A COMPARISON OF THE ACTIVITY BUDGETS OF WILD AND CAPTIVE SULAWESI CRESTED BLACK MACAQUES (*MACACA NIGRA*)

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Abstract *Animal Welfare 2002, 11*: 213-222

*One aim of environmental enrichment techniques is to replicate 'wild-like' behaviour in captivity. In this study, three captive troops of Sulawesi crested black macaques (*Macaca nigra*) were each observed for 100 h in large naturalistic enclosures. Activity budgets constructed from these observations were compared with published data collected from wild troops in the DuaSudara Nature Reserve, Sulawesi (O'Brien & Kinnaird 1997). No significant difference was found between the activity budgets of the wild and the captive macaques, although social, resting and feeding behaviours were significantly different between zoos. There was more rest and less movement and feeding in captivity, although these differences were not significant. The relatively large number of individuals, the wide variety of age–sex classes and the large and complex naturalistic enclosures provided for them may have been important factors in promoting wild-like behaviour. This study shows that captive primates can exhibit wild-type activity budgets.*

Keywords: *activity budgets, animal welfare, enclosure design, Sulawesi crested black macaque, wild versus captive*

Introduction

Defining 'natural' behaviour is difficult, even in the context of behaviours occurring in the wild or which are part of an animal's 'normal' repertoire, as the behaviour of a species may change over its geographical range (Chamove 1988; Boinski & Mitchell 1992). In addition, the degree of difference between wild and captive environments is highly variable. Wild areas vary from those that receive minimal impact from humans to intensively managed reserves, and in captivity some animals are semi-free-ranging over areas measured in hectares and some are kept in small 'traditional' cages (Carlstead 1996). Carlstead (1996) highlighted that a dichotomy between wild–captive environments is false, and Chang *et al* (1999) proposed a continuum along which animals live in conditions that tend towards being more 'wild' or 'captive'. Throughout this paper, we define 'wild-like' behaviours or levels of behaviours as those performed in the species' native habitat. The preservation of more wild-like behaviours may be necessary for conservation and re-introduction of endangered species. By actively conserving wild-like behaviours, behavioural adaptation to captive environments and loss of behaviours necessary for survival in the wild can be avoided (Frankham *et al* 1986).

Environmental enrichment can be used to manipulate the captive environment in order to increase the incidence of natural behaviours (Chamove 1988; Shepherdson 1994; Carlstead 1996). Three approaches to enrichment are: first, providing a suitable surrounding to allow wild-like behaviours (termed passive); second, active manipulation using apparatus to stimulate the desired behaviour using rewards; and third, manipulating social composition (second and third approaches termed active enrichment; Hancock 1980; Markowitz 1978; Visalberghi & Anderson 1993). The provision of naturalistic enclosures can have long-lasting effects on behaviour (Forthman-Quick 1984; Maple & Finlay 1989). Naturalistic enclosures have been associated with wild-like activity budgets and low frequencies of psychopathologies (Schilder & Boer 1987; Kerridge 1996; Perkins 1992). These 'enriched' environments are considered to improve animal welfare through the modulation of stress and the maintenance of physical fitness and psychological well-being (Bercovitch & Ziegler 1989; Maple & Finlay 1989; Chamove & Moodie 1990; Beck *et al* 1991; Redshaw & Mallinson 1991; Carlstead & Shepherdson 1994; Shepherdson 1994; Carlstead 1996). In addition, naturalistic conditions promote informal education of the public, who view these types of enclosures positively (Wolf & Tymitz 1981; Carlstead *et al* 1991; Reade & Waran 1996). Many managers of captive animals acknowledge the benefits of exhibits that allow the expression of wild-like behaviours and accordingly are trying to provide them (Seidensticker & Doherty 1996).

Activity budgets are widely recognised as a source of valuable information which should be incorporated into the management of captive animals (Bercovitch & Ziegler 1989; Maple & Finlay 1989; Lees 1993). The use of wild activity budgets may be useful in setting guidelines and illustrating the types of behaviour or level of expression that has been shaped through natural selection (Stolba & Wood-Gush 1984). The activity budget of a wild animal can be used to determine whether the frequency of behaviours observed in captivity has diverged significantly from that expressed in the wild.

Sulawesi crested black macaques (*Macaca nigra*) are highly endangered in the wild; their habitat is dwindling and they are prey to human hunters, despite being protected under Indonesian law (Kinnaird & O'Brien 1996; Hilton-Taylor 2000). Activities for the conservation of *M. nigra* involve both *in situ* (habitat protection and a reduction in hunting pressure) and *ex situ* (the use of captive breeding programmes in zoos) strategies. For example, there is a large captive population of *M. nigra* in Europe managed as part of a conservation programme (Carman 1995; Norcup 2001).

The captive population of *M. nigra* serves as a useful model to investigate the effectiveness of naturalistic environments as a form of enrichment. The aim of this study was to compare activity budget data from captive groups of macaques with those collected from groups in the wild by O'Brien and Kinnaird (1997).

Animals, materials and methods

Study sites

O'Brien and Kinnaird (1997) compiled activity budgets for wild *M. nigra* in Tangkoko DuaSudara National Reserve in north Sulawesi. Out of the eight troops regularly observed in all habitats and elevations of the reserve, three troops (Rambo, Malonda and Dua) comprising 50–97 individuals were habituated and followed for 18 months.

Three differently managed captive troops of *M. nigra* were observed in Chester, Jersey and Marwell zoos in May and June 1997. The macaques were all housed in enclosures made up of two areas, one inside (a sheltered house) and one outside (exposed to the elements).

The outside areas had been designed in a 'naturalistic' fashion, which provided enclosure furniture representing structures seen in the wild including natural vegetation and movable above-ground features (Hancock 1980; Forthman-Quick 1984). The inside enclosures were all divided into three dens, to allow for separation of individuals. A comparison of the study sites and management of the captive *M. nigra* is presented in Table 1.

Table 1 A comparison of the captive study sites and management of *M. nigra*.

Enclosure	Chester Zoo	Jersey Zoo	Marwell Zoo
Inside floor area (height)	190 m^2 (5.7 m)	33.2 m^2 (3.2 m)	20 m^2 (3 m)
Outside area	1660 m^2	1000 m^2	375 m^2
Inside furniture	A pond, three caves in a rendered wall, two walls and the ceiling made of mesh (useable surface), six wooden uprights with limb-like protrusions, movable sisal ropes.	Movable sisal ropes, automatic drinkers.	Static metal frame of nine uprights, six of which had circular platforms.
Outside — plants	Long grasses and wild flowers (1 m), several trees (silver birch, horse chestnut), bushes (holly, hebes).	Tall grasses (1 m), nettles (in flower), bushes (gorse).	Grass (20 cm).
Outside — furniture	Waterfall, large horizontal logs, large rocks.	Waterfall, stream, pond, natural tree trunks (both vertical and horizontal, up to 7 m high), cargo net, sisal ropes.	Waterfall, cargo net, large horizontal logs, upright metal structure (8 m high).
Perimeter	Moat and electric fence.	Electric fence.	Moat and electric fence.
Access to the outside	Access permitted between the inside and outside 0800h–1600h, after which they were locked inside.*	24 h access in and out (except brief period for indoor cleaning).	Locked out 0800h–1800h, then locked in for the night.
Feeding regime	Two feeds daily: 0800h concentrate feed; 1600h fruit and vegetable feed.	Four feeds daily: 0830h fruit and concentrate feed; 1200h forage feed; 1400h and 1600h fruit and vegetable feed.	Two feeds daily: 0900h concentrate feed; 1800h fruit and vegetable feed (occasionally eggs given at noon).

* As the enclosure was new, the macaques only had access to the island two days before the study and access outside was very restricted for the next five days.

Data collection

In the wild, five individuals from each age–sex class (adult male, adult female, large juvenile, small juvenile) were observed using scan sampling (total of 20 individuals per scan), in the first 10 min of every half-hour between 0600h and 1740h (O'Brien & Kinnaird 1997). To compare the captive activity budgets with the wild data, similar methodology was used here. The zoo groups did not contain five representatives in each age–sex class, so all of the macaques present in the zoo groups were observed, except those under one year old, who were dependent on their

mother (Rowell 1967). As the age–sex classes were not defined by O'Brien and Kinnaird (1997), we used the following criteria: small juvenile, 1–2 years old; large juvenile, males 3–7 years old, females 3–4 years old; adult, males > 7 years old, females > 5 years old.

Scan sampling at 30 min intervals was used to observe the zoo macaques and each individual was scanned (n = 14, 16 and 9 individuals at Chester, Jersey and Marwell, respectively; see Table 2). These scan observations took place over 10 h between 0700h and 1900h, evenly balanced over time of day. Animals that could not be located in the larger enclosures were recorded as 'not seen'. The observations were carried out over 10 days per troop, to amass 300 h of behavioural data divided equally between the three groups. Behavioural data were collected on zoo macaques using an extended version of the categories used by O'Brien and Kinnaird (1997; Table 3), allowing for more detailed data collection. However, for direct comparison with the wild data, categories were collapsed and comparisons made using the original categories.

Table 2 Captive group compositions, their age ranges and the age–sex class categories assigned to them.

Zoo	Sex ratio of troop	Age–sex categories of individuals studied				Age range
	m:f:unk*	Adult male	Adult female	Juvenile		
				Large	Small	
Chester	4:10:0	2	4	4	4	2–18 years
Jersey	7:9:1	3	6	3	4	2 weeks–26 years
Marwell	2:7:1	1	4	1	3	4 months–13 years

* m:f:unk = male:female:unknown

NB: Individuals under a year old were not included in the study

Table 3 Behavioural categories scored. Italics indicate where categories and definitions have been expanded from O'Brien and Kinnaird 1997.

Behaviour	Description
Social	Allogrooming, play, non-copulatory mounting and copulation (excluding manipulation of objects). Fights (chasing including attacks, usually associated with vocalisations), strutting, yawning, biting, pulling hair (usually from the crest) and grimacing (submissive) (Dixson 1977).
Moving	Locomotion, including walking, running, climbing and jumping.
Resting	Body stationary, usually sitting or lying and not engaged in social activity. Autogrooming included.
Foraging	Moving slowly with attention directed toward potential food source or manipulating substrates in search of potential foods. Manipulation of the environment (eg furnishings).
Feeding	Reaching for, picking, manipulating, masticating, placing food in mouth, or manipulating cheekpouch contents.
Miscellaneous	Behaviours that cannot be described in any of the above categories, but are identified on the checksheet.
Not seen	Individual not visible.

Statistical analysis

Analysis was divided into two sections:

1) Zoo versus wild comparison of the troops' activity budgets. The mean percentage of time observed performing each categorised behaviour was compared between the wild and captive troops (n = 3,3). The mean percentage of behaviour for each captive troop was calculated from the mean percentage of each individual in the troop (Chester 14, Jersey 16, Marwell 9).

The mean percentage for each individual was calculated from 20 scan observations per day averaged over 10 days (200 scans per individual in each captive troop), which were then turned into percentages. The wild data were collected and published by O'Brien and Kinnaird (1997). As there were only three sampling points in each sample (wild, captive) a non-parametric Mann-Whitney *U*-test was carried out. Although the Mann-Whitney *U*-test is usually carried out on medians, the wild data were published as means, so for comparative purposes means were calculated and used in the analysis for the captive troops as well.
2) Inter- and intra-site comparison of behaviours between the age–sex classes and zoos. The same mean values of behaviour described above were used. These were normally distributed, and therefore a parametric two-way ANOVA was carried out with Bonferroni *post hoc* analysis (Fowler & Cohen 1996; SPSS 1999). All analyses were carried out in SPSS for Windows, Release 8.0.

Results

Comparison of wild and captive activity budgets

The activity budgets for the wild and captive Sulawesi macaques are shown in Figure 1. There was no significant difference between the activity budgets of the wild and captive macaques (W = 9 social, 7 moving, 7 resting, 10 foraging, 7 feeding; $P > 0.05$). Rest increased and moving and feeding behaviours decreased with decreasing enclosure size and from the wild to the captive sites (Figure 1).

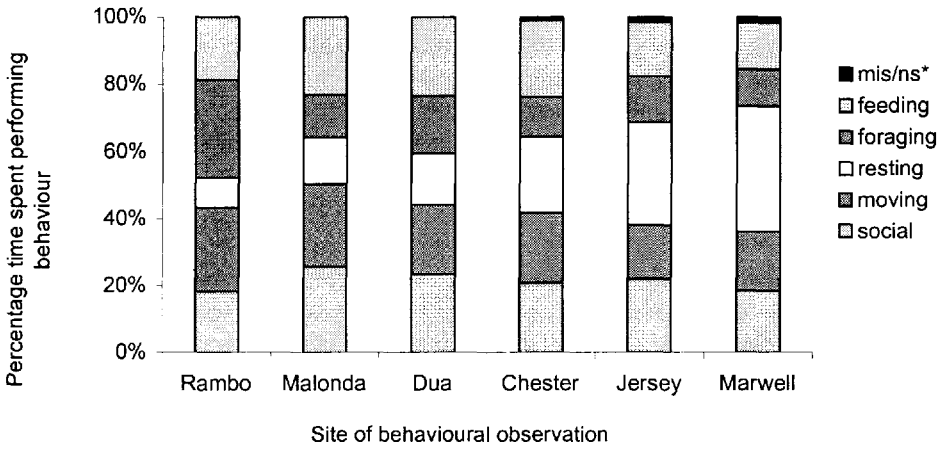

Figure 1 **The percentage of time spent performing categorised behaviours, in captivity and in the wild (mean ± SEM).**
* mis/ns, miscellaneous and not seen behavioural category.
The zoos are in order of enclosure size, Chester's enclosure covering the largest area and Marwell's the smallest (Table 1) and the wild troops are in order of home range size, Rambo covering the largest area (km^2 home ranges: Rambo = 2.42; Malonda = 1.13, Dua = 0.69, reported by O'Brien & Kinnaird 1997).

Effects of site and age–sex class on behaviour

Both zoo and age–sex class had significant effects on captive macaque behaviour (Table 4). Feeding behaviour was significantly influenced by an interaction of zoo and age–sex class, whereas resting and miscellaneous behaviours were significantly affected by differences between zoos, and social, moving, resting and foraging behaviour were significantly affected

by the age–sex class of the macaques (Table 4). The results from Bonferroni *post hoc* analysis identified that macaques at Chester Zoo rested significantly less than those at Jersey and Marwell but scored significantly higher in the miscellaneous behaviour and 'not seen' category than both Jersey and Marwell (Table 4).

Table 4 Summary of two-way ANOVA and *post hoc* analysis results investigating the effects of zoo and age–sex class on behaviour.

		F-value for each behaviour					
IV	***df***	**Social**	**Moving**	**Resting**	**Foraging**	**Feeding**	**Mis**
*Zoo*Age–sex*	6	1.16	1.15	0.74	1.88	9.89***	0.53
Zoo	2	0.84	2.7	8.12*	0.06	39.99***	8.47**
Post hoc results				C<J*		M<J***	C>M**
				C<M***		M<C***	C>J*
Age–sex	3	4.24*	6.27**	9.52***	9.34***	5.32**	1.6
Post hoc results		AF>A	AF<SJ**	AM>SJ***	AM<LJ**		
		M*	AF<LJ*	AM>LJ*	AM<SJ**		
				AF>SJ**			

IV, independent variable; Mis, miscellaneous behaviour

*$P<0.05$, **$P<0.01$, ***$P<0.001$

C, Chester Zoo; J, Jersey Zoo; M, Marwell Zoo

AM, adult male; AF, adult female; LJ, large juvenile; SJ, small juvenile

Discussion

This study shows that there are no significant differences in the activity budgets of wild and captive Sulawesi crested black macaques, which is a very positive comment on the quality of animal management in the three zoos. This lack of difference between wild and captive behaviours may be partly attributable to the variation seen in the activity budgets and habitats of the wild macaques. However, the complex and relatively spacious nature of the zoo enclosures and the social groupings of the captive troops provided opportunities for wild-like activity levels to be achieved.

Although the aim of providing a naturalistic enclosure is to create an environment that mimics many features of the wild, it is impossible to provide a complete simulation. As behaviour is partly a product of the environment, wild and captive animals would be expected to behave differently. Research has demonstrated that the inclusion of wild-like environmental stimuli may increase animal welfare and so we can tentatively assume that their absence may also compromise animal welfare (Chamove 1988; Chamove & Moodie 1990; Wiepkema & Koolhaas 1993; Wemelsfelder 1993; Carlstead & Shepherdson 1994; Carlstead 1996).

The wild troops varied significantly in many aspects of their behaviour because of variations in geography and food abundance (O'Brien & Kinnaird 1997). Similar behavioural differences were observed between zoos. A genetic basis for the behavioural difference between the captive troops is unlikely. European-held *M. nigra* have been managed for some years as one population, with individuals being exchanged between zoos to minimise inbreeding and maintain genetic diversity. The environmental differences at the participating zoos in this study, which included different enclosure dimensions and contents, daily husbandry routines and social composition, are a more likely explanation for behavioural differences. The significantly low level of feeding seen at Marwell zoo was probably artificially low because the animals' main feed was provided late in the day, outside the

observation periods. It appeared that increases in enclosure size were inversely related to the expression of resting behaviour (Figure 1). The argument for 'quality' space over quantity has been addressed in previous research. It is generally accepted that primates are better served by complex environments with opportunities to exercise, hide from conspecifics and fulfil appetitive behaviours (Hediger 1964; Wilson 1982; de Waal 1989; Carlstead & Shepherdson 1994; Maple & Finlay 1989; Woolverton *et al* 1989). Enclosure complexity was not quantified in this study and therefore may confound the links between enclosure size and activity, so this area is currently under further study.

Significant behavioural differences were found between age–sex classes in both captive and wild troops. Patterns of behaviour seen in wild macaques were similar to those observed in the captive troops, with adult males foraging the least, adult females socialising the most, and juveniles moving and foraging the most and resting the least (O'Brien & Kinnaird 1997). This similarity suggests that the captive environments provided opportunities for different classes to express behaviours independently of each other.

The decline of moving and feeding, with an increase in resting behaviour, in the captive troops compared to the wild was a trend apparent in all zoos. As the time spent in social and foraging behaviour remained similar across zoos, the additional time spent in resting must have been compensated for by a decrease in time moving or feeding. These findings support the idea that time commitments to certain behaviours are fixed, whereas those to other behaviours are more elastic (Bubier 1996). This study suggests that moving, resting and feeding behaviours are the more elastic behaviours, and social behaviour is more 'fixed'. Feeding increased with time spent moving (or with decreased resting), so it seems likely that movement is not just for exploration or territorial purposes, but also for food collection. Marwell's macaques fed and moved significantly less than those at Chester and Jersey. This may be due to a number of factors including differences in social composition, feeding regime, size and complexity of the enclosure, and weather (Wilson 1982; Chamove *et al* 1982; Bernstein & Baker 1988; de Waal 1989; Shepherdson 1994). Further research is underway to identify the environmental features that affect behavioural expression, and to investigate the effects of naturalistic enclosure design and wild-like social organisation.

There are limitations inherent in wild–captive comparative studies (Veasey *et al* 1996). However, the methodology used in this study sought to minimise variation between the wild and captive data. Interest in the observer was minimal because of habituation in both cases. The same behavioural categories were used at the wild and captive sites and they were simple and well defined, thus reducing inter-observer variation. The wild data were collected from three different troops, providing a representative sample from wild macaques.

It is generally agreed that it is good if captive animals exhibit wild-like behaviour. Such individuals, maintained in naturalistic environments, are likely to be behaviourally flexible and exhibit a broader repertoire of behaviours, suggesting that they can adapt to novel situations and have improved perceptual skills, and may thus be of higher quality as reintroduction candidates (Carlstead & Shepherdson 1994; Kleiman *et al* 1986). Activity budget data give a broad, although simplistic, overview of behavioural expression, which could be used to determine whether captive individuals are deviating from the wild-type pattern.

Conclusions

The similarities in wild and captive activity budgets found in this study demonstrate that it is possible to maintain captive Sulawesi macaques that express wild-like behaviours. The

stimulation of these wild-like behaviours was not explored in this study; however, a feature common to all three captive troops was a naturalistic approach to zoo enclosure design, and frequent and varied opportunities for locomotion and foraging.

Previous studies have identified that changes in activity budget may cause no concern over the short term, but in the long term may compromise welfare (Bubier 1996). Our study shows an increasing trend towards wild-like behaviour as the enclosures became larger and more complex, although further work is necessary to define the exact features of a naturalistic environment that lead to wild-type activity budgets. This study also demonstrates that naturalistic environments in zoos do allow the expression of wild-type activity budgets, as has previously been suggested (Forthman-Quick 1984; Carlstead & Shepherdson 1994).

Animal welfare implications

Replication of 'wild-like' behaviours in captivity must be seen as an advance in zoo animal welfare, which may benefit individual animals as well as the captive population as a whole through the conservation of survival skills needed in the wild (Box 1991; Newberry 1995; Carlstead 1996). Animals that express wild-like behaviour are more meaningful subjects for research and provide a positive addition to public education and captive-breeding programmes (Eisenberg & Kleiman 1977; Coe 1985; Snowdon 1989; Kleiman 1992; Reade & Waran 1996).

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