008) to be more important for primates than the size of the enclosure (Line *et al* 1991). Avoidance provision, especially adequate routes or visual barriers to escape from conspecifics and visitors, is also considered important (Wood 1998; Blaney & Wells 2004), since it can alleviate problems created by artificial group sizes and/or structures. Similarly, the importance of the provision of full spectrum, natural light has been realised in recent years (O'Neill 1989; Poole 1995; Wolfensohn & Honess 2005; Honess & Marin 2006).

Other issues, such as diet, staff quality and the availability of plants in the enclosure, have sometimes been advocated as important components of husbandry. Plants are often discussed in terms of increasing the naturalness of a zoo exhibit for the visitors' benefit (Price *et al* 1994). Their importance to primates has been rarely investigated (Chamove 2005), although one study with Great Apes has found that the addition of plants to an exhibit reduced the severity of a stereotyped behaviour, regurgitation and reingestion (*t/r*) (Struck *et al* 2007). Plants could also be used to extend feeding time, hide from visitors or conspecifics, provide shelter, tactile stimulation and an opportunity to make tools (Worstell 2003). Control, in which an animal's behaviour influences events, has recently been recognised as of potential welfare importance (Mineka & Kelly 1989; Sambrook & Buchanan-Smith 1997), particularly in the highly cognitive captive Great Apes (Bloomsmith *et al* 2001; Bassett & Buchanan-Smith 2007). Primates find it especially rewarding to have control over food delivery (Line *et al* 1991) and auditory stimuli (Hanson *et al* 1976). If control is not possible, human distribution of food should be spontaneous and unpredictable to avoid stereotypies when expecting a meal (Morgan & Tromborg 2007). In the wild, Great Apes spend 40–60% of their day feeding (Goodall 1986; Mitani 1989; Boesch & Boesch-Achermann 2000). Consequently, zoos often aim to promote and lengthen foraging behaviour (Maki & Bloomsmith 1989) by providing whole rather than chopped foods (Smith *et al* 1989; Elsner 2002), scattering food in the enclosure substrate (Anderson & Chamove 1984; Elsner 2002), and by packaging food items in containers (Elsner 2002).

Previously, no studies have assigned a weighting or rank for the husbandry attributes of Great Ape enclosures, and so it is impossible currently to make any comparisons between

enclosures in terms of the standard of husbandry they may provide. The extant scientific evidence is inadequate to enable a comprehensive index of husbandry needs to be constructed for evaluating captive environments, and so the opinion of a significant number of experts with different involvement in Great Ape husbandry was sought. The aim of this study was therefore to determine the perceived relative importance of the various husbandry options for captive Great Apes to the stakeholders involved indirectly or directly in their care.

Materials and methods

Stakeholder selection

A review panel to consider the identification of the relevant stakeholder groups that were either directly or indirectly involved with the husbandry of captive Great Apes was established, consisting of the UQ team and the convener of the primate Taxon Advisory Group (TAG) of ARAZPA. Previous studies of captive wildlife husbandry were reviewed and seven groups were selected for inclusion in the study: zoo management staff, zoo keepers, zoo education staff, Great Ape research colony technicians and managers, veterinarians, animal welfare organisation representatives and scientists known to be working with Great Apes. Suitable members of these groups were then identified by searching member lists and the websites of relevant organisations. The appropriate representatives of welfare organisations were identified by using the Google search engine to find 'animal welfare organisation' and by searching the websites of relevant organisations. Other stakeholder groups were invited to participate, using Primate Info Net (<http://pin.primate.wisc.edu/idp/>), the International Primatological Society (IPS), the Australasian Primate Society (APS), the South East Asian Zoos Association (SEAZA) membership lists and zoo websites. A total of 1,782 potential respondents were invited to participate in the survey. The largest group, with over 900 people, was the 'scientist' stakeholder group, deliberately chosen to be large because of the potentially heterogeneous nature of responses from this group. For other groups we anticipated a more homogenous set of responses, that is, most respondents within a group would rank the husbandry attributes in a similar fashion because of the similarity of their training and job specifications. Although heterogeneity of responses was hard to estimate, we considered that each group should contain 330 respondents for a sampling error of 5.5% at 95% confidence interval (de Vaus 1995).

Creation of the attributes and assigned levels

Seventeen attributes of Great Ape husbandry were selected by reviewing the scientific literature regarding captive animal husbandry and in discussion with the TAG Convener of ARAZPA. These were social structure, enclosure appearance, enclosure furnishings, group size, avoidance provision, duration of feeding, competition with conspecifics, enclosure size, lighting, feeding interval, temperature, diet, the apes' control over their environment, staff qualifications, enrichment rotation, enclosure plants,

Table 1 Attributes and levels included in the survey and utility values of each level. Attributes are listed in a random order within the four categories, diet, social environment, physical environment and management. Levels are listed from best scenario to worst (as ranked by respondents).

Attributes	Levels	Orangutan	Gorilla	Chimpanzee	Bonobo
<i>Diet</i>					
Diet	Diet which is adequate nutritionally and diverse	45.6	42.3	45.5	50.4
	Diet which is adequate nutritionally but not diverse	-45.6	-42.3	-45.5	-50.4
Feeding interval	Routine includes activity feeds at random intervals through the day	45.7	43.3	34.0	36.6
	Being fed four times per day at set times	-5.8	-6.1	-0.83	3.3
	Being fed twice per day at set times	-39.8	-37.2	-33.2	-39.9
Duration of feeding	Lengthening feeding time by having to forage/manipulate the food before consumption	52.7	49.3	49.6	49.0
	Having to forage/manipulate food somewhat before consumption but able to consume quickly	8.9	8.2	8.4	9.7
	No foraging/manipulation of food required, food able to be consumed very quickly	-61.6	-57.5	-57.9	-58.7
<i>Social environment</i>					
Competition with conspecifics	Not having to compete with other individuals for minimal amount of food required	27.7	34.6	34.2	23.7
	Some competition for an individual to get minimal amount of food required	20.4	21.6	21.2	23.4
	Intense and constant competition for food	-48.1	-56.2	-55.4	-47.0
Social structure	Well balanced species-specific housing	60.6	73.4	71.9	70.7
	Unbalanced social group	-1.2	-0.2	1.4	-0.2
	Solitary housing	-59.5	-73.2	-73.3	-70.5
Avoidance provision	Being able to escape from other dominant conspecifics or visitors at all times	37.1	40.5	39.4	34.9
	Having sufficient space to avoid dominant conspecifics or visitors most of the time	30.7	33.6	34.8	34.0
	Unable to escape from conspecifics or visitors and not sufficient room to avoid them	-67.8	-74.2	-74.2	-68.8
Group size	Group size matches that found in the wild	45.5	54.2	52.0	54.8
	Group size is bigger or smaller than that found in the wild	13.0	19.5	18.5	21.1
	Ape is kept solitary	-58.5	-73.7	-70.5	-75.9
Apes' control over their environment	Able to control several aspects of their environment	42.4	37.3	39.9	37.5
	Able to control some aspects of their environment	8.8	8.0	9.1	8.2
	Apes have no control over their environment	-51.2	-45.3	-49.0	-45.7
Enclosure size	Enclosure size greater than defined standard	49.4	50.2	50.2	53.5
	Enclosure size equal to standards	1.6	2.8	3.1	1.0
	Enclosure size less than defined standard	-51.0	-53.0	-53.2	-54.0
Lighting	Natural and artificial lighting provided (access to indoor and outdoor enclosure)	38.0	38.2	39.2	45.6
	Only natural lighting provided (outdoor enclosure)	14.5	16.1	13.0	11.2
	Only artificial lighting provided (indoor enclosure)	-52.5	-54.3	-52.2	-56.8
Temperature	Ape always has access to a temperature in comfort zone (18–30°C)	49.0	47.8	47.7	39.9
	Temperature is occasionally higher or lower by 5°C then comfort zone	3.4	7.7	9.1	15.1
	Temperature regularly is lower than comfort zone by 5°C or more	-33.8	-34.1	-34.0	-35.4
	Temperature regularly exceeds comfort zone by 5°C or more	-18.6	-21.4	-22.8	-19.6

Table 1 (cont)

Attributes	Levels	Orangutan	Gorilla	Chimpanzee	Bonobo
<i>Physical environment</i>					
Enclosure furnishings	A highly enriched environment with many furnishings (logs, platforms, ropes)	63.3	59.4	60.0	57.0
	Partially enriched environment with some furnishings	-0.2	0.2	0.6	1.9
	Minimal environmental enrichment or enclosure furnishings	-63.1	-59.7	-60.6	-58.9
Enrichment rotation	Changing environmental enrichment before the animals are habituated	44.0	37.3	37.2	36.0
	Not changing environmental enrichment until after the enrichment is no longer enriching	-44.0	-37.3	-37.2	-36.0
Enclosure appearance	An enclosure which closely reflects the natural environment	54.3	55.5	53.3	53.9
	An artificial enclosure	-14.7	-15.8	-14.9	-15.5
	A sterile environment	-64.0	-64.5	-64.7	-64.4
	A stimulating enclosure that does not reflect the natural environment	24.4	24.8	26.3	25.9
<i>Management</i>					
Outdoor enclosure availability	Ape can choose to spend up to 24 h per day in outdoor enclosure	32.3	31.1	31.6	29.8
	Ape can choose to spend up to 14 h per day in outdoor enclosure	3.8	4.5	4.4	4.0
	Ape is kept in outdoor enclosure for 8 h per day	-36.0	-35.6	-36.0	-33.2
Enclosure plants	An array of edible plants/foilage is grown in or provided in the enclosure	39.7	36.2	33.9	37.5
	Some edible plants/foilage are grown in or provided to the enclosure	5.1	4.7	3.7	4.9
	No edible plants/foilage grown in or provided to the enclosure	-44.8	-41.0	-37.5	-42.4
Staff qualifications	Team includes keepers with extensive experience/education with the species	38.0	35.8	36.9	41.7
	60–75% of keepers have education or experience with the species	6.8	6.6	6.6	8.9
	20% of keepers have education or experience with the species	-44.8	-42.4	-43.5	-50.6

outdoor enclosure availability. The different possible levels of each attribute were selected as, first, the ideal situation for a species of captive Great Ape, and then between one and three other scenarios that would provide less desirable husbandry options for all or some of the Great Ape species that are exhibited (Table 1).

Although every effort was made to include attributes that were deemed important in terms of the husbandry of Great Apes, the list could not be exhaustive. We also recognised that particular stakeholders may have a view on the inclusion of certain enclosure or husbandry elements, and that only a very wide consultation, and a critical and rigorous analysis of the attributes proposed could ensure that the most relevant variables were covered for each of the Great Ape species. However, in order to maintain the questionnaire response time at below 30 min and thereby maximise the response rate, the number of attributes was kept to below twenty, as advised by the software manufacturers (Sawtooth Software®, Evanston, IL, USA).

The online survey

An online survey of the respondents' preferences for captive ape husbandry methods was created using non-leading questions for each of the 17 attributes. The attributes were grouped into the following four categories: social environment; physical environment; diet; and management (Table 1). Respondents could answer the survey for one of any of the Great Ape species and the questions asked were not species-specific. The survey incorporated a consent form, a brief explanation, instructions on completing the survey, the survey itself and an opportunity to comment on the survey.

Respondents were instructed initially to answer the survey for the Great Ape species with which they were most familiar. They were asked to identify that species, and to provide background demographic and other information: their gender, primary involvement with the species, the amount of practical and educational experience they had had with their chosen Great Ape species, the country in

which they had gained that experience and the highest level of education they had achieved.

Respondents were then asked to select the attributes that they felt were most or least important for their species' welfare, and then to rank the levels of each of the 17 attributes, from most to least desirable. In the next stage of the survey, the respondent was asked to decide how important, in terms of welfare, the difference between two randomly selected levels of an attribute was if all other aspects of the Great Apes' husbandry were ideal. Respondents were presented with a series of individually customised (derived from previous answers by the computer programme), paired comparison trade-off questions (in the form of scenarios) and asked to choose which of the two provided the better welfare. Using the 13 most highly rated indicators for each respondent, determined during the initial ranking of attributes, the Adaptive Conjoint Analysis (ACA) software combined pairs of indicators by examining all the possible ways that the levels could be combined and selecting those with similar utilities and for which, based on previous responses, it was expected that the two indicators would be of similar merit. The software then used the information obtained from each paired comparison to update the estimates of each respondent's utilities and to select the next pair of options for trade-off. The advantages of using this questioning technique for surveys relating to animal welfare have been discussed previously (Phillips *et al* 2009). In brief, the ACA technique allows attributes to be considered jointly rather than in isolation, thus enabling trade-offs to be made between the different resources indicated by the levels within attributes. The technique is based on the assumption that complex decisions are not based on a single factor or criterion but on several factors considered jointly (Johnson 1974).

Finally, the survey asked the respondent to select which statement best represented their position on the captive management of Great Apes, with the four categories ranging from 'I disapprove of the keeping of Great Apes in captivity' to 'I am comfortable with the current methods used to keep Great Apes in captivity', with a box for any further comments on the survey.

A pilot survey was conducted with ten people who had practical and/or academic experience with captive primates. In the subsequent survey, which lasted four months, potential respondents were sent an email containing information about the online survey and a letter of support from the primate convener of the TAG of ARAZPA. They were invited to complete it with a unique username provided in the email. A reminder was sent six weeks later to individuals who had not completed the survey. Only completed surveys were included in the analysis. The survey was approved by the University of Queensland Human Ethics Committee (approval number 2005000355) and adhered to the legal requirements of Australia. All respondents were forwarded a summary of the major findings.

Statistical analysis

The overall weight attached to each level was deconstructed into an importance value, that indicated the importance attached to the attribute containing the level, and a utility value, which indicated the value attached to the level within the attribute.

Utility values

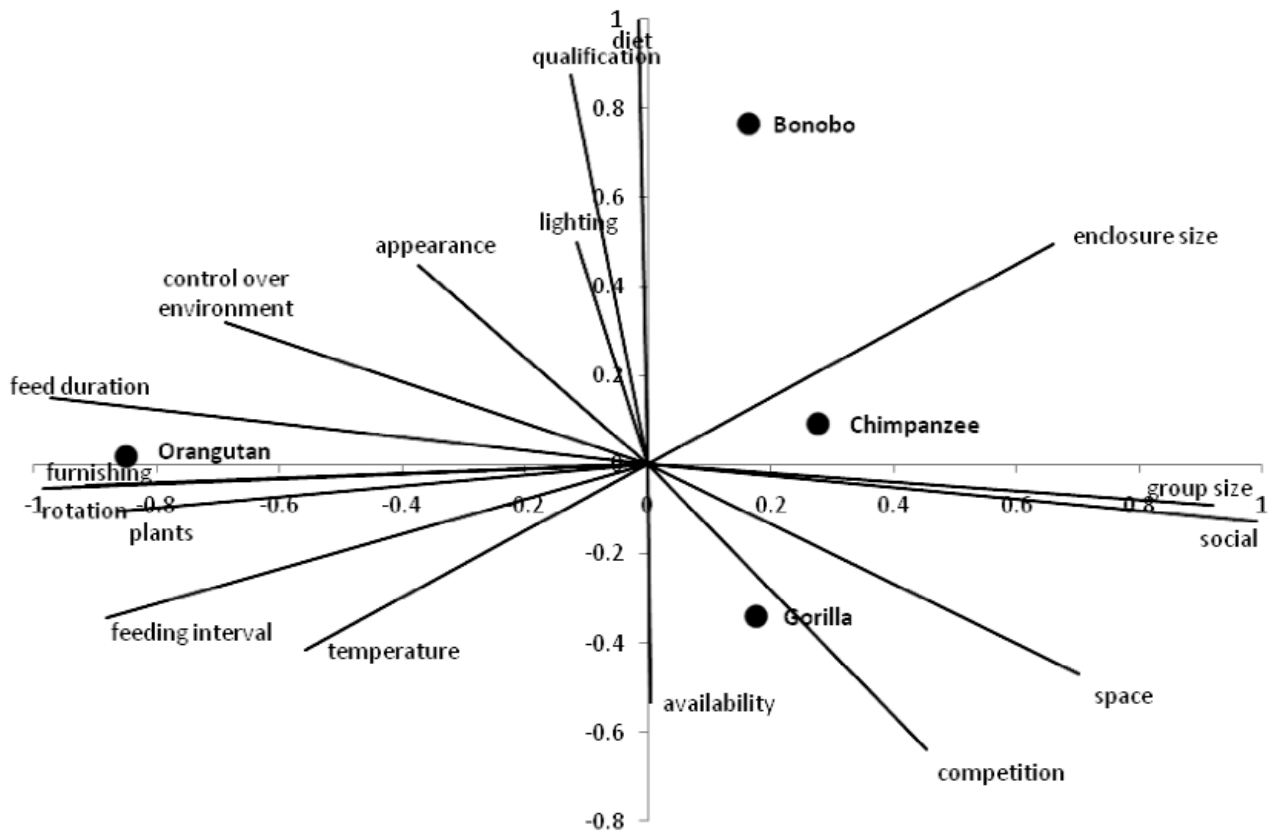
Utility values were determined for each level of the different attributes, after importing respondents' preferences for each level into an ACA software analysis programme (Sawtooth Software, North Orem, Utah, USA). This employed a hierarchical Bayes algorithm to analyse the data. First, the data were normalised across respondents by zero-centring the utility values within each attribute so that the sum of the utility values within each attribute was equal to zero. Levels of an attribute which a respondent rated highly are indicated by a positive utility value, and those with a low rating, a negative value.

Importance values

The relative importance of each attribute was determined and indicated in an importance value. These were a measure of how much difference each attribute makes in the total score for each respondent. Importance values are ratio data, so an attribute with an importance value of 10% is twice as important as an attribute with a value of 5%. The importance values for each respondent were extracted from the Sawtooth Software for further analysis. Two General Linear Models were run in SAS to calculate the least square means, standard errors and pair-wise differences in importance values for the following terms, species and stakeholder group. Prior analyses had evaluated the significance of level of education and experience, but there were many missing values and the variables were dropped from further analysis. Residuals were examined for each attribute and were normally distributed by the Anderson-Darling test at $P > 0.05$. We considered the risk of Type 1 statistical errors because of the significant number of attributes that were tested separately. The degree of correlation between variables was inspected and found to be low, adding validity to the analysis of the attributed independently. We considered the inclusion of a multiple comparison adjustment to probability values by the Bonferroni or Omnibus Permutation test, but after inspecting this and similar datasets for other ACA analyses we concluded that it was too stringent and would potentially lead to many Type 2 statistical errors (Perneger 1998). Instead, we reduced the critical P -value to indicate a significant response from the usual 0.05 to 0.01. In addition, no attempt was made to make inferences or do pair-wise comparisons when $0.05 > P < 0.10$.

A perceptual map was created using the statistical package SAS to display visually the preference of respondents in terms of the attributes most important for each species of Great Ape (Figure 1). These provided a graphical description of relationships among the observations (or rows) and relationships among the variables (or columns) in the data set (Armitage & Colton 1998).

Figure 1



Perceptual map of means for each Great Ape species and attribute loadings. The x- and y-axes represent the two ideal vectors that best characterised how the attributes were differentiated for the four Great Ape species by the respondents. Abbreviations for attributes names have been used as follows: appearance = Enclosure appearance; availability = Outside enclosure availability; competition = Competition with conspecifics; plants = Enclosure plants; rotation = Enrichment rotation; qualification = Staff qualification; social = Social structure; and space = Avoidance provision. The position of the four species is presented in relation to the two axes.

Table 2 The number of stakeholder responses for each Great Ape species.

Stakeholder	Number sent	Number responded	% response rate	% of total respondents	Orangutan	Gorilla	Chimpanzee	Bonobo
Animal welfare organisation representative	134	10	7	3	4	1	5	0
Great Ape research colony technician/manager	109	13	12	4	1	1	11	0
Keeper	159	46	29	13	11	19	14	2
Scientist	902	190	21	53	31	39	109	11
Veterinarian	153	37	24	10	10	14	13	0
Zoo education staff	155	15	9	4	4	5	5	1
Zoo management staff	142	48	34	13	17	13	13	5
Total	1,782	359	-	-	78	92	170	19
Percentage of total sent	100	20	-	100	21	26	48	5

Table 3 Respondents' characteristics (n = 359).

Personal characteristic	Number of respondents (%)
Female	206 (57)
<i>Highest education achieved</i>	
High school education	6 (2)
Technical Further Education	18 (5)
Bachelor's degree	88 (25)
Masters	91 (25)
Doctoral degree	132 (37)
Veterinarian	25 (7)
<i>Experience</i>	
No experience with chosen Great Ape	190 (28)
1–6 months experience with chosen Great Ape	31 (11)
7–12 months experience with chosen Great Ape	28 (8)
13–48 months experience with chosen Great Ape	61 (17)
Over 48 months experience with chosen Great Ape	120 (33)
<i>Education</i>	
No education with chosen Great Ape	91 (25)
1–6 months education with chosen Great Ape	52 (14)
7–12 months education with chosen Great Ape	34 (9)
13–48 months education with chosen Great Ape	73 (20)
Over 48 months education with chosen Great Ape	190 (28)
<i>Region(s) where experience had been gained with Great Apes</i>	
Africa	124 (35)
Asia	63 (18)
Australia	37 (10)
Europe	88 (25)
South America	21 (6)
North America	212 (59)
<i>Statement selected regarding keeping Great Apes in captivity</i>	
I disapprove of the keeping of Great Apes in captivity	39 (11)
I approve of the keeping of Great Apes in captivity providing welfare is good	228 (80)
I approve of the keeping of Great Apes in captivity providing they are involved in an endangered species breeding programme	83 (23)
I am comfortable with the current methods used to keep Great Apes in captivity	9 (3)

Results

Response rates and respondents' characteristics

A total of 359 completed surveys were returned online, with another 204 surveys completed partially but excluded from the analyses as the ACA software was unable to use incomplete responses. The overall response rate (%) of the people sent a link to the survey who had active email addresses was thus 359/1,782 or 20.1%, with the best response rate coming from zoo management staff and keepers (Table 2), and the

lowest response rate coming from zoo education staff and representatives of animal welfare organisations. The majority of the respondents identified themselves as 'scientists' (Table 2), and some of these were thought originally to belong to other stakeholder groups but selected 'scientist' when asked to describe their primary involvement with the species. We believe that the term 'scientist' is sufficiently distinct from the nomenclature for other expert groups in this study to be able to trust individual's classification of their role. Details of the respondents' characteristics are

Table 4 Least square mean (± SEM) importance values for the attributes by Great Ape species (df = 3, 355), listed in order of declining mean importance value.

Attribute	Chimpanzee	Gorilla	Bonobo	Orangutan	Weighted mean	F-value	P-value
Social structure	8.56 (± 0.13) ^a 1	8.62 (± 0.18) ^a 1	8.30 (± 0.39) ^a 1	6.97 (0.19) ^b 3	8.22	18.0	< 0.0001
Enclosure appearance	7.47 (± 0.12) 2	7.37 (± 0.17) 3	7.39 (± 0.37) 3	7.48 (0.18) 2	7.42	0.10	0.96
Enclosure furnishings	7.09 (± 0.08) ^a 5	7.01 (± 0.11) ^a 5	6.82 (± 0.24) ^a 4	7.49 (0.12) ^b 1	7.13	4.33	< 0.01
Group size	7.21 (± 0.16) ^a 3	7.52 (± 0.21) ^a 2	7.69 (± 0.47) ^a 2	6.17 (0.23) ^b 6	7.08	7.25	< 0.0001
Avoidance provision	7.19 (± 0.12) 4	7.14 (± 0.16) 4	6.56 (± 0.35) 5	6.83 (0.17) 4	7.04	1.74	0.16
Duration of feeding	6.33 (± 0.11) 6	6.28 (± 0.15) 6	6.33 (± 0.33) 7	6.65 (0.16) 5	6.40	1.08	0.36
Competition*	6.18 (± 0.15) 7	6.15 (± 0.20) 7	5.31 (± 0.44) 11	5.90 (0.22) 8	6.05	1.43	0.23
Enclosure size	6.08 (± 0.11) 8	6.08 (0.14) 8	6.35 (± 0.32) 6	5.95 (0.16) 7	6.05	0.45	0.72
Lighting	5.65 (± 0.11) 9	5.74 (± 0.15) 9	6.24 (± 0.33) 8	5.74 (0.16) 10	5.71	0.93	0.42
Feeding interval	5.10 (± 0.14) ^a 13	5.52 (± 0.19) ^{ab} 10	5.27 (± 0.41) ^{ab} 12	5.88 (0.20) ^b 9	5.37	3.65	< 0.01
Temperature	5.32 (± 0.11) 11	5.27 (± 0.15) 11	4.87 (± 0.32) 14	5.45 (0.16) 12	5.31	0.91	0.43
Diet	5.36 (± 0.10) ^a 10	4.97 (± 0.13) ^b 12	5.93 (± 0.29) ^a 9	5.30 (0.14) ^{ab} 13	5.29	3.60	< 0.01
Control over environment	5.22 (± 0.12) ^{ab} 12	4.86 (± 0.16) ^a 13	4.89 (± 0.35) ^{ab} 13	5.50 (0.17) ^b 11	5.18	2.77	0.04
Staff qualifications	4.71 (± 0.13) 14	4.60 (± 0.18) 14	5.43 (± 0.40) 10	4.77 (0.20) 16	4.77	1.23	0.30
Enrichment rotation	4.38 (± 0.11) ^a 15	4.39 (± 0.15) ^a 16	4.24 (± 0.33) ^a 16	5.06 (0.16) ^b 14	4.55	4.69	< 0.01
Enclosure plants	4.19 (± 0.11) ^{ab} 16	4.54 (± 0.15) ^a 15	4.70 (± 0.34) ^{ab} 15	4.90 (0.17) ^b 15	4.48	4.62	< 0.01
Enclosure availability	3.96 (± 0.09) 17	3.92 (± 0.13) 17	3.67 (± 0.28) 17	3.94 (0.14) 17	3.96	0.34	0.79

LSM importance values within rows followed by the same superscript are not significantly different ($P > 0.05$). Number in italics indicates order of importance placed on that attribute for each species. * With conspecifics.

Table 5 Least square mean (± SEM) importance values for the attributes by stakeholder group (df = 6, 352).

Attribute	Zoo management staff	Keeper	Scientist	Animal welfare organisation representative	Great Ape research colony personnel	Veterinarian	Zoo education staff	F-value	P-value
Social structure	7.59 (± 0.26) ^b 1	7.71 (± 0.27) ^b 1	8.49 (± 0.13) ^a 1	8.21 (± 0.57) ^{ab} 1	8.55 (± 0.50) ^{ab} 1	8.34 (± 0.30) ^{ab} 1	7.62 (± 0.47) ^{ab} 2	2.70	0.01
Enclosure appearance	7.57 (± 0.23) 2	7.11 (± 0.23) 3	7.47 (± 0.12) 2	7.47 (± 0.50) 3	7.69 (± 0.44) 3	7.31 (± 0.26) 3	7.87 (± 0.41) 1	0.67	0.68
Enclosure furnishings	7.25 (± 0.15) 3	7.41 (± 0.15) 2	7.09 (± 0.08) 4	7.38 (± 0.33) 2	7.35 (± 0.29) 4	6.85 (± 0.17) 5	7.00 (± 0.27) 5	1.39	0.22
Group size	6.68 (± 0.30) 5	6.75 (± 0.31) 6	7.29 (± 0.15) 3	6.26 (± 0.67) 7	6.95 (± 0.58) 5	7.18 (± 0.35) 4	7.29 (± 0.54) 4	1.10	0.36
Space allowance	7.10 (± 0.22) 4	6.81 (± 0.23) 5	6.93 (± 0.11) 5	7.14 (± 0.49) 4	7.71 (± 0.43) 2	7.69 (± 0.25) 2	7.30 (± 0.40) 3	1.90	0.08
Duration of feeding	6.57 (± 0.21) 6	6.89 (± 0.21) 4	6.29 (± 0.10) 6	6.41 (± 0.45) 6	6.38 (± 0.40) 6	6.33 (± 0.23) 7	5.66 (± 0.37) 9	1.87	0.09
Enclosure size	5.73 (± 0.20) 10	5.72 (± 0.20) 10	6.19 (± 0.10) 7	5.91 (± 0.43) 9	6.15 (± 0.38) 8	6.07 (± 0.23) 8	6.57 (± 0.35) 6		
Competition	6.40 (± 0.28) 7	6.13 (± 0.28) 7	5.94 (± 0.14) 8	5.45 (± 0.60) 11	6.26 (± 0.53) 7	6.45 (± 0.31) 6	5.65 (± 0.49) 10	0.95	0.46
Lighting	5.84 (± 0.21) 9	5.88 (± 0.21) 9	5.58 (± 0.11) 9	6.44 (± 0.46) 5	5.40 (± 0.40) 10	5.84 (± 0.24) 9	6.17 (± 0.37) 7	1.22	0.29
Feeding interval	5.86 (± 0.26) ^{ab} 8	6.09 (± 0.26) ^a 8	5.12 (± 0.13) ^b 13	5.98 (± 0.57) ^{ab} 8	5.53 (± 0.50) ^{ab} 9	5.14 (± 0.29) ^b 12	5.20 (± 0.46) ^{ab} 12	2.80	0.01
Temperature	5.16 (± 0.20) 13	5.25 (± 0.21) 13	5.21 (± 0.10) 10	5.67 (± 0.44) ^a 10	5.22 (± 0.39) 14	5.82 (± 0.23) 10	5.77 (± 0.36) 8	1.48	0.18
Diet	5.28 (± 0.19) 12	5.48 (± 0.19) 11	5.19 (± 0.09) 12	4.90 (± 0.41) 13	5.38 (± 0.36) 11	5.44 (± 0.21) 11	5.57 (± 0.34) 11	0.71	0.64
Control over environment	5.44 (± 0.22) 11	5.39 (± 0.23) 12	5.20 (± 0.11) 11	4.83 (± 0.48) 14	5.38 (± 0.42) 12	4.47 (± 0.25) 14	5.13 (± 0.39) 13	1.84	0.09
Staff qualifications	4.34 (± 0.25) 16	4.56 (± 0.25) 15	4.89 (± 0.13) 14	4.29 (± 0.55) 17	4.49 (± 0.48) 13	4.75 (± 0.28) 13	5.05 (± 0.45) 14	0.98	0.44
Enrichment rotation	4.60 (± 0.21) 15	4.70 (± 0.21) 14	4.57 (± 0.12) 16	4.93 (± 0.46) 12	4.17 (± 0.40) 15	4.38 (± 0.24) 15	3.58 (± 0.38) 17	1.55	0.16
Enclosure plants	4.67 (± 0.21) ^a 14	4.32 (± 0.22) ^{ab} 16	4.63 (± 0.11) ^a 15	4.32 (± 0.46) ^{ab} 16	3.47 (± 0.41) ^b 17	3.86 (± 0.24) ^b 17	4.42 (± 0.38) ^{ab} 15	2.74	0.01
Enclosure availability	3.91 (± 0.17) 17	3.80 (± 0.18) 17	3.90 (± 0.09) 17	4.42 (± 0.38) 16	3.93 (± 0.33) 16	4.08 (± 0.20) 16	4.17 (± 0.31) 16	0.59	0.74

LSM importance values within rows followed by the same superscript are not significantly different ($P > 0.05$). Number in italics indicates order of importance placed on attribute.

presented in Table 3. Only 18 (5%) respondents indicated High School or technical further education to be their highest education level attained, most of whom were keepers and zoo management staff that had not completed a Bachelors degree. A total of 116 (32%) of the scientists had a doctoral degree, with the remainder either having completed a Masters or Bachelors degree. The respondents had a varying level of experience with Great Ape husbandry, with the majority (51%) having more than 13 months experience with their selected Great Ape species. We investigated the possibility of a relationship between the ranking of the attributes and the respondents' level of education and experience, but none was found. Most respondents approved of Great Apes being kept in captivity providing that their welfare is good (Table 3).

The majority of respondents answered the survey for chimpanzees (*Pan troglodytes*), followed by gorillas (*Gorilla gorilla*), and then orangutans, while the least number of respondents answered the survey about the husbandry of bonobos (*Pan paniscus*) (Table 2).

Utility and importance values

The greatest variation in utility values within an attribute was seen for the attributes 'enclosure furnishings', 'social structure' and 'duration of feeding'. Others, such as 'outdoor enclosure availability' and 'enclosure plants' and 'feeding interval', showed less variation between levels. Importance values attributed to the attributes ranged from 3.96 for enclosure availability to 8.22 for social structure (with the maximum possible score for an attribute being 10) (Table 4). Overall, the attributes considered in the 'management' category ('staff qualification', 'enrichment rotation', 'control over environment' and 'outdoor enclosure availability') were ranked as least important.

Species differences

The order in which the attributes were ranked differed for each species, with the order for orangutans being most different to the others. The ranking of the attributes: 'diet'; 'feeding interval'; 'social structure'; 'group size'; 'enclosure furnishings'; 'enrichment rotation'; and 'enclosure plants' were influenced significantly by species (Table 4). Physical attributes of an environment were rated as more important for orangutans and social attributes were considered more important for the other species. The respondents for gorillas and chimpanzees had similar responses, with 'social structure', 'group size' and 'enclosure appearance' being the top three for both species, and 'avoidance provision' and 'enclosure furnishings' being fourth and fifth, respectively.

When investigating the means for each species and attribute loadings, the attributes: 'duration of feeding'; 'enclosure furnishings'; 'enrichment rotation'; 'enclosure plants'; and 'feeding interval' received higher ratings from the respondents for African Great Apes than the respondents for orangutans, who focused more on 'group size', 'enclosure size', 'social structure' and 'avoidance provision' (Table 4, Figure 1).

Stakeholder differences

Only three attributes showed significant differences between stakeholder groups in importance scores (Table 5). 'Social structure' was rated more highly by the scientists than keeper and zoo management staff ($P < 0.01$). 'Feeding interval' was rated more highly by keepers than scientists or veterinarians ($P < 0.01$). 'Enclosure plants' was rated more highly by zoo management staff and scientists than research colony personnel and veterinarians ($P < 0.01$).

Discussion

Survey method

As no previous studies have assigned a weighting or rank for the husbandry attributes of Great Ape enclosures it is difficult to support the rankings found as a result of this study with the literature, however we were able to establish that the opinions of the stakeholders surveyed placed high importance on those aspects of captivity considered in the *Introduction* that have been demonstrated as important for Great Ape welfare. There were several different techniques that could have been adopted for this survey, including focus groups, a Delphi study and a scientific literature review. Focus groups were considered impractical because the limited number of experts in any one region would preclude large group meetings, giving rise to the risk of individuals deferring to the views of most experienced members. Delphi studies are prone to a high rate of attrition, and if bribes are offered to retain experts this may bias the results. They assume experts are willing to have their views reformed by the opinions of others, running the risk of adherence to the median view to save time or embarrassment that might arise from holding a minority view. Scientific literature review has not demonstrated a sufficient depth of knowledge on this topic to rely on this assessment of husbandry requirements, and it is unclear how to rank attributes with such a process. Hence, we chose the most expedient method of research, an online expert opinion survey, as it was believed that this could most effectively and efficiently gather opinions from a wide range of stakeholders worldwide. The widespread agreement between stakeholder groups in their ratings suggests that a consensus was reached. The discrepancies observed appear to relate to the involvement of the different groups. Social structure is often the subject of scientific investigation, whereas keepers are more involved in feeding than scientists or veterinarians. Zoo management staff were more likely to appreciate the aesthetic benefit of enclosure plants to zoo visitors than research colony personnel or veterinarians.

Response rate

The low number of responses from zoo education staff (9%) was probably because members of this group forwarded the survey on to the relevant keeper instead of completing the survey themselves, thus increasing keeper response rate (29%) (Table 2). The number of respondents answering for each Great Ape species mirrors the unequal captive Great Ape population, with a large number of chimpanzees (1,200) and gorillas (788), and a small number of bonobos (171) held in International Species Information System member zoos (ISIS 2010).

Species

The higher perceived importance for the attribute 'feeding interval' for orangutans than for chimpanzees may be due to the fact that orangutans are usually kept in smaller numbers than chimpanzees due to their more solitary nature, so the stimulation provided by regular feeding may be perceived as more important for orangutans. This agrees with the greater importance of 'enclosure furnishings' and 'enrichment rotation' for orangutans and the lower ranking of 'social structure' and 'group size' than the African apes, as orangutans use the vertical dimension more (Perkins 1992; Hebert & Bard 2000) and may be perceived as requiring more physical stimulation as they have less social stimulation from conspecifics. The lower perceived importance for the attribute 'avoidance provision' for bonobos than the other Great Apes could be due to their more tolerant behaviour of each other. Studies have shown them to be much more co-operative with conspecifics when asked to work for a food reward and frequently share food, something chimpanzees will rarely do (Hare *et al* 2007).

Validation of the overall rankings with scientific evidence

The attributes perceived by the stakeholders as having higher importance have been demonstrated in the scientific literature as being essential for animal welfare, however as the majority of the respondents fell into the 'scientist' group this was to be expected. For example, studies have consistently shown the provision of an appropriate social structure is of critical importance in terms of the adequate behavioural development of Great Apes in captivity (Davenport & Rogers 1970; Bloomsmith & Baker 2001; Nakamichi *et al* 2001; Martin 2002), and this attribute was assigned the highest importance by the respondents.

The five elements identified in the USDA report (USDA-APHIS-AC 1999) correspond directly with the prime position given to these attributes, with 'social structure' being ranked most with importance, followed directly by 'enclosure appearance', and 'enclosure furnishings', with 'duration of feeding' in sixth place. The high ranking of 'social structure' by the respondents is supported by many papers in the literature asserting its importance (eg Davenport & Rogers 1970; Böer [1983; p 279]; Traylor-Holzer & Fritz 1985; Woolverton *et al* 1989). Both the survey results and the current literature confirm that the physical appearance of an enclosure can encourage both activity budgets that are similar to wild Great Apes and low frequencies of psychopathologies (eg Perkins 1992; Kerridge 1996). 'Enclosure furnishings', the third most important attribute, are supported by scientific literature for their ability to provide a complex environment (Carlsted *et al* 1993; Brent & Stone 1996; Hebert & Bard 2000; Caws *et al* 2008). Similarly, group size is supported because it influences the formation and maintenance of successful social groups (National Research Council 1998; USDA-APHIS-AC 1999; Price & Stoinski 2007) and has a large impact on behaviour, welfare and reproductive success. Sub-optimal group size has been associated with increased abnormal behaviours (Price & Stoinski 2007), with solitary

housing associated with high levels of stereotypic behaviours, incompetent social and reproductive behaviours and chronic stress (Erwin & Deni 1979; Carlstead 1996; Reimersa *et al* 2007).

The attribute 'competition with conspecifics' was given an identical importance value to 'enclosure size'. High levels of competition with conspecifics can cause a monopolisation of resources in captive Great Apes (Tarou *et al* 2004), and thus should be avoided in the captive environment. Competition to mate occurs in captivity (Price & Stoinski 2007), as well as competition for favoured items and locations (Tarou *et al* 2004). Of similar importance was small 'enclosure size', with respondents probably recognising that an increase in cage size has little to no effect on behaviour and activity levels (Line *et al* 1990; Crockett *et al* 1995), unless it is associated with increased enclosure complexity (Perkins 1992; Crockett *et al* 2000).

Aspects of 'feeding interval' were given a moderate level of importance (5.37), and random presentation was favoured over regular feeding times perhaps because of preprandial stereotypies (Morgan & Tromberg 2007). Four times presentation was rated better than twice daily, decreasing the time that the animals spend inactive and reducing the occurrence of abnormal behaviours (Elsner 2002).

'Diet' was ranked of relatively low importance, even though it is often addressed in relation to regurgitation and reingestion (r/r). However, there are specific reasons for this, as fruit-based diets containing high levels of water and excessive amounts of sugar may be responsible for causing r/r in gorillas (Popovich & Dierenfeld 1997). Both Aspinall (1980) and Struck *et al* (2007) support the high rating to a diverse diet.

The low importance placed on 'staff qualifications' corresponds with the very limited information in the Great Ape husbandry literature. The similarly low ranking of 'enrichment rotation' was contradicted by a study that found increased activity when chimpanzees were provided initially with enrichment, but habituation developed quickly (Celli *et al* 2003). The least importance was placed on 'outdoor enclosure availability' by the respondents, despite the fact that marmosets (*Callithrix jacchus*) have been shown to prefer outdoor enclosures to indoor (Pines *et al* 2007).

Animal welfare implications

Understanding expert opinion in relation to Great Ape husbandry requirements in captivity is valuable in the light of inadequate scientific studies on the major species to allow issues to be ranked for importance effectively. Obtaining such information is the first stage in developing an effective welfare assessment tool to use in captive situations. Further development of such a tool requires: i) validation, in part by comparison with literature data, but also by direct evaluation of the welfare outcomes of captive environments with different levels of provision of the husbandry issues investigated; and ii) evaluation of performance of establishments keeping captive Great Apes, both of which are the subject of a subsequent paper from this research group.

Conclusion

The stakeholders of Great Ape husbandry ranked the attributes of husbandry in a consistent and useful manner, indicating that those involved with the care of captive apes hold similar opinions. Expected differences were found between the attribute rankings for the different species, with a survey of relevant literature confirming the value of the attributes believed to be of most importance.

Acknowledgements

We thank the many respondents worldwide who contributed their time to this study, Hung Vu (The University of Queensland Information Technology Services) for assistance with uploading the survey onto the internet, Ms Amanda Embury of ARAZPA for invaluable comments and support for the survey. This Great Ape Husbandry survey was approved by The University of Queensland Human Ethics Committee and adhered to the legal requirements of Australia.

References

- Anderson JR and Chamove AS** 1984 Allowing captive primates to forage. *Standards in Laboratory Animal Management* pp 253-256. UFAW: Wheathampstead, Herts, UK
- Armitage P and Colton T** 1998 *Encyclopedia of Biostatistics*. John Wiley & Sons: Chichester, UK
- Aspinall J** 1980 The husbandry of gorillas in captivity. *Journal of Reproduction and Fertility Supplement* 28: 71-77
- Bartussek H** 1999 A review of the animal needs index (ANI) for the assessment of animals' well-being in the housing systems for Austrian proprietary products and legislation. *Livestock Production Science* 61: 179-192. [http://dx.doi.org/10.1016/S0301-6226\(99\)00067-6](http://dx.doi.org/10.1016/S0301-6226(99)00067-6)
- Bassett L and Buchanan-Smith HM** 2007 Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science* 102: 223-245. <http://dx.doi.org/10.1016/j.applanim.2006.05.029>
- Blaney E and Wells D** 2004 The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare* 13: 111-118
- Bloomsmith MA and Baker KC** 2001 Social management of captive chimpanzees. In Brent L (ed) *The Care and Management of Captive Chimpanzees* pp 205-242. American Society of Primatologists: San Antonio, TX, USA
- Bloomsmith MA, Baker KC, Lambeth SP, Ross SK and Schapiro SJ** 2001 Is giving chimpanzees control over environmental enrichment a good idea? *The Apes: Challenges for the 21st Century* pp 88-89. Brookfield Zoo: Brookfield, IL, USA
- Böer M** 1983 Several examinations on the reproductive status of lowland gorillas (*Gorilla g. gorilla*) at Hannover Zoo. *Zoo Biology*, 2: 267-280. <http://dx.doi.org/10.1002/zoo.1430020403>
- Boesch C and Boesch-Achermann H** 2000 *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford University Press: Oxford, UK
- Brent L and Stone A** 1996 Long-term use of televisions, balls, and mirrors as enrichment for paired and singly caged chimpanzees. *American Journal of Primatology* 39: 139-145. [http://dx.doi.org/10.1002/\(SICI\)1098-2345\(1996\)39:2<139::AID-AJP5>3.0.CO;2-#](http://dx.doi.org/10.1002/(SICI)1098-2345(1996)39:2<139::AID-AJP5>3.0.CO;2-#)
- Carlstead K** 1996 Effects of captivity on the behavior of wild mammals In: Kleiman DG, Allen ME, Thompson KV and Lumpkin A (eds) *Wild Mammals in Captivity* pp 317-332. The University of Chicago Press: Chicago, USA
- Carlsted K, Brown JL and Seidensticker J** 1993 Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology* 12: 321-331. <http://dx.doi.org/10.1002/zoo.1430120403>
- Caws CE, Wehnelt S and Aureli F** 2008 The effect of a new vertical structure in mitigating aggressive behaviour in a large group of chimpanzees (*Pan troglodytes*). *Animal Welfare* 17: 149-154
- Celli ML, Tomonaga M, Udono T, Teramoto M and Nagano K** 2003 Tool use task as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science* 81: 171-182. [http://dx.doi.org/10.1016/S0168-1591\(02\)00257-5](http://dx.doi.org/10.1016/S0168-1591(02)00257-5)
- Chamove AS** 2005 Environmental enrichment for monkeys using plants. *Laboratory Primate Newsletter* 44: 1-5
- Crockett CM, Bowers CL, Shimoji M, Leu M, Bowden DM and Sackett GP** 1995 Behavioural responses of long-tailed macaques to different cage sizes and common laboratory experiences. *Journal of Comparative Psychology* 109: 368-383. <http://dx.doi.org/10.1037/0735-7036.109.4.368>
- Crockett CM, Shimoji M and Bowden DM** 2000 Behavior, appetite, and urinary cortisol responses by adult female pigtailed macaques to cage size, cage level, room change, and ketamine sedation. *American Journal of Primatology* 52: 63-80. [http://dx.doi.org/10.1002/1098-2345\(200010\)52:2<63::AID-AJPI>3.0.CO;2-K](http://dx.doi.org/10.1002/1098-2345(200010)52:2<63::AID-AJPI>3.0.CO;2-K)
- Davenport RK and Rogers CM** 1970 Differential rearing of the chimpanzee: a project survey. In Bourne GH (ed) *The Chimpanzee* pp 337-360. Karger: Basel, Switzerland
- de Vaus DA** 1995 *Surveys in Social Research*. Allen & Unwin: Melbourne, USA
- Elsner R** 2002 Techniques that promote the psychological well-being of captive primates and their application in the husbandry and management of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*) at Lincoln Park Zoo and at Lester E Fisher Great Ape House. *Animal Keeper's Forum* 29: 66-84
- Erwin J and Deni R** 1979 Strangers in a strange land: abnormal behaviors or abnormal environments? In: Erwin J, Maple T and Mitchell G (eds) *Captivity and Behavior* pp 1-28. Van Nostrand Reinhold Co: New York, USA
- Fraser D** 1995 Science, values and animal welfare: exploring the inextricable connection. *Animal Welfare* 4: 103-117
- Goodall J** 1986 *The Chimpanzees of Gombe. Patterns of Behavior*. The Belknap Press of Harvard University Press: Cambridge, USA
- Hanson JD, Larson ME and Snowden CT** 1976 The effects of control over high intensity noise on plasma cortisol levels in rhesus monkeys. *Behavioral Biology* 16: 333-340. [http://dx.doi.org/10.1016/S0091-6773\(76\)91460-7](http://dx.doi.org/10.1016/S0091-6773(76)91460-7)
- Hare B, Melis AP, Woods V, Hastings S and Wrangham R** 2007 Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology* 17: 619-623. <http://dx.doi.org/10.1016/j.cub.2007.02.040>
- Hebert P and Bard K** 2000 Orangutan use of vertical space in an innovative habitat. *Zoo Biology* 19: 239-251. [http://dx.doi.org/10.1002/1098-2361\(2000\)19:4<239::AID-ZOO2>3.0.CO;2-7](http://dx.doi.org/10.1002/1098-2361(2000)19:4<239::AID-ZOO2>3.0.CO;2-7)

- Honess PE and Marin CM** 2006 Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews* 30: 390-412. <http://dx.doi.org/10.1016/j.neubiorev.2005.04.003>
- International Species Information System (ISIS)** 2010 *ISIS Species Holdings*. <http://app.isis.org/abstracts/abs.asp>. (Accessed 20 September 2010)
- Johnson R** 1974 Trade-off analysis of consumer values. *Journal of Marketing Research* May: 121-127. <http://dx.doi.org/10.2307/3150548>
- Kerridge FJ** 1996 *Behavioural enrichment of ruffed lemurs (Varecia variegata) based upon a wild-captive comparison of their behaviour*. PhD Thesis, University of Manchester, UK
- Line SW, Markowitz H, Morgan KN and Strong S** 1991 Effects of cage size and environmental enrichment on the behavioural and physiological responses of rhesus macaques to the stress of daily events. In: Novak MA and Petto AJ (eds) *Through the Looking Glass: Issues of Psychological Well-being in Captive Nonhuman Primates* pp 160-179. American Psychological Association: Washington DC, USA. <http://dx.doi.org/10.1037/10080-016>
- Line SW, Morgan KN, Markowitz H and Strong S** 1990 Increased cage size does not alter heart rate or behavior in female rhesus monkeys. *American Journal of Primatology* 20: 107-113. <http://dx.doi.org/10.1002/ajp.1350200205>
- Maki S and Bloomsmith MA** 1989 Uprooted trees facilitate the psychological well-being of captive chimpanzees. *Zoo Biology* 8: 79-88. <http://dx.doi.org/10.1002/zoo.1430080110>
- Martin J** 2002 Early life experiences: activity levels and abnormal behaviours in re-socialised chimpanzees. *Animal Welfare* 11: 419-436
- Mineka S and Kelly KA** 1989 The relationship between anxiety, lack of control and loss of control. In: Steptoe A and Appels A (eds) *Stress, Personal Control and Health*. John Wiley & Sons Ltd: Chichester, UK
- Mitani JC** 1989 Orangutan activity budgets: monthly variations and effect of body size, parturition, and sociality. *American Journal of Primatology* 18: 87-100. <http://dx.doi.org/10.1002/ajp.1350180203>
- Morgan KN and Tromborg CT** 2007 Sources of stress in captivity. *Applied Animal Behaviour Science* 102: 262-302. <http://dx.doi.org/10.1016/j.applanim.2006.05.032>
- Nakamichi M, Silldorff A and Sexton P** 2001 Behavioral responses of an infant gorilla to maternal separation in a captive social group of lowland gorillas (*Gorilla gorilla gorilla*). *Primates* 42: 245-252. <http://dx.doi.org/10.1007/BF02629640>
- National Research Council** 1998 *The Psychological Well-being of Nonhuman Primates, Committee on Well-being of Nonhuman Primates*. National Academy Press: Washington, USA
- O'Neill P** 1989 A room with a view for captive primates: issues, goals, related research and strategies. In Segal EF (ed), *Housing, Care, and Psychological Wellbeing of Captive and Laboratory Primates* pp 135-160. Noyes Publications: Park Ridge, NJ, USA
- Perkins LA** 1992 Variables that influence the activity of captive orangutans. *Zoo Biology* 11: 177-186. <http://dx.doi.org/10.1002/zoo.1430110306>
- Perneger TV** 1998 What's wrong with Bonferroni adjustments. *British Medical Journal* 316: 1236-1238. <http://dx.doi.org/10.1136/bmj.316.7139.1236>
- Phillips CJC, Wojciechowska J, Meng J and Cross N** 2009 Perceptions of the importance of different welfare issues in livestock production in Australia. *Animal* 3: 1152-1166. <http://dx.doi.org/10.1017/S1751731109004479>
- Pines MK, Kaplan G and Rogers LJ** 2007 A note on indoor and outdoor housing preferences of common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science* 108: 348-353. <http://dx.doi.org/10.1016/j.applanim.2006.12.001>
- Poole TB** 1995 Guidelines and legal codes for the welfare of non-human primates in biomedical research. *Laboratory Animals* 29: 244-249. <http://dx.doi.org/10.1258/002367795781088379>
- Popovich DG and Dierenfeld ES** 1997 Nutrition. In: Ogden J and Wharton D (eds) *Management of Gorillas in Captivity* pp 138-146. Gorilla Species Survival Plan and the Atlanta/Fulton County Zoo Inc: Atlanta, GA, USA
- Price EC, Ashmore LA and McGivern AM** 1994 Reactions of zoo visitors to free-ranging monkeys. *Zoo Biology* 13: 355-373. <http://dx.doi.org/10.1002/zoo.1430130409>
- Price EE and Stoinski TS** 2007 Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science* 103: 255-264. <http://dx.doi.org/10.1016/j.applanim.2006.05.021>
- Reimersa M, Schwarzenbergera F and Preuschoft S** 2007 Rehabilitation of research chimpanzees: stress and coping after long-term isolation. *Hormones and Behavior* 51: 428-435. <http://dx.doi.org/10.1016/j.yhbeh.2006.12.011>
- Sambrook TD and Buchanan-Smith HM** 1997 Control and complexity in novel object enrichment. *Animal Welfare* 6: 207-216
- Savini T and Bigatti MP** 2000 Nutrition of *Gorilla gorilla graueri* in captivity. *Folia Primatologica* 71: 292
- Smith A, Lindburg DG and Vehrencamp S** 1989 Effect of food preparation on feeding behavior of lion-tailed macaques. *Zoo Biology* 8: 57-66. <http://dx.doi.org/10.1002/zoo.1430080108>
- Struck K, Videan EN, Fritz J and Murphy J** 2007 Attempting to reduce regurgitation and reingestion in a captive chimpanzee through increased feeding opportunities: a case study. *Laboratory Animals* 36: 35-38. <http://dx.doi.org/10.1038/labani0107-35>
- Tarou L, Kuhar C, Adcock D, Bloomsmith M and Maple T** 2004 Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). *Animal Welfare* 13: 445-453
- Traylor-Holzer K and Fritz P** 1985 Utilization of space by adult and juvenile groups of captive chimpanzees (*Pan troglodytes*). *Zoo Biology* 4: 115-127. <http://dx.doi.org/10.1002/zoo.1430040205>
- United States Department of Agriculture, Animal & Plant Health Inspection Service/Animal Care (USDA-APHIS-AC)** 1999 *Final Report on Environment Enhancement to Promote the Psychological Wellbeing of Non-Human Primates*. Department of Agriculture, Animal and Plant Health Inspection Service, Animal Care: Riverdale, MD, USA
- Wolfensohn S and Honess P** 2005 *Handbook of Primate Husbandry and Welfare*. Blackwell Publishing: Oxford, UK. <http://dx.doi.org/10.1002/9780470752951>
- Wood W** 1998 Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology* 17: 211-230. [http://dx.doi.org/10.1002/\(SICI\)1098-2361\(1998\)17:3<211::AID-ZOO5>3.0.CO;2-C](http://dx.doi.org/10.1002/(SICI)1098-2361(1998)17:3<211::AID-ZOO5>3.0.CO;2-C)

Woolverton WL, Ator NA, Beardsley PM and Carroll ME

1989 Effects of environmental condition on the psychological well-being of primates. A review of the literature. *Life Sciences* 44: 901-917. [http://dx.doi.org/10.1016/0024-3205\(89\)90489-X](http://dx.doi.org/10.1016/0024-3205(89)90489-X)

Worstell C 2003 *Reconciling user needs in animal exhibit design: gorilla exhibits as a case study*. <http://www.zoolex.org/publication/worstell/gorilla/content.html>. (Accessed 10 June 2007)

Zubkowicz R and Kaleta T 2005 The investigations concerning an evaluation great apes exhibits in selected European zoological gardens. *Annals of Warsaw University, SGGW, Animal Science* 43: 47-53

Zucker EL, Mitchell G and Maple T 1978 Adult male-offspring play interactions within a captive group of orangutans (*Pongo pygmaeus*). *Primates* 19: 379-384