

Investigation of the behavioural response of a colony of group-housed
hamadryas baboons (*Papio cynocephalus hamadryas*) to relocation to a more
naturalistic enclosure

by

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ABSTRACT

As part of Wellington Zoo's current management philosophy to reduce the number of species and increase enclosure size, quality and appropriateness for those remaining animals, the zoo's colony of hamadryas baboons (*Papio cynocephalus hamadryas*) was relocated within the zoo to a purpose-designed and more naturalistic exhibit.

The primary objective of this investigation was to determine group and individual responses of five of these baboons to their new enclosure. In so doing, this investigation was intended to address the shortage of quantitative, species-specific information on environmental enrichment for *Papio* baboons (Kessel and Brent 1996).

The data collection method used in this investigation consisted of fifteen-minute focal sampling of each of the five focal animals in the two months before and the month following the colony's relocation. For the purposes of this investigation, these focal samples were initially analysed together, prior to each focal animal being considered independently. Analysis of data extracted from these focal samples included consideration of:

- The overall occurrence of individual behaviours between the former and new enclosures;
- Additions to the animals' behavioural repertoires upon relocation; and,
- Time the animals spent alone and interacting socially.

Upon the colony's relocation, changes in the combined focal animals' behaviour were anticipated as a result of greater space, areas of privacy, and increased environmental variation. Focal sampling revealed increasingly naturalistic behaviours, including a reduction in vacuum and vestigial behaviours, and an increase in species-typical behaviour. Results also indicated that the combined focal animals experienced unexpectedly low levels of "agonistic" (i.e. aggressive) behaviour in both enclosures. However, there was a reduction in some associated behaviours upon the colony's relocation. This included a decline in male rivalry over females.

Differences in the responses of individual focal animals to relocation were also anticipated. Of particular interest were results indicating an increasing similarity of individual roles within one-male units to those of free-ranging hamadryas baboons. These roles were associated with both age and sex.

This study raises implications for improving the current management of the Wellington Zoo colony and other captive hamadryas baboon colonies. These include emphasising the importance of appropriate husbandry and feeding schedules. It also raises implications for the future management of other captive *Papio* baboon colonies in terms of enclosure redesign. These include the benefit of incorporating naturally occurring environmental factors, such as natural leaf litter.

This study is also of value from a management perspective as a baseline for future investigations. Such investigations could include long-term monitoring of this colony's use of environmental enrichment in the new enclosure and consideration of the animals' behaviour as the colony is encouraged to expand.

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CHAPTER 1: INTRODUCTION

1.1 BACKGROUND TO STUDY

The relocation of a captive colony of hamadryas baboons (*Papio cynocephalus hamadryas*) into a more spacious and naturalistic enclosure within the same zoo provided an opportunity to study the effects of enclosure enrichment on the behaviour of group-housed baboons. Studying the same colony in two different exhibits provided the additional benefit of mitigating the effects of genetic behavioural differences in sample populations (Altman, S A 1974).

While information pertaining to wild baboons is plentiful, studies regarding behavioural and physical effects of enrichment for captive *Papio* species, and especially group-housed baboons, are limited to a few abstracts (Kessel and Brent 1996). Furthermore, unlike many baboon enrichment techniques that are borrowed from studies of macaques (*Macaca* sp.) (Kessel and Brent 1996), this study was specific to enrichment designed expressly for group-housed hamadryas baboons. While information from investigations involving other species can be of value in designing enrichment for captive baboons, differences in interspecies responses to environmental change are common (Brent and Long 1995).

In assessing the welfare of captive animals, behavioural observations are advantageous because they can be undertaken non-invasively, without complicated equipment (Duncan and Poole 1990). In addition, changes in the animals' conditions may present themselves more subtly and quickly than physiological and biochemical changes (Duncan and Poole 1990).

Behavioural observations made in this investigation were compared with those made by various authors of wild hamadryas baboons and other captive colonies. According to Duncan and Poole (1990:203), there is validity in comparing the behaviour of captive animals with that of wild conspecifics because wild animals will have adapted to their natural environment. This provides a “benchmark” against which to compare the behaviour of captive animals.

1.2 SPECIES BACKGROUND


1.2.1 Genera

Papio cynocephalus hamadryas belong to one of two genera of baboons, each containing a single living species; the *Theropithecus* baboons [of which the gelada baboon (*Theropithecus gelada*) is the only existing species] and the *Papio* baboons (Barrett 2000). Initially characterised as five independent species due to physical differences, the five *Papio cynocephalus* baboons are now commonly considered a single species divided into five subspecies. This is because these subspecies can successfully interbreed (Barrett 2000). However, in the literature there remains the occasional taxonomic inconsistency.

1.2.2 Distribution

Baboons occupy a variety of habitats from West African rainforests to the semi-desert coasts of the Red Sea (Kummer 1968). Hamadryas baboons inhabit the northerly reaches of the broad *Papio* range. They are found in the scrublands of Sudan and Somalia, south to Ethiopia where their distribution merges with that of the olive baboon (*Papio cynocephalus anubis*) (Barrett 2000) (Figure 1.1). Hamadryas baboons also inhabit the coastal mountains of southern Arabia, although there is speculation as to whether this is part of their natural distribution, (via a submerged land bridge), or is a consequence of human transportation (Barrett 2000).



Figure 1.1.  Distribution of *Papio cynocephalus hamadryas* (Kummer 1995)

1.2.3 Habitat and ecology

Unlike their nocturnal predators, specifically leopards, baboons have poor night vision (Barrett 2000). Sleeping sites must, therefore, not only be sheltered and dry to protect the animals from cold overnight temperatures but, also, be secure against surprise predation attacks (Barrett 2000). As such, hamadryas baboons shelter overnight on steep cliff faces, central to a large home range that is characteristically devoid of tall trees (Sigg and Stolba 1981). Other predators of hamadryas baboons include spotted hyenas, jackals, dogs and fish eagles (Sigg 1980).

Sigg and Stolba (1981:43) deduced a home range of 28 square kilometres for a wild Erer-Gota hamadryas baboon band. This area is larger than the average home ranges deduced for other baboons, with the exception of estimates by DeVore and Hall [1965] (Sigg and Stolba 1981). Such a broad home range led to the suggestion that hamadryas baboons occupy a habitat with a low food density that necessitates significant daily travel (Sigg and Stolba 1981) in order to sustain a predominantly vegetarian diet (Kummer 1995). Clutton-Brock and Harvey (1977, cited in Kummer 1995:253) determined that there is a correlation between length of daily march and the proportion of leaves in a species' diet. Specifically, the lower the proportion of leaves, the longer the daily travel. Their typically low population density is also indicative of low resource availability (Kummer 1968).

Hamadryas baboons are the only baboons specialised to semi-desert, scrub land, and open savannah environments (Kummer 1995). Hamadryas baboons have been found to use the space within their home range non-randomly in such a way as to best utilise feeding sites and large water supplies, which are limited in the dry season to predominantly underground sources (Sigg and Stolba 1981).

1.2.4 Social organisation

An outstanding feature of the hamadryas baboon's ability to survive its arid habitat is its complex, four-layered social structure, considered to be unique amongst animals (Kummer 1995). Known as the "fusion-fission system", this social structure provides a flexible solution to resource acquisition and protection from predators (Kummer 1995:10). It is thought that hamadryas baboons employ this fusion-fission system in a variety of ways and to varying degrees, depending upon prevailing ecological conditions (Kummer 1968).

The primary social unit of the hamadryas baboon is the harem, consisting of a single adult male, a group of between one and ten females (Kummer 1995), and their associated immature offspring (Sigg and Stolba 1981). Harems retain their integrity despite fusion (Kummer 1968). When two or three one-male units join at small feeding sites, a clan is formed. Typically, males within a clan are related (Barrett 2000). At permanent water sources, clans combine to form a band of approximately 60 individuals. Several such bands come together overnight to form a troop (Sigg and Stolba 1981).

A number of differences exist between hamadryas baboons and gelada baboons, which also have a multi-layered social structure. Unlike gelada baboons, female hamadryas baboons within harems are typically not closely related and spend little time socialising with one another (Barrett 2000). Furthermore, adolescent hamadryas baboon females become separated from their natal group upon being sequestered into harems by adult males. Such transfers have been interpreted as a means of preventing inbreeding (Sigg et al. 1982). The consequent lack of kin support results in greater control by male hamadryas baboons over their females (Barrett 2000). Another point of difference between hamadryas baboons and gelada baboons is that gelada baboon harems sleep alone or in small clusters overnight and come together into large herds at feeding sites in the morning (Altman, S.A 1974). This is the opposite to the fusion-fission system employed by hamadryas baboons.

1.2.5 Physical appearance

Hamadryas baboons exhibit pronounced sexual dimorphism at maturity (Figure 1.2). This is typical of polygynous species (Kummer 1995). Although substantially smaller than the average size of baboons [i.e. 22 to 30 kg for males and 12 to 15 kg for females (Barrett 2000)] the hamadryas baboon is still large for a monkey.

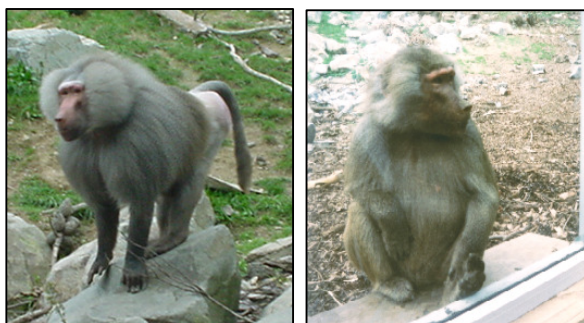


Figure 1.2. Adult male (left) and adult female (right) *Papio cynocephalus hamadryas* baboons

Adult male hamadryas baboons weigh approximately 17 kg (Barrett 2000) and may be 65 cm in height when seated (Sigg et al. 1982). Like other *Papio* subspecies, the male hamadryas baboon has immense upper canines that are used in antagonistic displays. These upper canines are kept sharp by a grinding action against a specially adapted lower tooth (Barrett 2000). A thick mantle of flecked hair capes the mature males shoulders and midriff, exposing a naked red posterior. Mantles develop between 6.8 and 10 years of age, during which time the male almost doubles in weight (Sigg et al. 1982). Until this time, the juvenile male is small and brown. Full maturity occurs between seven and 10.3 years of age (Sigg et al. 1982). It has been estimated that males may remain harem leaders for only three to six years before being defeated by a younger rival (Sigg et al. 1982).

Females at maturity have a coat of short brown hair, weigh 9 kg to 10 kg (Barrett 2000), and measure between 50 cm and 55 cm when seated (Sigg et al. 1982). Oestrus occurs at four to five years and pregnancy lasts approximately six months (Sigg et al. 1982). A female can give birth every 22 months, although this inter-birth interval can be shorter if an infant dies (Sigg et al. 1982). The duration of the oestrous cycle of hamadryas baboons, determined from a captive study, is approximately 30 days (with extremes ranging from 23 to 40 days) (Zuckerman and Parkes 1930, cited in Kummer 1968:176). A few days prior to ovulation, the sexual skin of all *Papio* females begins to swell and pheromone olfactory signals are produced (Kummer 1995), indicative of the female's reproductive condition. When a female is not in oestrus the sexual skin remains flat, and copulation is almost impossible (Kummer 1995).

Both males and females have dark to reddish hairless faces with dog-like muzzles (Barrett 2000). Hamadryas baboon pigmentation varies according to location, with those in the west of their natural range being considerably darker than those in the east (Kummer 1968). Periodic interbreeding with the darker anubis baboons (*Papio cynocephalus anubis*) may cause the dark pigmentation of the hamadryas baboon in the west (Kummer 1968). Adapted to ground living, hamadryas baboons have hands and feet specialised for walking, although they remain efficient climbers (Barrett 2000).

1.3 STUDY COLONY

1.3.1 Wellington Zoo

The present behavioural study was conducted at Wellington Zoo, where a colony of 14 hamadryas baboons was transferred from a small and old enclosure into a purpose-designed exhibit almost 23 times the size of the former enclosure.

Wellington Zoo focuses on providing “safe natural environments for animals at risk”, with the hope that the public will “come away with a stronger appreciation of the world around us” (Wellington Zoo foyer display). As a member of the Australasian Species Management Program (ASMP), Wellington Zoo is co-operative in in-situ support programmes, gene-pool databases and other strategic planning. The zoo can receive additional assistance through specialist groups within the ASMP, such as that provided by Primate Tag, which offers expertise about individual species.

The new baboon enclosure is part of the Zoo's objective to gradually reduce its number of species, whilst grouping species according to geographic area and increasing the size and authenticity of the enclosures provided for its remaining inhabitants (G. Strachan, pers. comm.).

1.3.2 Previous enclosures

Wellington Zoo has housed hamadryas baboons for 30 years, during which time the colony has experienced three types of enclosures.

The initial colony was comprised of four individuals. Built at a time when zoos were measured according to the number of species they held in their collection (Tarpy 1993), the first enclosure was a small, basic concrete display. Directly adjoining the hamadryas baboon enclosure, in classic taxonomic arrangement (Tarpy 1993), was the chacma baboon (*Papio cynocephalus ursinus*) exhibit. The hamadryas baboon colony at this time was extremely agitated (G. Strachan, pers. comm.).

In 1987 the hamadryas baboons were relocated to a bigger enclosure that had been built in the 1930's as a tiger exhibit. They remained in this second enclosure until February 2000. New animals were introduced from Adelaide for the purpose of breeding. At this time, it was observed that young females, breeding for the first time, had limited reproductive success, there being numerous infant deaths (G. Strachan, pers. comm.). In 1994, when the colony had reached the enclosure's carrying capacity of 14, measures were taken to stop further reproduction and reduce the deleterious effects of inbreeding.

This second enclosure (Figure 1.3) was a rectangular outdoor exhibit measuring 12 metres by 9 metres, with a cement floor and central concrete, two-tiered platform. The sides and rounded roof were broad wire mesh. A rain shelter covered the den entrance and a resting bench that was set at approximately two-metre elevation against the back wall. Two separate, fully covered den areas were provided at the back of the enclosure, each containing two platforms for the animals to rest on. Two permanent wooden climbing structures were set on either side of the concrete platform.

Bark-chip was provided over approximately 60 percent of the total floor space to encourage foraging activities, which were enhanced by a daily scattering of grain mixture. In addition, leafy branches, rotting logs, pinecones, clumps of long grass and 'boomer' balls filled with seed mix were frequently provided as further enrichment.

1.3.3 New enclosure

Construction on the new enclosure began in 1999. At the time, there was concern that the baboons' existing enclosure might no longer have been structurally strong enough to house animals as robust as hamadryas baboons (G. Strachan, pers. comm.).

The new enclosure (Figure 1.4) was intended to provide space for the colony's expansion, through reproduction, to 30 to 35 individuals, as well as room to increase the gene pool by introducing individuals from captive colonies elsewhere. The purpose-built enclosure and den area were designed for ease of daily maintenance and hygiene. The new enclosure was intended to meet the animals' physical and emotional needs by providing

increased space and authentic enrichment in order to elicit species-typical behaviours. This is particularly relevant for non-human primates understood to suffer “social, physiological and intellectual pathologies when important environmental considerations are neglected” (McGrew 1981, cited in Chamove et al. 1982:308).

In an attempt to replicate the arid highlands of North Africa, this expansive new area was designed after considering other open-air baboon enclosures, specifically those at Yemen Zoo and Rhine Zoo (G. Strachan, pers. comm.). Set on a north-facing hillside, the sloping, irregularly shaped enclosure is fenced with an approximately five-metre high wire mesh, recessed 800 mm beneath ground level. The fence is topped with a metal barrier, angled inwards to prevent the animals from escaping. Fine electric wires sit below this upper metal barrier as an additional deterrent.

The large den area is in two sections. An outdoor covered area, containing a single wooden climbing structure, leads into a fully covered den area with resting benches set against the interior walls. The den area is the only part of the enclosure with concrete floors. The remainder of the area is predominantly grass, with bark-chip along the front of the enclosure. Refinement of antibiotics, and more sophisticated veterinary care, has reduced the need for sterile, disinfected enclosures (Hutchins et al. 1984) like those used in the past at Wellington Zoo to house baboons.

The enclosure encompasses a scrub vegetation area, an authentic dried-up creek bed, and the occasional mature tree. At the time of the data collection, a small pond existed towards the middle of the enclosure and a number of large boulders and logs were distributed around this area.

1.3.4 Reducing captivity stress

The new enclosure exemplifies numerous ways in which Wellington Zoo endeavours to reduce captivity stress and abnormal behaviour. For example:

- The enclosure design and additional enrichment is intended to stimulate natural behavioural patterns, such as foraging excursions (Sigg and Stolba 1981), by taking into account the species natural history (Duncan and Poole 1990), thereby better complementing the animals’ anatomical and behavioural adaptations (Hutchins et al. 1984);
- Ample room for the colony’s expansion is expected to prevent an ageing population, allow for an appropriate social setting and minimise aggression. For example, the interaction of adult male hamadryas baboons with immature conspecifics may reduce hostility and facilitate social interaction amongst adult males. This phenomenon has been referred to as “agonistic buffering” (Seyfarth 1978:244). In addition, wild sub-adult or adult hamadryas baboon males have been described as establishing their first bonds with immature females prior to forming harems (Sigg et al. 1982);
- The additional space also provides flight distance. This is especially relevant for hamadryas baboons whose flight response is heightened in captivity (Kummer and Kurt 1965);

- The enclosure is designed in such away as to provide areas of privacy for the animals, from both each other and the viewing public. Refuge areas, which are particularly important for primates, enable animals to distance themselves from dominant conspecifics, as they would in the wild (Bostock 1993);
- Staring is a threat gesture to many primates (Bostock 1993), including hamadryas baboons. The size of the new enclosure, which provides public viewing from only one side, enables the animals to distance themselves from such human disturbance (Bostock 1993);
- Observations by Wellington Zoo staff suggest that, the more naturalistic the enclosure, the greater the respect and consideration shown towards animals by the public. Visitor reaction towards inhabitants of the Great Ape House in Seattle support these anecdotal observations, in that naturalistic enclosures generated a more positive, less disruptive response towards the animals (Hutchins et al. 1984).

1.3.5 Daily husbandry

The daily husbandry routine and schedule remained constant between the former and new exhibit.

Food remnants and faeces were removed and each area's concrete surface was disinfected daily between 8:00 am and 10:30 am, during which time the animals were confined to each enclosure's den area.

Each morning, the animals received clean water and a main feed of fruits, cooked vegetables and porridge. A smaller afternoon feed of cooked vegetables was provided daily. Twice a week the animals' diet was supplemented with chicken pieces or hard-boiled eggs.

1.3.6 Colony demographics

At the time of the study, the colony consisted of 14 captive born individuals, ranging in age from 4.1 years to 32.8 years (Appendix A, Figure 6.1). Table 1.1 illustrates the age/sex classes present within the Wellington Zoo colony at the time of the study. These classes are based on age classifications and physical descriptions given by Sigg et al. (1982:475) and Abegglen (in press, cited in Sigg et al. 1982:475).

In line with observations made at London Zoo and Zurich Zoo, Wellington Zoo's hamadryas baboon colony had established harems (i.e. one-male units) comparable to harem organisation amongst wild populations (Kummer 1968). Each leader of the two established units within the colony had two associated females. These females could be identified because only their corresponding males led and herded them during the initial observation period. Such herding is a characteristic of male leadership (Kummer 1973). Additionally, these males were observed grooming their respective females, a practise rarely seen outside of sexual consortship (Seyfarth 1978).

The eldest colony member, a female, was a previous member of an existing harem. While still interacting socially with her former one-male unit leader, she exhibited much greater independence from him than did his current females. The remainder of the colony were immature and had not yet established, or been sequestered into, harems.

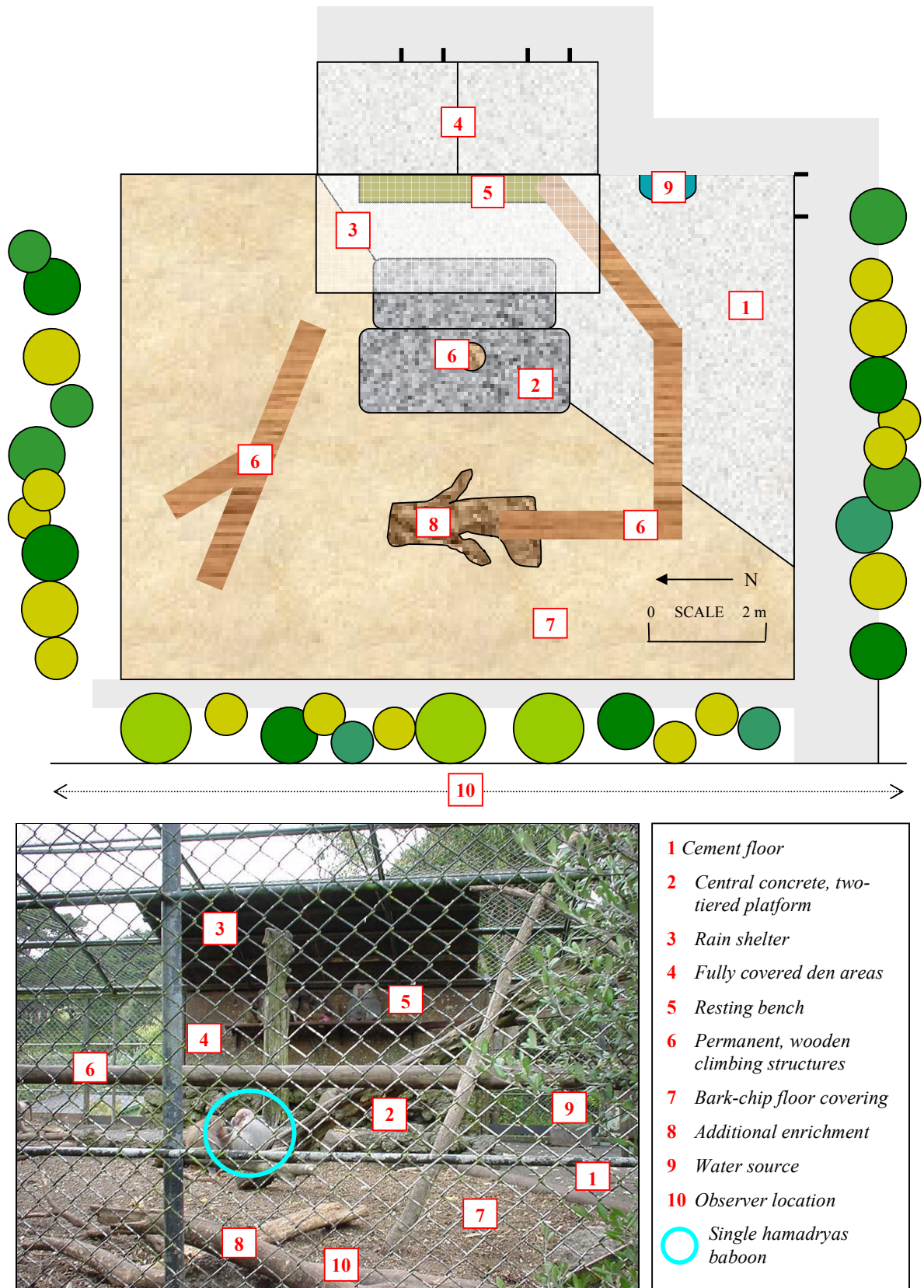
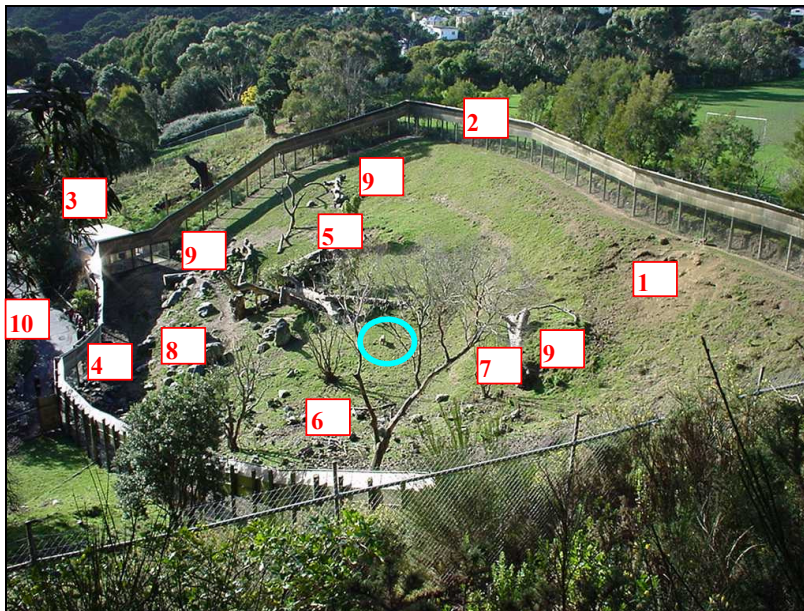
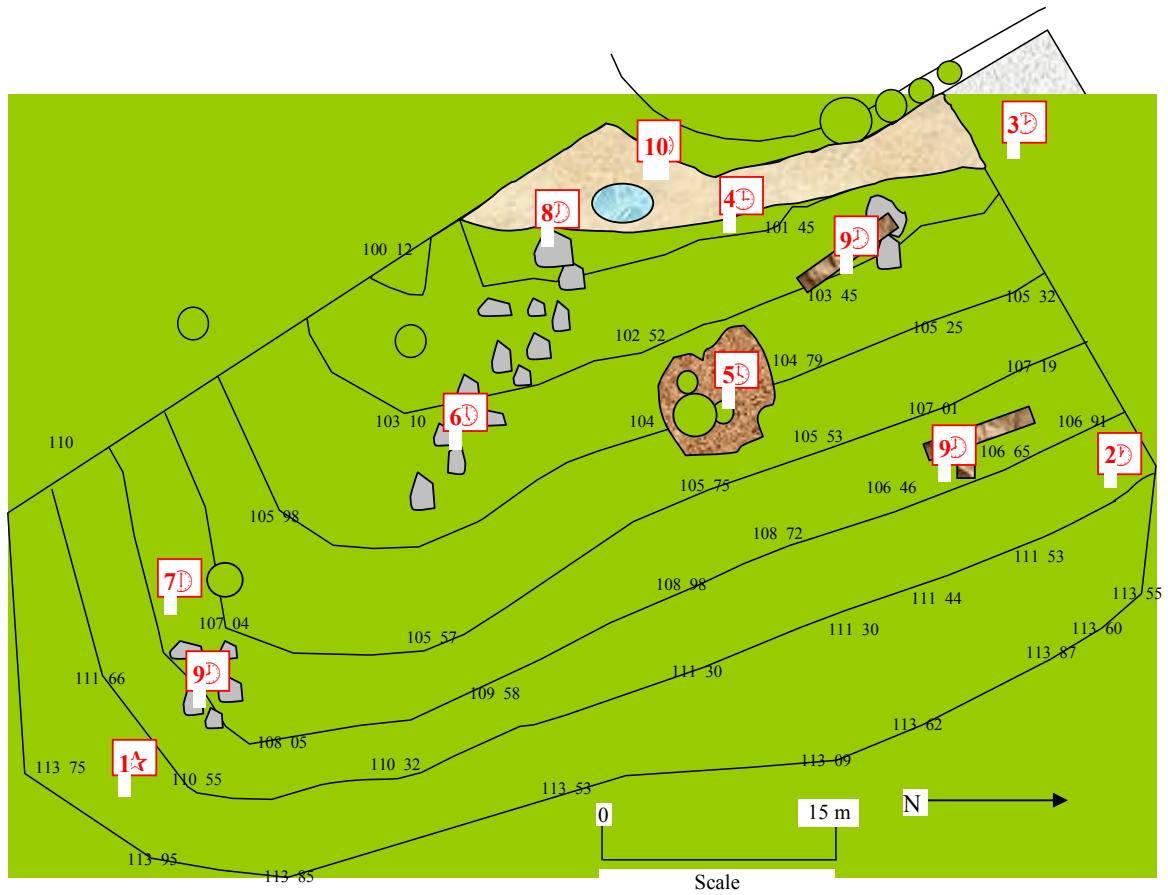


Figure 1.3. Overhead perspective and close-up photograph of the majority of the former enclosure, with corresponding key points



- 1 Sloping grass hillside
- 2 Baboon proof fence
- 3 Den area
- 4 Bark-chip
- 5 Scrub vegetation area
- 6 Dried-up creek bed
- 7 Mature trees
- 8 Small pond
- 9 Additional enrichment (large boulders and logs)
- 10 Observer location (glass viewing area)
- Single hamadryas baboon

Figure 1.4. Overhead topographic perspective detailing gradient and elevation, and distant photograph of the entire new enclosure, with corresponding key points

Table 1.1. Age/sex classifications of the Wellington Zoo hamadryas baboon colony at commencement of study compared with age/sex classifications for hamadryas baboons proposed by previous authors, as tabulated in Sigg et al. (1982:475).

Classifications	Abbreviated physical description derived from Sigg et al. (1982:475)	Age range (years)			Wellington Zoo*	Number at Wellington Zoo*
		Wild (estimated Sigg et al 1982)	ABEGGLEN (in press)	KUMMER (1968)		
Infant N	Hair predominantly black. Rounded head with short snout and pink face.	0-0.7	0-1.0	0-0.5	-	0
Infant B	Hair brown. Rounded head, short snout. 25 cm sitting height.	0.7-1.3	0-1.0	0.5-1.5	-	0
Juvenile 1	Snout length lengthens and head becomes more “dog-like”. Sitting height 30 cm. Males and females remain almost analogous.	1.3-3.0	1.0-2.5	0.5-1.5	-	0
Juvenile 2	Individual characteristics develop in both males and females. Sitting height 40 cm.	Female 3.0-4.3	2.5-3.7	1.5-2.5	-	0
		Male 3.0-4.8	2.5-4.0	1.5-2.5	4.1-4.4	2
Juvenile 3 females	Approaching adult size. First swellings begin. Sitting height 45-50 cm.	4.3-5.6	3.7-4.8	2.5-3.5	5.2-5.5	2
Juvenile 3 males	Hair lengthening around sides of face. Sitting height 50 cm.	4.8-6.8	4.0-5.5	2.5-3.5	5.1-6.1	2
Adult females	Regular cycling, pregnancy or lactation. Sitting height 50-55 cm.	5.6-	4.8-	5.0-	9.1-32.8	5
Sub-adult males	Development of mantle, with colour change from brown to silver grey. Hair around face remains undeveloped. Sitting height 50-60 cm.	6.8-10.3	5.5-10.0	3.7-7.0	6.6	1
Adult males	Fully developed mantle and hair around face. Mantle may be silver or brown, according to clan. Sitting height 65 cm.	10.3-	10.0-	7.0-	10.1 – 19.2	2

* Classifications based on ranges of age/sex from Sigg et al. (1982:475) and Abegglen (in press, cited in Sigg et al. 1982:475) and the corresponding physical description that fits each classification according to these authors.

1.4 THESIS OUTLINE, OBJECTIVES AND HYPOTHESIS

The primary objective of this investigation was to determine group and individual responses of focal animals to their new enclosure.

In addition to the primary objective, this investigation also aimed to:

- Provide further insights into how confinement alters animal behaviour. Such behavioural alteration is considered to be a challenging and ongoing problem (Morris 1964);
- Contribute to the limited body of empirical research on environmental enrichment in relation to captive *Papio* species (Kessel and Brent 1996); and,
- Generate implications for improving the management of captive *Papio* baboons.

Chapter 2 presents results and discussion in relation to the combined focal animal group. The specific objective of this chapter was to investigate the major responses of group-housed *Papio* baboons to broad scale environmental enrichment.

Ho: There is no change in the combined focal animals' behaviour between the former and new enclosures.

Ha: There is a difference in the behaviour of the combined focal animals between the former and new enclosures.

Ha₁: Upon relocation to the new, more expansive and naturalistic enclosure, the combined focal animals demonstrate a broader repertoire of species typical behaviour.

Ha₂: The provision of more space and areas of privacy in the new enclosure reduce the incidence of aggression and, consequently, the need for appeasement behaviour.

Ha₃: The provision of increased space, and the greater variety of environmental enrichment in the new enclosure, impact upon levels of social interaction.

Chapter 3 presents results and summary discussion of the response of each of the five focal animals. The specific objective of this chapter was to develop a more detailed understanding of the impact of broad scale environmental enrichment on group-housed *Papio* baboons.

Ho: There is no difference in the responses of individual focal animals to relocation.

Ha: There is a difference in the responses of the individual focal animals to relocation.

Ha₁: Gender plays a part in the different responses of the individual focal animals.

Ha₂: Age plays a part in the different responses of the individual focal animals.

Chapter 4 summarises some of this investigation's major findings. It also records implications derived from this investigation for the purpose of:

- Further improving the management and welfare of the Wellington Zoo hamadryas baboon colony;
- Improving the management and welfare of captive *Papio* baboon colonies in their existing enclosures at other facilities; and,

- Providing insights and suggestions for other facilities considering enclosure redesign for group-housed *Papio* baboons.

This final chapter also details suggestions for future studies, as well as the problems and limitations encountered during the current investigation. It is anticipated that any resulting refinements and improvements of the methods used will facilitate future studies.

CHAPTER 2: METHODOLOGY

2.1 FIELD METHODS

2.1.1 Preliminary observations

Wellington Zoo was visited regularly from mid November 1999 until the end of March 2000, directly before and directly after the animals were relocated.

An initial two weeks of observation was used to gain familiarity with the former exhibit and the new enclosure under construction, as well as to learn how to recognise each of the 14 colony members. Identifying features (Appendix A, Figure 6.1) were discovered for each individual in the same manner as described by Kummer (1995) in relation his studies of the Zurich Zoo hamadryas baboon colony.

This initial observation period was also used to determine the best sampling times to use for data collection. Due to regular keeper disturbance (specifically, enclosure maintenance and feeding between 8:00 am and 10:30 am daily, during which time the animals were confined to the den area), it was decided that the first daily sampling period should commence at midday in order to minimise the influence of such disturbance on the colony's behaviour.

The two data collection periods were 12:00 noon to 2:00 p.m. and 3:00 p.m. to 5:00 p.m. Starting data collection at midday also accommodated daylight saving. When daylight saving ended, the two sample periods were adjusted to 11:00 a.m. to 1:00 p.m. and 2:00 p.m. to 4:00 p.m. Consequently, they remained uninterrupted by the keepers, whose schedules remained unchanged.

2.1.2 Behavioural repertoire

This initial observation period allowed for the construction of a preliminary ethogram. It was decided that this behavioural repertoire should be constructed specifically for the Wellington colony. Construction of an independent ethogram by the observer meant that behaviours were not incorrectly assigned to written descriptions by previous authors. In addition, the Wellington Zoo colony's behavioural repertoire was unusual as it was developed in the absence of infants and juvenile class 1 individuals.

The behavioural repertoire was constructed to a detail appropriate for video analysis, videotaping being the principle method of data recording. Many behaviours from other ethograms, such as one finger grooming (Kummer and Kurt 1965), would not have been clearly discernible through a video camera lens and the wire mesh viewing area of the former enclosure. The ethogram employed was flexible and allowed for new behaviours as they arose. This was critical in comparing repertoire changes as a consequence of the colony's relocation. The complete ethogram (Table 2.1) was finalised with consideration to observer fatigue, which is affected by the number, rapidity and subtlety of the categories recorded (Altman, J 1974).

Only positively identifiable vocalisations were recorded, specifically those that clearly accompanied agonistic, appeasement and solicitation displays. It is difficult to assign a precise meaning to calls, regardless of species, and there is lack of information supporting intentional knowledge-sharing by non-human primates (Cheney et al. 1996).

Table 2.1. Full ethogram derived from behavioural observations of the Wellington Zoo *Papio cynocephalus hamadryas* colony. Asterisks mark behaviours that can be undertaken “socially”.

“MAJOR” ACTIVITY	“MINOR” ACTIVITY		DESCRIPTION
	Abbreviation	Behaviour	
Solicitation			Sexual and pseudo-sexual behaviours
	Dpg	* Visual presentation	Displaying genitals - hindquarters turned towards receiver, giver crouched or standing.
	Dpr	* Receiving visual presentation	Responding to visual presentations – observing, turning away, touching ‘giver’s’ rump or tail, lips quivering.
	Dvg	* Vocal presentation	Clucking or shrieking, generally (although not exclusively) associated with visual presentation.
	Dvr	* Receiving vocal presentation	Responding to vocal presentations - observing, turning away, touching ‘giver’s’ rump or tail, lips quivering.
	M	* Mating	Partaking in heterosexual mating activity.
	Ms	* Simulated mating	Partaking in homosexual mating activity.
	Thg	* Tail holding	Actively herding another by the tail.
	Thr	* Herded by tail	Actively being led by the tail.
	P	* Pursuit	Following the same path.
Agonistic			Hostile or fearful behaviour
	Avi	* Visual aggression	Displaying aggression without physical contact - brow-raising, teeth bearing, ground-beating, lunging and ‘feinting’.
	Aph	* Physical aggression	Displaying aggression by physical contact, fighting and contesting, or attempting physical contact by prolonged chasing.
	Avo	* Vocal aggression	Shrieking, screeching and kecking, generally (although not exclusively) associated with aggression.
	Sh	* Shaking	Vigorously shaking branches, structural poles or wire netting.
	Av	* Avoidance	Moving or turning away upon approach of conspecific, or avoiding crossing path of conspecific.
	Sp	* Supplanting	The approach or activity of sample animal causes another to move or turn away.
	Mi	* Intervention	Physically intervening in hostile situations – forcing contesting conspecifics apart by positioning or chasing.
	Al	* Alert	Being alerted by disturbance - upright and vigilant, facing direction of disturbance.
Feeding activity			Behaviour relating to the investigation, acquisition and consumption of food
	Fe	Feeding	Taking repetitive bites from a single item of food.
	F	Foraging	Repeatedly searching for small items of food and transferring these directly to the mouth.
	Rout	Reaching out	Extending arm beyond peripheral fence to grasp at surrounding vegetation.
	LF	Relocating food	Moving food from one location to another - walking, running or climbing.

“MAJOR” ACTIVITY	“MINOR” ACTIVITY		DESCRIPTION
	Abbreviation	Behaviour	
Feeding activity cont.	Hu	Hunting	Pursuing and/or catching wild birds or insects.
	Dr	Drinking	Lapping from water sources provided.
	Li	Licking	Licking inanimate items.
Grooming			Preening behaviours
	GS	Grooming self	Continuous period of self-preening.
	Gor	* Receiving grooming	The focal animal groomed by one or more others.
	GOg	* Grooming other	The focal animal, alone or accompanied by an additional individual/s grooms another.
Appeasement			Non-grooming examples of calming, pacifying and reassuring gestures (including reconciliation between former opponents) following threatening events
	TaAp	* Tactile appeasement	Physical placation by non-aggressive mutual hugging or touching.
	VoAp	* Vocal appeasement	Vocal placation, generally (although not exclusively) associated with tactile appeasement.
Inactivity			Stationary and without any of the other behaviours
	S	Sitting	Sitting without additional activity - eyes open or closed.
	R	Resting	Lying, sleeping, or basking in sunshine, without additional activity.
	SS	Standing still	Standing (quadrupedal or bipedal) for longer than a momentary pause and possibly observing.
Locomotion			Moving from one destination to another
	W	Walking	Terrestrial quadrupedic locomotion - walking on four legs.
	Ru	Running	Terrestrial quadrupedic locomotion - running on four legs.
	C	Climbing	Ascending or descending from climbing structures or wire mesh.
	J	Jumping	Leaping onto, down from, or over structures.
	Wob	Relocating object	Moving non-food items from one location to another - walking, running or climbing.
	Tm	* Troop movement	Moving with majority of colony in same direction.
Play	Tp	* Troop patrol	Moving in line ahead by groups larger than a single harem.
			Non-food enrichment-directed and play behaviours
	ME	Manipulating environment	Forcibly rocking, pushing or tipping substantial enrichment items - logs, branches, water dishes - within enclosure.
	Di	Digging	Burrowing into bark chip or soil using front feet.
	Pf	* Play fighting	Tussling or challenging without physical or vocal aggression.
Out of sight	Sch	Scraping	Scraping non-edible objects along the ground.
	OoS		Periods where observation not possible

2.1.3 Data collection period

The animals were observed for data collection in their former enclosure between 2 December 1999 and 28 January 2000, with a total of eighty-four 10 to 15 minute samples collected. During this observation period a total of 2402 “minor” behaviours were sampled.

Data collection resumed upon the animals’ release into their new enclosure after two weeks of confinement in the den area, which overlooks the entire new exhibit. This two weeks of confinement was intended to habituate the animals to their new surroundings, to ensure their health after transportation and to reduce their stress associated with the relocation (G. Strachan, pers. comm.). Sampling began on 29 February 2000, a day after their release from the den area (whereupon the animals’ daily husbandry routine resumed) and concluded on 31 March 2000. A total of seventy-five 10 to 15 minute focal samples from the new enclosure were collected incorporating a total of 2122 “minor” behaviours. Sampling of the animals in their new enclosure was done rapidly upon their release in order to sample during mid summer only. This was intended to reduce the influence of weather conditions on the colony’s behaviour.

2.1.4 Sampling method

Focal samples were selected as the method of behavioural sampling for this investigation specifically because this type of sampling provides data relevant to a broad range of questions (Altman, J 1974). It was anticipated that these samples would also provide additional information relevant to future investigations of the study colony.

Initial sampling was done manually with a digital stopwatch and notepad. After a number of samples had been attempted the results were reviewed and their verity questioned. It was apparent that the simultaneous recording of an animal’s actions or interactions, duration of each behaviour and social state was not feasible. Consequently, in order to improve the accuracy of the data, sampling was repeated with a hand-held video camera (a Sony Handycam Video 8). (An additional benefit of using a video camera was the ability to make frequent and accurate audio notes). Data from the samples was transferred manually from the video record onto spreadsheet for analysis (Table 2.2).

The video record provided information on the number and categories of behaviours represented per sample. Video sampling also provided the length of each behaviour. This was determined by playing the video on slow play and then pausing at the end of each activity and noting the time on the video recorder. From this, the duration of individual behaviours could be calculated to the nearest second.

2.1.5 Duration of samples

Focal samples were intended to be 15 minutes in duration, during which time the focal animal was to be followed as closely as possible. Due to the nature of the analysis, samples between 10 to 15 minutes were also considered viable if, as a result of disturbance, 15-minute samples could not be completed. The most frequent type of disturbance was weather related, specifically rain, which prevented video sampling, as it would have damaged the camera. To get enough samples of each animal given such disturbances, the order of individual sampling was rotational so that the same animal was not continuously missed when disturbance caused a premature end to daily sampling.

Table 2.2. Example of focal sample data recorded on spreadsheet

Animal name: Toka Date: 29/02/00 Temperature: 26.6 °C Cloud cover: 5% + Wispy Time: 3.55 Rainfall: Nil Other Comment: Light, warm breeze Humidity: 54%

Behaviour	Location	Giver	Receiver	Receivers behaviour	Finishing time on counter	Duration of behaviour	Other comment
Tp	2P-5P				0:00:00		
					0:00:13	00:00:13	Following group down left-hand side periphery.
S c	5P				0:00:24	00:00:11	Next to Inubus.
W	5P-12				0:00:38	00:00:14	Down to join others near to den opening.
SS c	12				0:00:48	00:00:10	Standing within 2m of Jackie and Sinead. All other troop members gathering in same general area.
Ru	12P				0:00:53	00:00:05	Down onto flat area outside dens. Whole troop still gathering.
Out of sight	12				0:01:19	00:00:26	
S c	Den (doorway)				0:01:41	00:00:22	Grouped with Randy.
W + P	12-5	Tina	Toka	Walking	0:01:52	00:00:11	
S	5				0:02:08	00:00:16	Inubus and Tina close-by.
Tp	5-5P				0:02:28	00:00:20	Not included in Tp were Rameses, Pharaoh and Suzy.
S c + Rout	5P				0:03:02	00:00:34	With Tina + Beth. Others approaching. Toka joining them in move up periphery.
Tp	5P – 2P				0:03:15	00:00:13	Tp involving majority of troop. Not Suzy or Randy.
S c	2P				0:03:22	00:00:07	Grouped together with most of troop except Suzy and Randy.
W	2P				0:03:28	00:00:06	
S	2P				0:03:39	00:00:11	
S c	2P				0:04:20	00:00:41	Human Disturbance at back periphery. Majority of troop Tp across back periphery past Toka to right of enclosure.
W	2P...9P				0:05:12	00:00:52	
W + P	9P...24P	Pharaoh	Toka	Walking	0:06:07	00:00:55	Pharaoh starting to pursue Toka as Toka walks past him at the periphery.
S c	24P				0:06:40	00:00:33	Sitting grouped with Pharaoh.
S	24P				0:06:43	00:00:03	
W	24P-23P				0:06:46	00:00:03	Walking down periphery
Ru	23P-21P-21				0:06:54	00:00:08	Running down periphery. Other troop members approaching 24P along back periphery in Tp.
W	21				0:07:03	00:00:09	
SS	21				0:07:14	00:00:11	
S	21				0:07:53	00:00:39	
W + F	21-22-16				0:08:14	00:00:21	
S	16				0:08:55	00:00:41	In shade. Chewing but not actively Fe or FI.
W	16-22				0:09:04	00:00:09	
Fe	22				0:09:34	00:00:30	Sitting, then standing browsing leaves of tree.
W + F	22-21				0:09:49	00:00:15	
GS	21				0:09:50	00:00:01	
Tp	21-20				0:09:57	00:00:07	Tp includes Tina and Randy + others. Most of troop moving over to den side.
F	20				0:10:08	00:00:11	Standing alone.
Tp	20-19				0:10:22	00:00:14	
Tp + Ru	19-19P				0:10:25	00:00:03	
Out of sight	19P				0:10:34	00:00:09	
TP	19P-12P outside den				0:10:41	00:00:07	
S	12P				0:10:41	00:00:00	With majority of troop close by but > 2m away.
W	12P-5P-5				0:11:20	00:00:39	
S	5				0:12:12	00:00:52	Majority of troop in den. Randy, Jackie, Tina and Albert close to Toka but not grouped with him.
Tp	5-5P-1P				0:12:25	00:00:13	Tp includes Randy, Jackie and Tina.
S c	1P				0:13:01	00:00:36	Within 2m of Tina.
Tp	1P-2P				0:13:12	00:00:11	
S c	2P				0:13:32	00:00:20	Human disturbance at back periphery.
S	2P				0:13:54	00:00:22	
Tp	2P...4P				0:14:21	00:00:27	Human disturbance at back periphery continues.
Tp + Ru + Al	4P...3P				0:14:24	00:00:03	Troop on alert with majority on Tp.
Tp	3P-2P-5P				0:14:49	00:00:25	
S	5P				0:15:00	00:00:11	

2.1.6 Observer location

The observer stood at the most accessible viewpoint i.e. the front of each enclosure, whilst taking video samples (Figures 1.3 and 1.4). It was from this position that the least obstructed view was available over the greatest distance. In addition, as the animals were accustomed to the public standing in front of their enclosures, it was considered that this position would generate the least observer disturbance.

Binoculars (Vivitar PV Services 10x25) were used to supplement the zoom capability of the video camera and were most frequently employed to locate the animals before sampling. A tele-conversion lens (Sony VCL-2046C), which increased the camera's magnification by a factor of two, was required when the animals were relocated to the new exhibit in order to record the same degree of detail over a larger space.

2.1.7 Additional information

Temperature, humidity and any additional comments on relevant external variables were also recorded. While these variables have not been directly investigated, they were frequently referenced in order to ensure that an extreme external variable, such as a particularly disruptive crowd, had not obviously influenced an individual's behaviour when this appeared erratic or uncharacteristic (Table 2.2). Information on the location of the animals during sampling was also recorded through a grid system for use in future investigations.

2.1.8 Focal animals

Five of the 14 baboons within the Wellington Zoo colony were selected for daily sampling in order to collect enough data on each animal, within a fixed time period, for meaningful comparisons between the enclosures. The five animals were chosen specifically to:

- Minimise changes in behaviour that may have occurred across the four month total sample period if maturing juveniles had been selected;
- Establish methods that can be repeated for comparison in the future on the same five individuals, thereby limiting maturation as an influencing variable.

The colony's two most mature males (i.e. Abu and Randy) were selected, along with one adult female from each of their harems (i.e. Sinead and Tina respectively). The fifth focal animal, Toka, the next oldest male and a bachelor, was selected due to ease of identification.

2.2 DATA ANALYSIS

2.2.1 Statistical methods

Raw data was processed through a categorisation software programme written specifically for this study by A. Ruthven in consultation with the observer. This created data sets suitable for analysis by the statistical software programme, SAS. Activity between the enclosures was tested against a null hypothesis of zero change, which would be expected if the new enclosure had little or no impact upon the colony's behaviour. A level of $p < 0.05$ was considered significant for all tests.

2.2.2 Patterns of behaviour for the combined focal animals

Analysis of the combined data for the five focal animals was intended to illustrate overall variations in the focal group's behaviour upon relocation. The animals' behaviour was considered in six ways:

2.2.2.1 Extent of behavioural repertoire

The combined focal animals' repertoire of behaviours prior to and following the colony's relocation was compared to determine the influence of relocation on the composition of behaviours in each repertoire.

2.2.2.2 Comparison of the number of "major" and "minor" behavioural categories occurring per unit of time between the former and new enclosures

A logit model was used to compare the odds of each of the "major" and "minor" behavioural categories occurring per sample between the former and new enclosures. This was then used to give an indication of the differences in the average number of these behavioural categories occurring per sample. For these comparisons only fifteen-minute video samples were used.

Note: The n-values can differ between "major" and "minor" behavioural analyses because an animal could have performed, consecutively, two or more "minor" behaviours under one "major" category (e.g. *grooming self* and *grooming other*). In such cases, these were recorded as a single instance of a "major" behaviour (e.g. "grooming" behaviour).

2.2.2.3 Comparison of overall occurrence of "major" and "minor" behaviours between the former and new enclosures

Chi-square tests comparing two log linear models were undertaken to test for significant differences in the overall occurrence of each behaviour between the former and new enclosures. This method of statistical analysis accounted for individual personalities within the combined focal animal data. Analyses was undertaken at two levels:

(i) Relative occurrence of "major" behaviours i.e. broad behavioural categories, namely: Solicitation, agonistic, feeding activity, grooming, appeasement, inactivity, locomotion, play, and time spent out of sight.

(ii) Relative occurrence of “minor” behaviours i.e. activity recorded with more specific detail, categorised within subgroups of appropriate “major” behavioural headings (Table 2.1.).

Notes:

“Out of sight” was recorded as both a “major” and a “minor” behaviour (i.e. it was the only “minor” behaviour for this “major” category). This meant that the overall occurrence of behaviours could be determined using 100 percent of available data from both “minor” and “major” behaviours.

As noted in 2.2.2.2 above, n-values may differ between “major” and “minor” analyses when two or more “minor” behaviours belonging to the same “major” category were performed consecutively.

2.2.2.4 Comparison of mean bout lengths of “major” and “minor” behaviours between the former and new enclosures

The average length of each “major” and “minor” behaviour was determined for comparison between the enclosures. Analysis of variance (ANOVA) was used to determine significant differences in the mean duration (or bout length) of each behaviour between the two enclosures. Only those occurrences for which the complete duration was visible were processed. Consequently, the first and last behaviours of each video sample, and those behaviours occurring immediately before and after the animals moved “out of sight”, were not processed.

Differences in mean bout length, together with changes in overall occurrence, of both “major” and “minor” behaviours were used to infer changes in the relative repetition of these behaviours between the former and new enclosures (Table 3.2).

2.2.2.5 Comparison of overall occurrence of social states between the former and new enclosures

Each of the animal’s activities was allocated to one of three categories according to the animal’s social situation. The latter was recorded next to each behaviour and additional comments on the spreadsheets. Chi-square tests comparing two log linear models were used to test for significant differences in the overall occurrence of each social state between the two enclosures. For the purposes of this investigation, these categories were as follows:

(i) “Solitary” - the animal was acting independently at a distance of greater than two metres from its nearest neighbour;

(ii) “Grouped” - the animal was acting independently within two metres of the nearest individual. This inter-individual distance was selected as one-male hamadryas baboon units have been observed to sit at a mutual distance of approximately two meters. Harem leaders rigorously enforce this segregation (Kummer and Kurt 1965) as mixing of units can lead to competition for females (Kummer 1968); and,

(iii) “Social” - the definition of social time used corresponds with that employed by Kummer and Kurt (1965:71). For the purposes of this investigation, an animal was considered to be acting socially if its behaviour was “motivated by the presence or the behaviour of a partner of the same species”, according the observer’s experience and regardless of its nearest neighbour distance. The ‘receiver’ is defined as experiencing the action

of the ‘giver’. Asterisks on the ethogram (Table 2.1) above indicate behaviours that could be undertaken socially by the focal animals.

Note: N-values for social states deviate from those collected for “major” and “minor” behaviours because social states did not necessarily change when an animal’s activity changed. Furthermore, n-values differ between the overall occurrence of “minor” behaviours and social states because an animal may have been performing two or more “minor” behaviours consecutively whilst remaining in a single social state.

2.2.2.6 Comparison of mean bout lengths of social states between the former and new enclosures

The average length of “solitary”, “grouped” and “social” behaviours was determined using the same method outlined for “major” and “minor” behaviours above. The ANOVA method was used to determine significant differences in the mean duration of each social state between the former and new enclosures.

2.2.3 Patterns of behaviour for the individual focal animals

Detailed analysis of the behaviour of each of the five focal animals was undertaken in the same manner outlined above (refer 2.2.2.1 to 2.2.2.6). This analysis was intended to ascertain individual responses to the focal animals’ relocation and, therefore, a more detailed understanding of the response of captive group-housed hamadryas baboons to broad-scale environmental enrichment.

CHAPTER 3: RESULTS

PATTERNS OF BEHAVIOUR FOR THE COMBINED FOCAL ANIMALS

3.1 EXTENT OF BEHAVIOURAL REPERTOIRE

The behavioural repertoire (Table 2.1) encompassing the full range of behaviours observed at the two study sites consisted of a total of nine “major” and 44 “minor” behaviours (including “out of sight”). For the combined focal animals, each of the nine “major” behaviours was recorded in both of the study sites. However, only 33 (i.e. 75 percent) of the “minor” behaviours were common to both enclosures. The remaining behaviours i.e. the 11 recorded exclusively in a single enclosure, were relatively evenly distributed between the two enclosures. Five of the 11 [i.e. *tail holding* and *herded by tail* (“solicitation” behaviours), *shaking* (“agonistic” behaviour), *vocal appeasement* (“appeasement” behaviour) and *digging* (“play” behaviour)] were recorded exclusively in the former enclosure. The remaining six [i.e. *hunting* and *licking* (“feeding activity” behaviours), *relocating object*, *troop movement* and *troop patrol* (“locomotion” behaviours) and *scraping* (“play” behaviour)] were recorded in the new enclosure.

3.2 COMPARISON OF THE NUMBER OF “MAJOR” AND “MINOR” BEHAVIOURAL CATEGORIES OCCURRING PER UNIT OF TIME BETWEEN THE FORMER AND NEW ENCLOSURES

Table 3.1 illustrates the mean number of “major” and “minor” behavioural categories occurring per fifteen-minute sample in the former and new enclosures for the combined focal animals. It also shows the p-values for statistical tests that compare the odds of each “major” and “minor” behavioural category occurring per sample in the former and new enclosures.

Logit model comparison for the combined focal animals determined that the odds of each of the “major” behavioural categories occurring per sample decreased significantly upon the colony’s relocation (χ^2 test, $p=0.0186$). Using the same test, no statistically significant difference was determined for the odds of each of the “minor” behavioural categories occurring per sample (χ^2 test, $p=0.4220$).

Table 3.1. Mean number \pm SE and p-value of odds of occurrence of a) “major” and b) “minor” behavioural categories occurring per 15 minute focal sample.

		a) “Major” behaviour	b) “Minor” behaviour
Former enclosure	No. of samples	57	57
	Mean \pm SE	5.175 \pm 0.143	7.842 \pm 0.320
χ^2 test p-value		0.0186	0.4220
New enclosure	Mean \pm SE	4.870 \pm 0.193	7.768 \pm 0.392
	No. of samples	69	69

3.3 COMPARISON OF OVERALL OCCURRENCE OF “MAJOR” AND “MINOR” BEHAVIOURS BETWEEN THE FORMER AND NEW ENCLOSURES

Figures 3.1 and 3.2 illustrate the mean percentage time per sample, in lieu of overall occurrence, spent by the combined focal animals on each “major” and “minor” behaviour respectively. The standard deviation of many of the mean values is large, indicative of a wide distribution in percentages. The statistical method employed to determine differences between the enclosures did not test for significant differences in the mean percentage values across the samples. Rather, chi-square comparisons of two log linear models were used to test for differences in the overall occurrence of each behaviour. As such, significant differences were found between the former and new enclosures for some “major” and “minor” behaviours for which little difference in mean and general spread was discernible from the graphical representation deemed most appropriate. (Precise p-values and degrees of freedom are recorded in Appendix B, Tables 5.1 and 5.2).

3.3.1 Relative occurrence of “major” behaviours

Analysis of the combined focal animal data, to determine changes in the overall occurrence of each “major” behaviour, produced statistically significant differences in six of the nine behavioural categories investigated (Figure 3.1).

Analysis indicated that the overall occurrence of *locomotion* and *out of sight* significantly increased upon the colony’s relocation (χ^2 test, $p = 0.0000$ and $p = 0.0000$ respectively). Conversely, the overall occurrence of *solicitation*, *grooming*, *inactivity* and *play* behaviour were all found to be significantly reduced upon the colony’s relocation (χ^2 test, $p = 0.0000$, $p = 0.0000$, $p = 0.0000$, $p = 0.0000$ respectively). The overall occurrence of *aggression*, *feeding activity* and *appeasement* by the combined focal animals did not significantly change between the former and new enclosures (χ^2 test, $p > 0.05$).

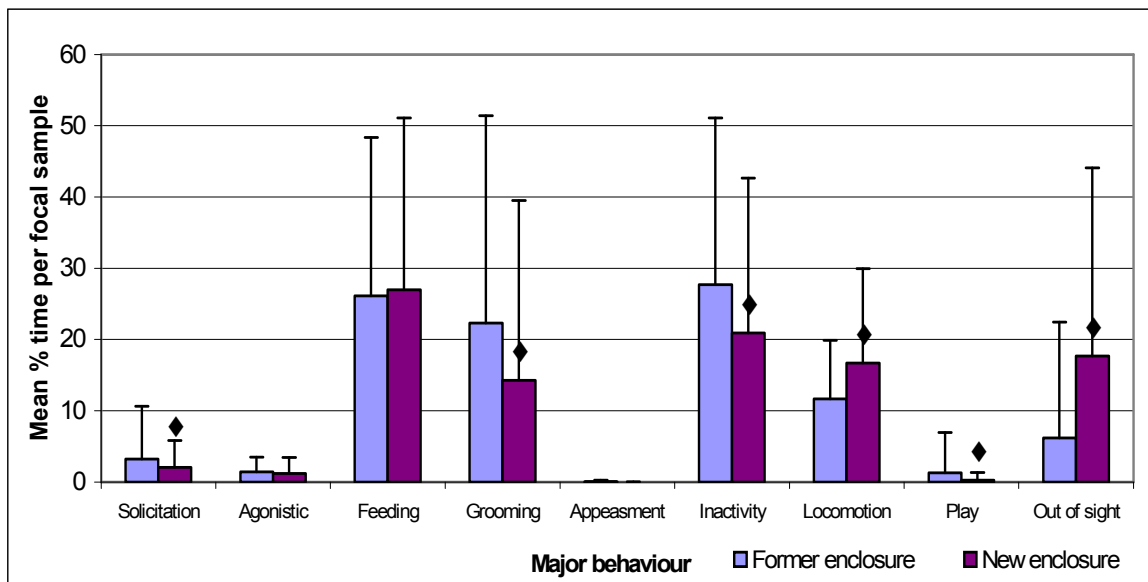


Figure 3.1. Activity budget for “major” behaviours for the combined focal animal group. Mean percentage time \pm SD per 10 to 15 minute focal sample for each “major” behaviour are shown. ♦ Indicates “major” behavioural categories with significant differences in overall occurrence between the former ($n=2,105$) and new ($n=1,754$) enclosures, where n = the total number of “major” behaviours sampled.

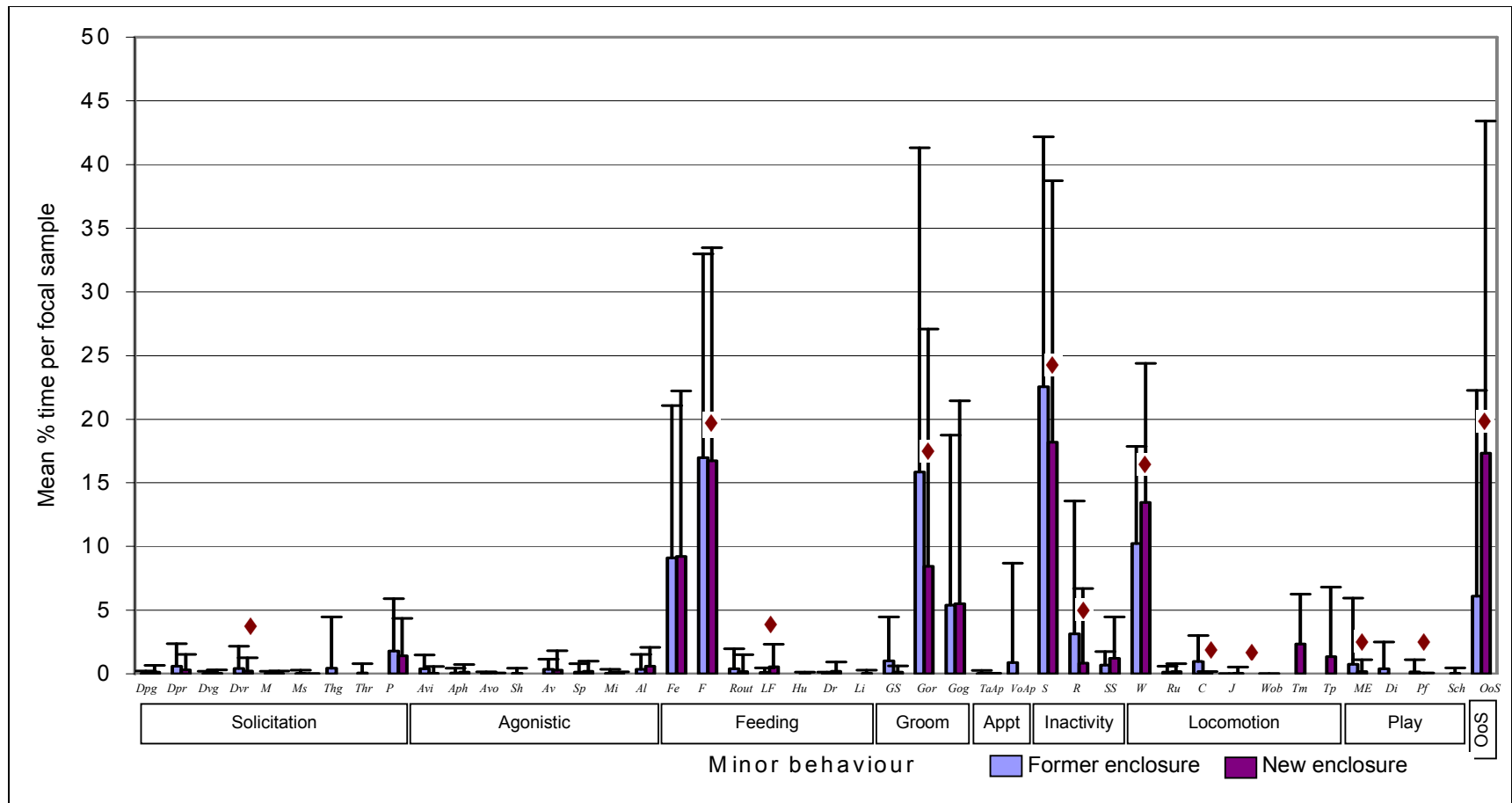


Figure 3.2. Activity budget for "minor" behaviours for the combined focal animal group. Mean percentage time \pm SD per 10 to 15 minute focal sample for "minor" behaviours are shown. "Minor" behaviours are grouped according to "major" behaviour categories. ♦ Indicates "minor" behavioural categories with significant differences in overall occurrence between the former ($n=2,402$) and new ($n=2,122$) enclosures, where n = the total number of "minor" behaviours sampled.

3.3.2 Relative occurrence of “minor” behaviours

Chi-square tests comparing two log linear models to determine changes in the overall occurrence of “minor” behaviours by the combined focal animals, produced significant differences between the former and new enclosures in 13 of the 33 “minor” behaviours common to both enclosures (Figure 3.2).

Of the seven “minor” behaviours categorised under the heading of “solicitation” in common to both enclosures, only one was found to demonstrate a significant difference in overall occurrence between the enclosures. Specifically, the occurrence of *receiving vocal presentation* declined significantly upon the animals’ relocation (χ^2 test, $p = 0.001$).

There were no statistically significant differences between the enclosures in the overall occurrence of any of seven the “minor” behaviours categorised as “agonistic” in common to both enclosures (χ^2 test, $p > 0.05$).

Two significant differences in overall occurrence were found between the enclosures among the five “minor” “feeding activity” behaviours seen to occur in both enclosures. *Foraging* and *relocating food* were found to significantly increase upon the colony’s relocation (χ^2 test, $p = 0.0294$ and $p = 0.0098$ respectively). The overall occurrence of three other feeding behaviours common to both enclosures (i.e. *feeding*, *reaching out* and *drinking*) did not significantly differ upon the colony’s relocation to the new enclosure (χ^2 test, $p > 0.05$).

Statistical differences between the former and new enclosures were found in two of the three “grooming” behaviours, of which each was seen to occur in both enclosures. The combined focal animals were found to perform significantly less *grooming self* upon relocation (χ^2 test, $p = 0.0000$). Similarly, the overall occurrence of *receiving grooming* declined (χ^2 test, $p = 0.0000$). There was no evidence of a significant difference in the overall occurrence of *grooming other* between the enclosures (χ^2 test, $p = 0.6432$).

The overall occurrence of *tactile appeasement* behaviour, the only “minor” “appeasement” behaviour in common to both enclosures was equally low in both enclosures, with no evidence of a statistically significant difference (χ^2 test, $p = 0.1553$).

Further chi-square tests comparing log linear models indicated significant differences between the enclosures in *sitting* and *resting* (χ^2 test, $p = 0.0002$ and $p = 0.0172$ respectively). Results indicated that the overall occurrence of these “minor” behaviours significantly decreased upon the combined focal animals relocation. There was no evidence of a relationship between time spent by the combined animals of the third “minor” “inactivity” behaviour i.e. *standing still* and the enclosure in which the behaviour was recorded (χ^2 test, $p = 0.0929$).

Significant differences were found between the enclosures in the overall occurrence of three of the four “locomotion” behaviours common to both exhibits. Log linear modelling determined that *walking* and *jumping* significantly increased in the new enclosure (χ^2 test, $p = 0.0000$ and $p = 0.0365$ respectively). By contrast, the overall occurrence of *climbing* behaviour significantly declined upon the animals’ relocation (χ^2 test, $p = 0.0000$). No significant difference between the enclosures was found for the percentage of time spent by the combined focal animals *running* (χ^2 test, $p = 0.01181$).

Chi-square tests comparing log linear models of the two “minor” “play” behaviours common to both enclosures, *manipulating environment* and *play fighting*, indicated that the overall occurrence of these behaviours was significantly lower upon the colony’s relocation (χ^2 test, $p = 0.0228$ and $p = 0.0139$ respectively).

3.4 COMPARISON OF MEAN BOUT LENGTHS OF “MAJOR” AND “MINOR” BEHAVIOURS BETWEEN THE FORMER AND NEW ENCLOSURES

3.4.1 Relative bout lengths of “major” behaviours

The distribution of bout lengths (i.e. duration in seconds) of “major” behaviours for the combined focal animals is illustrated in Figure 3.3. Analysis of variance failed to show any statistically significant difference in the mean duration of the eight “major” behaviours, for which there was sufficient data, between the former and new enclosures (ANOVA, $p > 0.05$). There were insufficient instances of “appeasement” behaviour in the former enclosure ($n_f = 1$) to test for a significant difference in mean bout length. (Precise p-values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.3).

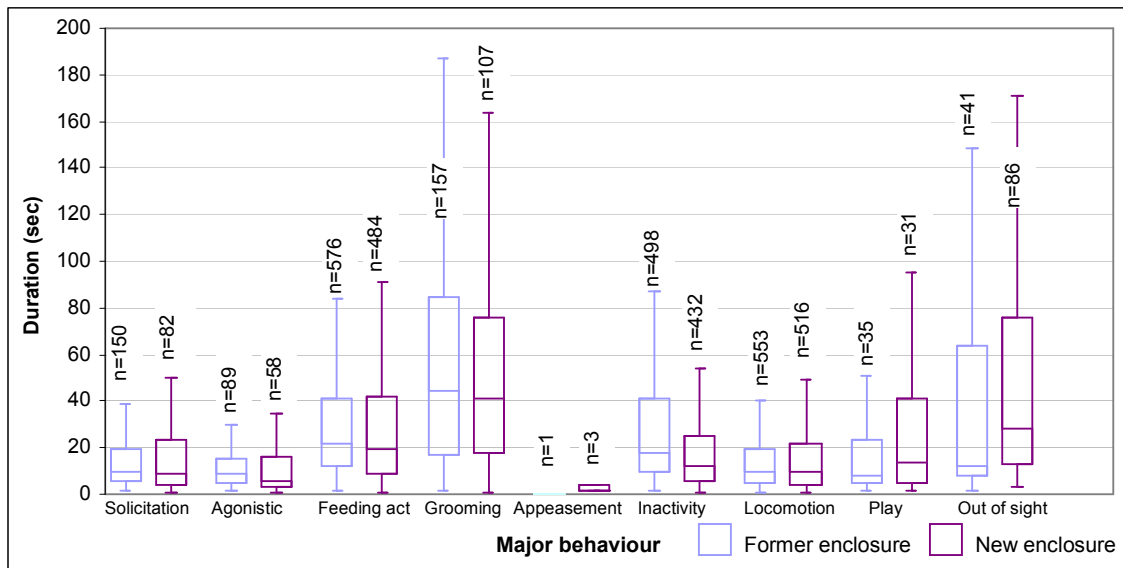


Figure 3.3. Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “major” behaviours for the combined focal group whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. N = the total number of “major” behaviours sampled.

3.4.2 Relative bout lengths of “minor” behaviours

The distribution of bout lengths (i.e. duration in seconds) of “minor” behaviours for the combined focal animals is illustrated in Figure 3.4. (Precise p-values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.4).

Analysis of variance comparing the mean bout lengths of “minor” behaviours between the former and new enclosures for the combined focal animals produced significant differences in only three “minor” behaviours common to both enclosures.

Five of the seven “minor” behaviours categorised as “solicitation” common to both enclosures were found to have no statistically significant differences in mean duration between the former and new enclosure (ANOVA, $p > 0.05$). The mean length of *pursuit* behaviour was statistically greater in the new exhibit (ANOVA, $p = 0.0032$). There were insufficient instances in the new enclosure of the remaining “minor” “solicitation” behaviour that occurred in both enclosures, i.e. *simulated mating* ($n_n = 1$), to test for a significant difference in mean bout length.

No significant differences in mean bout length were found for “minor” “agonistic” behaviours common to both enclosure for which data permitted statistical testing (ANOVA $p = 0.05$). There were insufficient episodes in the new enclosure of *visual aggression* ($n_n = 1$), *vocal aggression* ($n_n = 1$) and *intervention* ($n_n = 1$) by the combined focal animals to test for a significant difference in mean bout length between the former and new enclosures.

The difference between the two enclosures in the mean duration of “minor” behaviours categorised under “feeding activity” remained insignificant for all but *reaching out*. For this “minor” behaviour, it was found that the new enclosure elicited bouts of significantly greater mean duration (ANOVA, $p = 0.0236$).

Analysis of variance showed no relationship between the mean lengths of *grooming other* and *receiving grooming* and the enclosure in which they were observed (ANOVA, $p > 0.05$). The difference between the enclosures in the mean bout length of *grooming self* approached significance (ANOVA, $p = 0.0553$). In this instance, the lowest mean value was found in the new enclosure.

There were too few occurrences in the former enclosure of *tactile appeasement* ($n_f = 1$), the only “appeasement” behaviour recorded in both enclosures, to statistically compare mean bout lengths.

No significant differences in the mean bout lengths of “minor” behaviours categorised as “inactivity” were found between the enclosures (ANOVA, $p > 0.05$).

Of the four “minor” behaviours categorised as “locomotion” common to both enclosures, one significant difference was found in mean bout length. Analysis of variance indicated that the mean length of *climbing* was significantly reduced upon the combined focal animals relocation to the new enclosure (ANOVA, $p = 0.0009$). There were too few instances of *jumping* ($n_f = 1$, $n_n = 1$) in each enclosure to determine a significant difference in mean bout length.

The mean duration of *manipulating environment* and *play fighting* (the “minor” “play” behaviours common to both enclosures) did not significantly differ upon the colony’s relocation (ANOVA, $p > 0.05$).

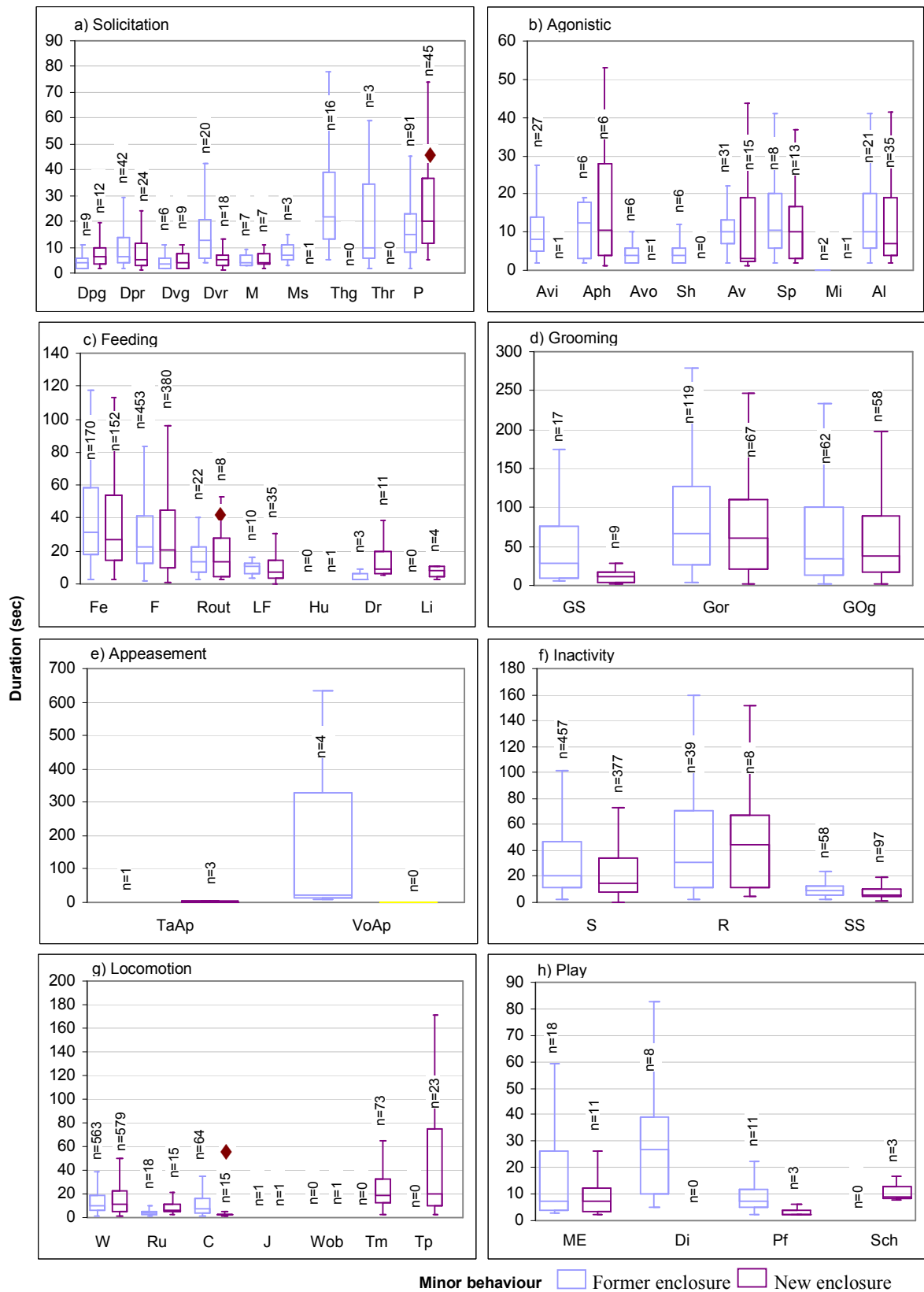


Figure 3.4a to 3.4h. Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for the combined focal group whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.

3.5 COMPARISON OF OVERALL OCCURRENCE OF SOCIAL STATES BETWEEN THE FORMER AND NEW ENCLOSURES

Figure 3.5 illustrates the mean percentage of time per sample, in lieu of overall occurrence, spent by the combined focal animals in “solitary”, “grouped” and “social” states. (Degrees of freedom are recorded in Appendix B, Table 6.5). Chi-square comparison of two log linear models, to determine changes in overall occurrence between the enclosures, produced significant results for each of the three social states. The occurrence of “solitary” increased significantly upon the colony’s relocation (χ^2 test, $p = 0.0000$). By contrast, the combined focal animals were found to spend significantly less time in “grouped” and “social” states in the new enclosure (χ^2 test, $p = 0.0000$ and $p = 0.0003$ respectively).

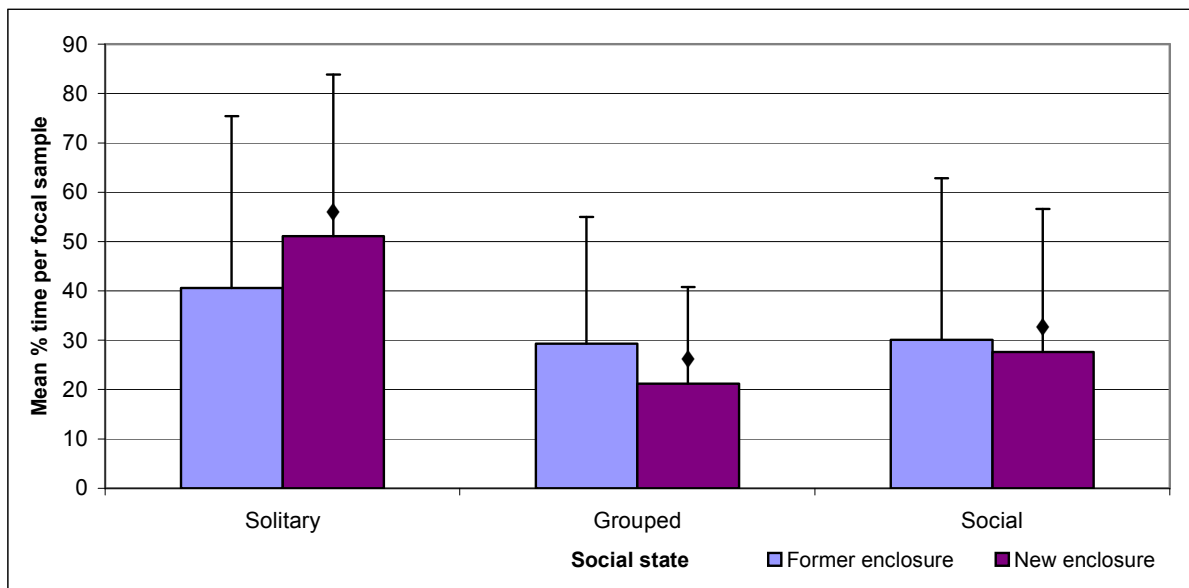


Figure 3.5. Activity budget of social states by the combined focal animals. Mean percentage time \pm SD per 10 to 15 minute focal sample for each social state are shown. ♦ Indicates social states with significant differences between the former ($n = 1750$) and new ($n = 1509$) enclosures, where n = the total number of states sampled.

3.6 COMPARISON OF MEAN BOUT LENGTHS OF SOCIAL STATES BETWEEN THE FORMER AND NEW ENCLOSURES

Figure 3.6 illustrates the distribution of bout lengths (i.e. duration in seconds) of “solitary”, “grouped” and “social” states for the combined focal animals in the former and new enclosures. (Precise p -values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.6). Statistical testing showed no significant difference in the average length of “solitary”, “grouped” or “social” states between the former and new enclosures (ANOVA, $p > 0.05$).

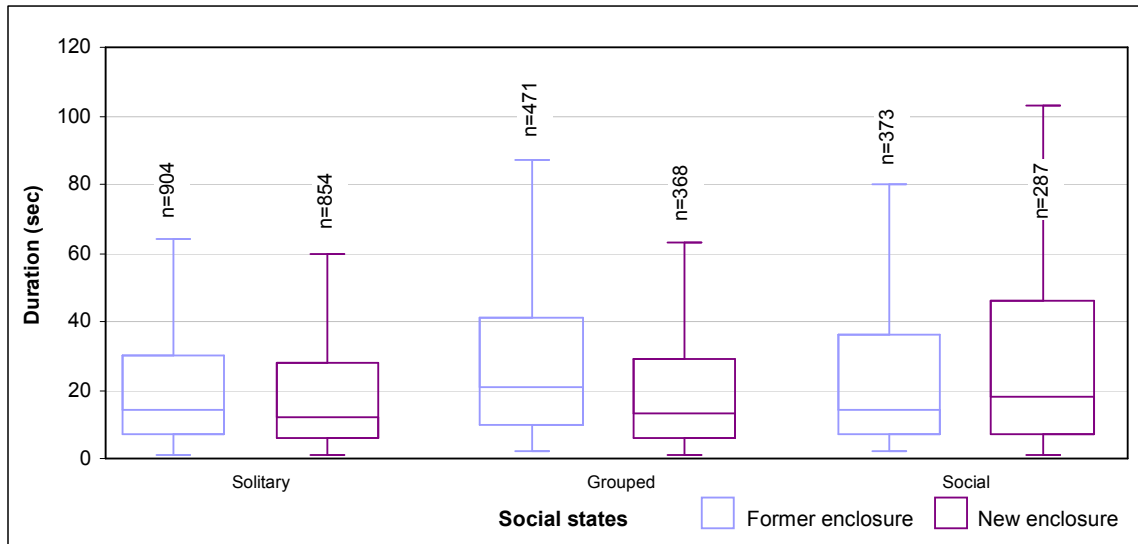


Figure 3.6. Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “solitary”, “grouped” and “social” states for the combined focal group whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. States were only included if their complete duration was visible. N = the total number of states sampled.

3.7 DISCUSSION ON THE COMBINED FOCAL ANIMALS' PATTERNS OF BEHAVIOUR

While the activity budgets of free-ranging baboons are shaped by “scheduled” activities, (i.e. those that must occur at a particular time and place, such as reaching safe sleeping sites before darkness), these animals also live in a structurally complex natural environment, experiencing temporal, geographic and habitat variability over space (Altman, S.A 1974:237). In addition, free-ranging baboons are exposed to localised hazards, including remoteness from water, carnivores and inter-group competition (Altman, S.A 1974). Differences in the ecological conditions experienced by groups within a local population may cause variations in intra-specific behaviour and group composition (Altman, S.A 1974).

Unfortunately, the environment provided in captivity is often comparatively simple and physically restrictive (Kessel and Brent 1996). The animals are sheltered from predation and the elements, and are provided with food and water (Kessel and Brent 1996). Their activity may come to be dictated by the daily schedule of husbandry and feeding. The time, type and location of food given to captive animals, for example, may be highly predictable (Hutchins et al. 1984). Hygiene, economy and exhibition requirements are such that it is not always possible to give captive animals a constantly changing environment and variable daily schedule (Morris 1964). Captive animals, therefore, may have everything they need to stay highly active with the notable exception of variability, novelty, and stimuli (Morris 1964).

Hamadryas baboons are opportunists and, as such, neophilic behaviour (including investigation and exploration) is predominant (Morris 1964). Unlike specialists, which fare better in the rigid and restricted captive environment, neophilic animals abhor inactivity (Morris 1964). Enclosure enrichment may serve to reduce such monotony, whilst providing additional exercise (Kessel and Brent 1996), and alleviating aberrant behaviours (Hutchins et al. 1984).

3.7.1 Extent of behavioural repertoire

In the wild, animals that live in diverse and unpredictable natural habitats may evolve extensive behavioural repertoires (Hutchins et al. 1984). By contrast, in captivity, the extensive repertoires necessary for coping with diverse surroundings in the wild, including exploratory, harvesting and danger response behaviours, are not required (Kummer 1995).

Upon the animal's relocation to the new, more naturalistic and expansive enclosure, it was anticipated that the size of the colony's behavioural repertoire would expand as the animals experienced greater spatial variation (i.e. “multi-dimensional surfaces of different materials such as rocks, soil, water and vegetation” (Hutchins et al. 1984:29).

The total repertoire of “minor” behaviours was found to increase only marginally upon the colony's relocation. Of the 11 “minor” behaviours recorded in a single exhibit, five were exclusive to the former enclosure. The remaining six behaviours were recorded exclusively in the new enclosure.

Of more significance than the extent of the behavioural repertoire at each enclosure was its composition. Four of the five behaviours exclusive to the former enclosure (i.e. *tail holding*, *herded by tail*, *shaking* and *digging*) have been attributed below to the physical restrictions imposed by the former enclosure.

By contrast, five of the six behaviours recorded exclusively in the new enclosure (i.e. *hunting*, *licking*, *troop movement*, *troop patrol* and *scraping*) have been described below as indicative of an increase in either favourable, natural exploratory tendencies or cohesive group behaviour.

Consequently, while the size of the colony's behavioural repertoire may not have expanded upon the animals' relocation, many of the disadvantageous behaviours occurring in the former enclosure were not replicated in the new enclosure. At the same time, the new enclosure elicited a broader repertoire of favourable behaviours.

It is to Wellington Zoo's credit that combatant, self-directed behavioural abnormalities, including self orality, hair pulling and eating, faeces manipulation and food regurgitation, highlighted in another study of *Papio* baboons (Brent and Belik 1996), were not recorded in either the former or the new baboon enclosures at Wellington Zoo. Such self-directed behaviours may be an indicator of frustration (Bareham 1973), or stress (Castles and Whiten 1998).

The provision of structural enrichment, resulting in more available space and escape routes (Kessel and Brent 1996), may have contributed to the absence of these stress-related behavioural abnormalities noted above.

In addition, the provision of varying degrees of foraging enrichment in each enclosure may also have reduced the likelihood of such behavioural abnormalities. In a study of single-housed female olive baboons (*Papio hamadryas anubis* [= *Papio cynocephalus anubis*]) and guinea baboons (*Papio hamadryas papio* [= *Papio cynocephalus papio*]), abnormal behaviours (including those listed above, as well as behaviours such as bizarre postures and pacing) were found to significantly decline upon the provision of increased foraging opportunities (Brent and Long 1995).

Additionally, abnormal sexual behaviour is likely to have been minimised by the provision of an appropriate social grouping (with consideration to the 'carrying' capacities of both enclosures) i.e. abnormal social groupings may generate aberrant activities (Morris 1964). For example, in captivity, single gender groupings of many species may produce abnormal sexual behaviour (Morris 1964). A non-human primate example of this involved two captive male orang-utan (*Pongo pygmaeus*) housed in a single enclosure, resulting in homosexual behaviour. This subsequently affected one of the male's ability to participate successfully in heterosexual activity (Morris 1964).

3.7.2 Comparison of the number of "major" and "minor" behavioural categories occurring per unit of time between the former and new enclosures

Each of the nine "major" behavioural categories on the complete ethogram was recorded in both the former and new enclosures. There was no obvious reason for the significant decline in the odds of each "major" behavioural category occurring per sample upon the colony's relocation.

No significant difference was found between the enclosures in the odds of each of the “minor” behavioural classifications occurring per sample. This indicated that the number of “minor” behaviours per sample for the combined focal animals did not change significantly upon the colony’s relocation.

3.7.3 Comparison of overall occurrence of “major” and “minor” behaviours between the former and new enclosures

Upon relocation to the more naturalistic and spacious enclosure, the behaviour of the combined focal animals at Wellington Zoo was seen to change in a variety of ways. These are detailed below and summarised in Figure 3.7.

3.7.3.1 “Solicitation” behaviour

The overall occurrence of “solicitation” in samples of the combined focal animals was found to significantly decrease upon the colony’s relocation. Heightened sexual behaviour found in captive hamadryas baboons has been related to greater attention being paid towards conspecific pen-mates, as a result of extra time and energy available as a consequence of the restrictive captive environment (Kummer 1995). Consequently, a reduction in “solicitation” upon the colony’s release into the new enclosure (with its increased complexity) can be regarded as a positive, albeit indirect, result of the relocation. More specifically, this reduction can be attributed to a decline in the mean percentage occurrence per sample of *receiving vocal presentation* and the absence of *tail holding* and *herded by tail* by the combined focal animals upon relocation.

Because of its low incidence of occurrence, the statistically significant reduction in *receiving vocal presentation* is best explained by considering the behavioural response of individual focal animals.

Tail holding and *herded by tail* (i.e. the giver and receiver forms of the same activity) were both recorded exclusively in the former enclosure. The function of these two “minor” behaviours can be likened to neck biting. Male hamadryas baboons threaten their mates when their units’ behavioural or spatial integrity has been compromised (Kummer 1968), for example:

- When the female has reached a separation distance of four to ten meters (Kummer and Kurt 1965);
- When she interacts with a conspecific beyond her immediate unit (Kummer 1968); or,
- If she was to let an ‘outsider’ come between herself and her unit leader (Kummer 1968).

The most serious form of threat administered by a unit leader in such cases is neck biting (Kummer 1968). Such behaviour exemplifies that the cohesion of a one-male unit is mostly reinforced by the aggressive herding behaviour of its leader (Kummer 1968). Kummer (1995) noted the absence of neck biting as a form of punishment for wandering females amongst the hamadryas baboon colony at Zurich Zoo. He attributed this to spatial confinement that prevented the females from straying. The opposite appears to be true for the Wellington Zoo colony when they were confined to the former, small enclosure. In this exhibit, the two mature focal males were recorded on several occasions administering neck bites to females in their respective harems. (Neck biting was recorded under the “minor” behaviour *physical aggression*). Such episodes were frequently followed by the

females walking or running in *pursuit* of their aggressor. Similar behaviour has also been observed in the wild (Kummer 1995). In the same way, *tail holding* and *herded by tail* episodes within the Wellington Zoo colony were frequently accompanied by the *pursuit* of the male by the female. Consequently, it would appear that *tail holding* and *herded by tail* behaviours serve a similar cohering function. This was reinforced by the observation that males are always the givers and never the receivers of this particular herding behaviour, just as neck bites are only administered by males for the reasons noted above. The observer suggests that neck biting and *tail holding* behaviour occurred in the former enclosure because of the reduced inter-individual distance between rival males relative to the new enclosure. The fact that social partners of many taxa, including primates, often prefer to remain together in order to reduce conspecific aggression (Cowlshaw 1999) would tend to support this contention.

3.7.3.2 “Agonistic” behaviour

The overall occurrence of “agonistic” behaviour was recorded at equally low levels in both the former and new enclosure. This was contrary to this study’s hypothesis that the provision of more space and areas of privacy would reduce the likelihood of hostility. No significant difference in overall occurrence of any of the seven “minor” “agonistic” behaviours common to both enclosures was discernible upon the colony’s relocation. A similar result i.e. where agonistic behaviour was found to remain unchanged upon the provision of toys as enrichment into a colony of captive *Papio* baboons, was reported by Brent and Belik (1996).

Physical fighting by hamadryas baboons is uncommon (Kummer 1973). Baboons avoid aggressive encounters whenever possible because, in the course of an aggressive episode, females may become isolated from their unit leader and forcefully sequestered into another harem (Sigg et al. 1982). However, Kummer and Kurt (1965) observed that threatening, submissive and flight behaviours occurred more often in Zurich Zoo’s captive hamadryas baboon colony than by their wild counterparts. In addition, captive adult baboons have been found to be more aggressive than baboons in the wild (Kummer 1973). Consequently, it had been expected that aggressive confrontations involving adult focal animals sampled at Wellington Zoo would be especially intensified in the former enclosure because the animals remained in full sight of one another and had little room to escape conflict. The latter was used to explain intensive confrontations in captive langurs (*Trachypithecus* sp.) (Dolhinow 1972). The observer proposes three reasons for the low overall occurrence of “agonistic” behaviour in focal samples of the combined focal group, as follows:

- (i) The provision of woodchip ground litter was shown to lower “agonistic” behaviour in seven of the eight non-human primate species investigated by Chamove et al. (1982). This outcome was further enhanced with the provision of grain or mealworms to the litter layer (Chamove et al. 1982). In a similar way, the provision of a woodchip litter layer, including grain mixture, in both enclosures featured in this study, was likely to have assisted in reducing levels of aggression.
- (ii) The isolation of both the former and the new baboon enclosures at Wellington Zoo from other species may also have minimised agonistic episodes. When the behaviour of a captive animal is frustrated by the presence of other animals in adjacent cages, aggression may be directed at pen-mates (Bareham 1973; Morris 1964).

(iii) The provision of an appropriate social setting, in addition to minimising the likelihood of abnormal sexual behaviour, may also have contributed to levels of aggression lower than expected in each enclosure. At the time of the current investigation, there were enough adult females within the Wellington Zoo colony for each of the two mature males to establish harems of naturalistic size. An example of an inappropriate social setting for hamadryas baboons, resulting in intensive aggression, occurred at London Zoo in the 1920s. In 1925, a naturalistic hamadryas baboon exhibit was opened with approximately 94 males and only six females. Notwithstanding that 30 more females were introduced into this colony in 1927, a great many deaths were reported to have occurred as the colony's males fought over possession of an insufficient number of females (Bostock 1993).

Shaking was the only "agonistic" behaviour recorded exclusively, (albeit infrequently), in one enclosure i.e. the former enclosure. One way in which animals may cope with a restricted environment, such as the former enclosure, is to perform 'vacuum' behaviours i.e. undertake normal responses to subnormal stimuli (Morris 1964). In the absence of correct stimuli, the range of factors that cause a response gradually increases (Bareham 1973). In the wild, some primates shake branches, to divert attention away from their group, when confronted with a stimulus such as a potential threat (Public Education Signage, Taronga Zoo, Sydney Australia). In the former enclosure, some troop members were seen to vigorously shake roof beams, even though their view beyond the enclosure was obstructed. By contrast, in the new enclosure, the sloped bank enabled greater views over a broader area. This meant that the colony could effectively survey the adjacent surroundings and see that no foreign troops, or other possible threats, were present. Any decline in the repertoire of "agonistic" behaviour upon the colony's relocation (such as the absence of *shaking*) can be viewed as favourable because aggression is stressful and dangerous (Castles and Whiten 1998).

3.7.3.3 "Feeding activity" behaviour

There was no significant difference between the former and new enclosures in the overall occurrence of "feeding activity" amongst the combined focal animals.

"The proportion of time spent feeding probably reflects the relationship between several factors, including the richness of food resources, their spatial proximity, the processing time required to utilize them, and the metabolic requirements of the animals" (Altman, S.A 1974:238). As the feeding schedule and process remained largely unchanged between the former and new enclosures, and the animals were provided with a majority of their food requirements, it was of no surprise that the overall occurrence of "feeding activity" did not change significantly upon the colony's relocation. The absence of a statistically significant difference in the "minor" behaviour *feeding* between the enclosures reinforces this contention.

Upon the combined focal animal's relocation, an increased amount of time was spent *foraging*. The new enclosure provided a greater assortment of foraging opportunities including grass, a shrub area and soil, as well as a bark chip litter layer (similar to that provided in the former enclosure). In this way, the new enclosure provided increased opportunities for the animals to display *foraging* behaviours in variety of ways more closely approximating those of free-ranging baboons in both quantity and form (Brent and Long 1995). Foraging occupies the greatest proportion of time in the activity budgets of wild baboons (Castles and Whiten 1998).

Distortions in a captive animal's natural activity patterns may be stressful to that animal and this may lead to behavioural abnormalities (Chamove et al. 1982). The provision of food, in particular, may deprive captive animals of the opportunity to seek their own food and, consequently, activities that promote a "sense of purposefulness" (Bostock 1993:70). An increase in *foraging* effort can, therefore, be viewed as a successful outcome of the colony's relocation, as the new levels of *foraging* in the new enclosure moved towards those in the wild. *Papio* species spend up to 70 percent of their time on the ground searching for food (Kessel and Brent 1996:37). Other studies have shown that feeding enrichment may increase the time spent foraging in a variety of non-human primates (Brent and Long 1995).

In the new enclosure, which offered increased foraging opportunities and a greater variety of objects, the overall occurrence of *relocating food* was found to significantly increase. The animals also began transporting non-edible items around their enclosure (i.e. *relocating object*). Logically, one could have been expected that the confinement of the former enclosure would see the animals move desired objects more frequently than in the new, more expansive enclosure in order to keep them away from potential competitors in close proximity. The increase in the overall occurrence of *relocating food*, in particular, in the new enclosure would appear to contradict the contention that spatial dispersion should increase where feeding competition is high (Cowlshaw 1999). However, in an investigation of the feeding behaviour of free-ranging desert baboons (*Papio cynocephalus ursinus*), feeding competition was found to effect spatial behaviour during foraging and, specifically, increase inter-individual distances (Cowlshaw 1999). The overall occurrence of *foraging* by the combined focal animals increased in the new enclosure. A subsequent increase in feeding competition may explain why the focal animals began to relocate food, and other (non-edible) items, more frequently upon the their relocation.

Upon the colony's relocation to the new enclosure, two additional "minor" "feeding activity" behaviours were recorded. Firstly, one animal was observed on a single occasion *hunting* a bird. In the same way, wild hamadryas baboons occasionally catch hares, young antelopes or locusts (Kummer 1995). Infrequent occurrences of *hunting* by the Wellington Zoo baboons was anticipated for the same reasons that hunting levels of wild hamadryas baboons are low [i.e. whilst males are most suited to hunting, in doing so, they would leave their females vulnerable to attack (Rosen 1974); furthermore, as baboons lack the social ability to surrender food, this method of obtaining food would be inefficient (Kummer 1995)]. Secondly, focal animals were recorded in two samples *licking* the new enclosure's glass viewing window. (*Scraping* non-edible objects along the ground - a "play" behaviour - was also observed exclusively, albeit infrequently, in the new enclosure). Under restricted, stable conditions such as in the former enclosure, exploration is unlikely to reveal anything new (Kummer 1995). However, the new enclosure offered opportunities for oral and manual exploration of unique surfaces (i.e. *licking* and *scraping*). Such exploration provides animals with the opportunity to discover new ways of processing food and alternative means of survival (Kummer 1995).

3.7.3.4 "Grooming" behaviour

Upon relocation to the more naturalistic enclosure, the combined focal animals were found to spend significantly less time overall on "grooming". Despite grooming, through the process of ritualisation, having the additional

function of appeasement (Kummer 1995), there was nothing in the data to suggest that the decline in “grooming” by the combined focal animals evidenced a decline in “appeasement” gestures upon the colony’s relocation.

While a reduction in “grooming” does not correspond directly with a similar decline in “agonistic” behaviour, a reduction the overall occurrence of *receiving grooming* can be attributed, at least in part, to reduced competition among males over their respective females as a result of the increased space and physical complexity of the new enclosure. As four of the five focal animals were members of a one-male unit, significantly more *receiving grooming* prior to relocation was consistent with the findings of Kummer (1973) that male-female pairs of hamadryas baboons groomed more when they could see a rival. This relates to the ‘early bird principle’ amongst hamadryas baboons, in which competitors are inhibited “by a perceived relationship between a subject and an object” (Kummer 1973:229) (in this instance, the subject was a male and the object its female). The above situation also illustrates how, in such a triadic situation (i.e. of subject, object and competitor), the subject may become less inhibited (Kummer 1973). For example, he may interact significantly more with his female (Kummer 1973). The relatively small size and physical simplicity of the former enclosure made it easier for colony members to see each other.

By contrast, the overall occurrence of *grooming other* remained unchanged upon the colony’s relocation. Together, a reduction in the overall occurrence of *receiving grooming* and no change in the overall occurrence of *grooming other* between the enclosures indicated that some of the five focal animals began grooming outside of their respective units more frequently upon relocation to the new enclosure. This is supported by results for individual focal animals.

In the new enclosure, the combined focal animals were found to spend significantly less time on *grooming self*. This correlates to the findings of Brent and Belik (1996:83) that increased enrichment for captive *Papio* baboons, resulting from the provision of manipulable objects, caused a reduction in similar self-directed behaviour (in this particular study “bite nails, groom self, lick self, manipulate self, play with self, scratch self”).

3.7.3.5 “Appeasement” behaviour

No change was discernible in the overall occurrence of “appeasement” behaviour between the former and new enclosures.

The overall occurrence of (non-grooming) *tactile appeasement*, which include gestures of reconciliation, was equally low in both the former and new enclosures. This finding correlates with the equally low levels of aggression in each of the enclosures.

Vocal appeasement was recorded exclusively, and infrequently, in samples in the former enclosure. This may have been related to the limitations of the audio recording capability of the video camera i.e. *vocal appeasement* may have been ‘missed’ simply because of the greater distances in the new enclosure.

3.7.3.6 “Inactivity” behaviour

The overall occurrence of “inactivity” by the combined focal animals was found to decrease upon the colony’s relocation. In the study referred to above (Brent and Belik 1996), the provision of toys for enrichment purposes was also found to reduce similar inactive behaviours amongst captive *Papio* species. Excessive inactivity has been shown to be common in captive animals due to predictable and often inappropriate captive environments (Hutchins et al. 1984). Consequently, decreased “inactivity” can be viewed as a positive effect of enrichment (Brent and Long 1995).

In particular, the combined focal animals spent significantly less time *sitting* and *resting* in the new enclosure. It is thought that these two responses were a consequence of more time spent on *foraging* and associated “locomotion”. This is supported by numerous examples in relevant literature whereby such decreased inactivity in captive primates has been associated with feeding enrichment. In an investigation of the effect of increased feeding enrichment in the behaviour of eight primate species, it was found that the percentage of time that the animals slept decreased for all species (Chamove et al. 1982). In another example, the provision of a PVC foraging device reduced inactive behaviours (i.e. bipedal stand, crouch, hang, lie, sit, stand) among four individually housed captive female baboons i.e. two olive baboons (*Papio hamadryas anubis* [= *Papio cynocephalus anubis*]) and two guinea baboons (*Papio hamadryas papio* [= *Papio cynocephalus papio*]) (Brent and Long 1995).

In contrast to the captive situation, foraging for food accounts for the majority of the activity budgets of wild baboons (Kessel and Brent 1996). The long daily march of hamadryas baboons serves the purpose of resource acquisition and reconnaissance (Sigg and Stolba 1981). Due to regular daily feeding at common locations within the new enclosure at Wellington Zoo, the animals are able to quickly locate (Sigg 1980) and consume the majority of the food provided (Chamove et al. 1982). Given the foregoing, it would seem unlikely that “inactivity” levels within the Wellington Zoo hamadryas baboon colony will reach naturally low levels under the current husbandry routine, despite the provision of a broader exploratory space.

3.7.3.7 “Locomotion” behaviour

Upon relocation, the combined focal animals were found to spend more time overall on “locomotion”. This increase in “locomotion” and, in particular, *walking* coincided with decreased “inactivity” and an increase in *foraging*. In addition, there was also the advent of several new, “minor” “locomotion” behaviours upon the colony’s relocation.

Increased “locomotion” can be regarded as a positive response of the animals to their new enclosure as it was indicative of increasingly naturalistic behaviour for the following reasons:

- (i) Wild hamadryas baboons travel on extensive daily journeys, thought to be longer than those of any other non-human primates (Altman, S.A 1974; Kessel and Brent 1996); and,

(ii) Increased “locomotion” also implies greater exploration. Exploration of the resource state is commonly seen in the daily marches of hamadryas baboons (Sigg and Stolba 1981). Encouraging such opportunist tendencies may alleviate monotony for captive neophilic species.

Another relevant finding was that the combined focal animals spent less time overall *climbing* upon relocation to the new enclosure. This occurred despite the provision of climbing structures, trees and a wire netting boundary fence in the new enclosure and may be coincident with an increase in foraging opportunities. Similar findings were found in an investigation conducted on the response of eight primate species to various degrees of foraging enrichment referred to above (Chamove et al. 1982). In this investigation, it was found that each of the eight species spent significantly more time on the ground upon the provision of a woodchip litter layer, a result enhanced by the scattering of grain mixture onto this litter layer (Chamove et al. 1982).

In addition, the increased landscape diversity in the new enclosure may have provided better observation points and more escape routes and refuges from social pressure that, in the former enclosure, could only be found on structural elements.

Of the “locomotion” behaviours that were exclusively recorded upon the colony’s relocation, *troop patrol* and *troop movement* were especially indicative of a positive response by the focal animal’s to the new, enriched and spacious enclosure. This is because these behaviours closely resembled species-typical behaviour of their wild counterparts, as described below.

Troop patrol activity, whereby individuals in groups larger than harems advanced in line, corresponds with the column formation observed amongst wild hamadryas baboons. This column formation behaviour in free-ranging baboons is the prevailing formation in non-foraging progression (Sigg 1980), providing convenient passage through rocks and vegetation (Kummer 1995). In addition, this formation bears some resemblance to the procession of two-male teams, such as those involving focal animals upon the colony’s relocation.

Troop movement was also exclusive to the new enclosure. This form of herding formation, whereby several one-male units join together (Sigg 1980), may indicate a defensive response. Predation risks in free-ranging hamadryas baboons usually results in reduced inter-individual spacing (Altman, S.A 1974). The resulting cluster formation provides increased protection for individuals in the middle (Altman, S.A 1974), increases the herd effect and provides greater defensive capabilities through the concentration of males (Sigg 1980). Alternatively, *troop movement* may be a form of the procession activity undertaken by free-ranging hamadryas baboons during their daily march. In the wild, hamadryas baboons travel in the same general direction towards a common destination, such as a midday water whole, in small and slow moving parties (Sigg and Stolba 1981). At the same time, individuals forage on single shrubs (Sigg and Stolba 1981).

Both *troop patrol* and *troop movement*, behaviours that, in the wild, are co-ordinated by the troop’s adult males (Kummer 1968), are group behaviours that were not recorded in the former enclosure. In a similar way, captive colonies of celebes macaques (*Macaca nigra*) and lion-tailed macaques (*Macaca silenus*), relocated to physically complex, naturalistic island enclosures, have been reported to show cohesive group behaviour that, because of space restrictions, was not possible in their smaller and traditional exhibits (Hutchins et al. 1984).

3.7.3.8 “Play” behaviour

The decrease in overall occurrence of “play” by the combined focal animals upon their relocation to the new enclosure may be attributable to the increased foraging opportunities available relative to the former enclosure. This correlates with the findings of the study referred to above i.e. an investigation of eight primate species, where the degree of foraging enrichment, manipulated with the provision of grain or mealworms to a woodchip litter layer, was found to reduce play (Chamove et al. 1982).

Digging was recorded exclusively in the former enclosure. Free-ranging baboons dig to uncover edible roots (Kummer 1995) and sources of water (Altman, S.A 1974). Because instances of this activity were not accompanied by “feeding activity”, *digging* was deemed to be vestigial and recorded as a non-food related, enrichment directed, “play” behaviour. In a comparison of the social behaviour of captive and wild hamadryas baboons, a similar behaviour was described (Kummer and Kurt 1965). In this investigation, the quantum of what was termed “exploring ground” (i.e. “digging in holes and cracks, turning stones without eating any particles”) by captive juvenile baboons was seen to be higher than the corresponding field values of any other non-social behaviour (Kummer and Kurt 1965:73). It was suggested that, in the absence of real foraging opportunities, captive juvenile baboons probably extended such “exploring ground” behaviours that are only part of the foraging repertoire in the wild (Kummer and Kurt 1965:73). As *digging* did not occur in the new enclosure, with its increased *foraging* and foraging-related exploration opportunities, a similar explanation may be the reason for the occurrence of vestigial *digging* in the former enclosure. In this way, vestigial *digging* by the Wellington Zoo baboons may have been a “supernormal” behaviour [i.e. “...richer manifestations of a natural disposition within the innate reaction norm” (Kummer 1995:132)].

The specific “minor” behaviours for which significant differences in overall occurrence were found between the former and new enclosures were *manipulating environment* and *play fighting*.

As the number of objects available to captive animals is much smaller and less varied than in the wild, the captive animal may compensate for this by using certain objects in one or more abnormal ways (Morris 1964). Instances of *manipulating environment* by the Wellington Zoo focal animals included the overturning of their water trough, rocking and pushing aside logs without foraging underneath, and rolling stones. Given the infrequency with which hamadryas baboons handle non-edible items in the wild (Kummer 1968), a reduction in such behaviour upon the colony’s relocation may, therefore, be attributable to the increased complexity of the new enclosure. Increased environmental complexity in the new enclosure, however, did appear to provide a greater number of novel objects for the animals to move. This explains the occurrence of *relocating object* (a “locomotion” behaviour) in focal samples upon the colony’s relocation.

Due to the low overall occurrence of *play fighting*, the results for this “minor” behaviour are more appropriately explained by the behavioural responses of individual focal animals.

3.7.3.9 “Out of sight”





The combined focal animals were found to spend more time “out of sight” upon their relocation. The observer suggests two possible reasons for this result. Both indicate increasingly naturalistic behaviour:

(i) An increase in “out of sight” by the combined focal animals reflects the increased physical complexity of the new enclosure and how this provided refuges from social pressure (Duncan and Poole 1990), like those that would be sought by animals in the wild (Bostock 1993). The new enclosure also provided a greater variety of beneficial spaces that enabled the animals to escape public view (Hutchins et al. 1984).

(ii) In the new enclosure, an increase in “out of sight” by the combined focal animals can be interpreted as the animals exercising a preference for shade cover and shelter. During much of the time that the sample animals were “out of sight” in the new enclosure they were in their den areas. Both the fully covered and outside den areas were sheltered from rain and direct sunlight. They were also less spatially restrictive than the double den area, and its overhanging platform, in the former enclosure (i.e. the two primary sources of permanent shade in the former enclosure). In the wild, hamadryas baboons prefer shady resting areas, which they may find under sparse *Dobera glabra* trees (Sigg and Stolba 1981). However, they would usually not share such sites with animals beyond their immediate units (Kummer 1968).

It is possible that “inactivity” in the new enclosure was greater than the observed value because of the increased amount of time that the animals could not be seen. However, as an independent behaviour, “out of sight” has value in emphasising the combined focal animals’ preference for shade cover, shelter and/or areas of privacy.

Figure 3.7. Diagram summarising changes in the overall occurrence of “major” and “minor” behaviours between the former and new enclosures by the combined focal animals.

		PRIMARY VARIABLES CONTRIBUTING TO CHANGE			
COMBINED FOCAL ANIMALS RESPONSE TO RELOCATION	NEW ENCLOSURE	More space	More physical diversity	More foraging enrichment	More enclosure complexity and naturalism
	 Behaviours exclusive to the new enclosure	<i>Troop movement</i> <i>Troop patrol</i>			<i>Licking</i> <i>Scrapping</i> <i>Relocating object</i>
	 Significant increase in overall occurrence upon relocation		“Out of sight”	<i>Foraging</i> <i>Relocating food</i> “Locomotion” <i>Walking</i>	“Solicitation”
	 Significant decrease in overall occurrence upon relocation		<i>Climbing</i> <i>Receiving grooming</i>	<i>Sitting</i> <i>Resting</i> <i>Climbing</i> “Play”	“Grooming” <i>Grooming self</i> “Inactivity” <i>Manipulating environment</i>
	 Behaviours exclusive to the former enclosure	<i>Herded by tail/tail holding</i>	<i>Shaking</i>	<i>Digging</i>	
	FORMER ENCLOSURE	Less space	Less physical diversity	Less opportunities for foraging	Less enclosure complexity and naturalism

3.7.4 Comparison of mean bout lengths of “major” and “minor” behaviours between the former and new enclosures

3.7.4.1 Relative bout lengths of “major” behaviours

No statistically significant differences were found between the former and new enclosures in the mean bout lengths (i.e. duration) of any of the eight “major” behavioural categories investigated in this study for which data permitted statistical comparison.

Consideration of significant differences in mean bout length, in conjunction with the overall occurrence of each of the “major” and “minor” behavioural categories at both study sites, provided some insight into the differences in the degree of repetition of these behaviours between the former and new enclosures (Table 3.2). From this, it becomes apparent whether a change in mean bout length and/or relative repetition caused significant differences in the overall occurrence of a specific “major” or “minor” behaviour upon the focal animals’ relocation to the new enclosure.

Table 3.2. Matrix of mean bout length and overall occurrence of “major” and “minor” behaviours and social states designed to show changes in relative repetition upon the colony’s relocation to the new enclosure.

Mean bout length (Y)	Increase	Less repetition ①	Less repetition ②	More repetition and/or Y may have caused X ③
	No change	Less repetition ④	No change in repetition ⑤	More repetition ⑥
	Decrease	Less repetition and/or Y may have caused X ⑦	More repetition ⑧	More repetition ⑨
		Decrease	No change	Increase
		Overall occurrence (X)		

The overall occurrence of “solicitation”, “grooming”, “inactivity” and “play” were all found to decline significantly upon the colony’s relocation, while their mean bout length remained unchanged. This indicated that the degree of repetition of these behaviours declined upon the combined focal animals’ release into the new enclosure, resulting in a decline in the overall occurrence of these behaviours, as illustrated in Table 3.2 above. Due to the high number of instances with which “grooming”, in particular, by the combined focal animals occurred in the former enclosure, as well as the evidence to suggest its greater repetition prior to relocation, this “major” behaviour in the former enclosure bore some resemblance to a stereotypical behaviour. This is because, in the wild, (during times equivalent to this study’s hours of observation), grooming only occurs when the animals stop occasionally during the daily march (Kummer 1968). Stereotypes may be adaptive to increase the quantity of stimulation to an animal that is otherwise bored as a result of lack of stimuli. [Some stereotypes

develop more directly from the absence of a natural habitat (Bareham 1973)]. In this respect, the reduction in the relative repetition of “grooming” can be seen as a favourable outcome. A reduction in the repetition of “grooming” was especially positive because repetitive behaviour or habits in captive animals may become ‘fixed’ and unable to be corrected, even when greater stimulation is provided (Bareham 1973; Bostock 1993).

Conversely, the overall occurrence of “locomotion” and “out of sight” were found to significantly increase upon the colony’s relocation, while the mean bout length of each of these behaviours remained unchanged. This would indicate that these behaviours occurred more repetitively in samples from the new enclosure. Given that wild *Papio* baboons spend a majority of their time travelling (in search of food) (Kessel and Brent 1996), an increase in the degree of repetition of “locomotion” in the new enclosure can be considered a positive effect of the new enclosure. Similarly, an increase in the repetition of “out of sight” can also be viewed as favourable. This is because the animals appeared to be exercising a preference for using the increased diversity of spaces as visual barriers or hiding places (Kessel and Brent 1996), in order to avoid being seen by the public and to isolate themselves from one other (Hutchins et al. 1984), as well as shady resting sites (Sigg and Stolba 1981).

No statistically significant differences between the enclosures were found in either the overall occurrence or mean bout length of “aggression” or “feeding activity”. This suggests that the degree of repetition of these behaviours was also unchanged between the former and new enclosures (Table 3.2).

There were insufficient occurrences of “appeasement” by the combined focal animals to make a comparison of mean bout lengths and, therefore, relative repetition between the former and new enclosures.

3.7.4.2 Relative bout lengths of “minor” behaviours

- “Solicitation” behaviour

For four of the seven “minor” “solicitation” behaviours common to both enclosures (i.e. *visual presentation*, *receiving visual presentation*, *vocal presentation* and *mating*) there was no statistically significant difference in mean bout length or overall occurrence. This implies that these behaviours also occurred at a similar degree of repetition in both enclosures (Table 3.2).

A significant decrease in the overall occurrence of *receiving vocal presentation* upon the colony’s relocation, coupled with statistically similar mean bout lengths, suggests that this behaviour occurred less frequently in samples from the new enclosure. This is interpreted in the discussion relating to individual focal animals.

Pursuit was the only “solicitation” behaviour for which a significant difference (in this case, an increase) in mean bout length was found upon the animals’ relocation. *Pursuit* behaviour resembles “following processions” observed in free-ranging hamadryas baboons, whereby males have been described as typically, but not exclusively, leading their respective unit females (Kummer 1968:72). In a similar way, the harem leaders at Wellington Zoo would stop intermittently during pursuit behaviour and turn back and stare at their females. The latter would then hasten to catch up (Kummer 1968). As no significant difference was found between the enclosures in the overall occurrence of this behaviour amongst the combined focal animals, these two results suggest that *pursuit* behaviour occurred less frequently in the new enclosure. This result further supports the

contention made previously that “solicitation” behaviours that reinforced the integrity of one-male units were intensified in the former enclosure.

There were too few instances of *simulated mating* in both enclosures to test for differences in mean bout length and therefore to determine the relative repetition of this “minor” behaviour between the former and new enclosures. The infrequency with which *simulated mating* was recorded corresponds with the limited co-ordination behaviour seen to be undertaken by the study's males during analysis of individual focal animals.

- “Agonistic” behaviour

The overall occurrence and mean bout lengths of *physical aggression*, *avoidance*, *supplanting* and *alert* were all found to be unchanged between the former and the new enclosure. These results indicated that each of these behaviours occurred with similar degrees of repetition in both enclosures (Table 3.2).

There were insufficient instances of *visual aggression*, *vocal aggression* and *intervention* to determine significant differences in mean bout length and, therefore, approximate relative repetition of these behaviours between the former and new enclosures.

In the case of the first two of these behaviours, *vocal aggression* and *visual aggression*, there were sufficient instances in the new enclosure only, thereby preventing statistical analysis between the former and new enclosures.

Data sets for mean bout length analysis for the combined focal animals contained 27 instances of *visual aggression* in the former enclosure. However, only one such instance was recorded in the new enclosure. This could have been expected to lead to a decrease in the overall occurrence of this “minor” behaviour. However, no statistically significant difference between enclosures was found for the combined focal animals. The single instance of *visual aggression* in the new enclosure was disproportionately longer than instances in the former enclosure and this caused this anomaly.

Six instances of *vocal aggression* were recorded in data sets for mean bout length analysis in the former enclosure and only one in the new enclosure. The similarity in overall occurrence of this “minor” behaviour in the former and new enclosures can be attributed to an additional and especially long occurrence of this behaviour. This featured only in data sets for overall occurrence (i.e. data sets that encompassed each sample's first and last behaviour and those behaviours occurring either side of “out of sight”). This resulted in a similar anomaly to that noted above.

While statistical testing could not be undertaken to determine mean bout lengths of either of these “minor” “agonistic” behaviours, the occurrence of too few of each in the new enclosure, and the frequency with which they were recorded prior to relocation, provided some indication that these “minor” behaviours occurred less frequently in samples from the new enclosure (notwithstanding that there were nine more focal samples collected prior to relocation). This may be attributable to the animals' spending more time “out of sight” from the observer and, therefore, by inference, one another. A similar outcome was experienced at the Great Ape House in Seattle, where the elimination of aggressive encounters, which had occurred in the gorillas' former enclosure,

has been associated with the physical diversity of the animals' current, more naturalistic enclosure (Hutchins et al. 1984).

In addition, the apparent decrease in the frequency of *visual* and *vocal aggression* would appear to correspond with anecdotal observations of reduced interaction between the animals and the viewing public in the new enclosure. The observer had noted that, when the public agitated the animals, the baboons invariably responded with visually and vocally aggressive behaviour. Animals may interact with passers-by in order to increase the frequency, intensity and range of activities outside their enclosure (i.e. to enhance environmental variability in an enclosure otherwise lacking in stimulation) (Morris 1964). A reduction in such interaction can be seen as a positive outcome of increased enclosure variability in the new exhibit.

Furthermore, a decrease in the frequency with which these two "minor" "agonistic" behaviours occurred upon the colony's relocation to the new enclosure may also be attributable to an increase in enclosure size. The latter enabled the animals to maintain more space between themselves and the public, such as that which would be maintained between themselves and potential enemies in the wild (Rowell 1972). This indicated that the new enclosure better provided for this species' flight distance.

A single instance of *intervention* by the combined focal animals in the new enclosure prevented statistical testing of the mean length of this behaviour between the former and new enclosures. Unlike above, no inference can be made from this about the relative frequency of *intervention* because this "minor" behaviour occurred infrequently in both enclosures.

- "Feeding" behaviour

There was no significant difference between the former and new enclosures in the mean bout length of either *feeding* or *drinking*. This, together with the absence of a significant difference in the overall occurrence of each "minor" behaviour upon the colony's relocation, suggests that the degree of repetition of these behaviours by the combined focal animals remained relatively consistent in samples from both enclosures (Table 3.2). This result for *feeding* supports the explanation pertaining to the regular provision of food noted above and emphasises how a similar feeding routine of major food items in the former and new enclosures corresponded with a similar rate of consumption.

By contrast, the absence of a difference between the former and new enclosures in the mean bout length of *foraging* and *relocating food* indicated that each of these behaviours occurred with a greater degree of repetition in samples from the new enclosure thereby causing an increase in their overall occurrence.

An increase in the mean bout length of *reaching out* was found in samples following the animals' relocation to the new enclosure. This, coupled with no significant difference in overall occurrence, indicated a reduction in the relative repetition of *reaching out* in the new enclosure samples. The observer speculates that, for the same reasons that the animals interacted aggressively with the public, *reaching out* in the former and less stimulating enclosure may have exemplified their attempts to increase environmental complexity by 'employing' external elements more frequently.

- “Grooming” behaviour

No statistically significant difference in mean bout length of *grooming self* was found between the former and new enclosures for the combined focal animals. In addition, a statistically significant decline in the overall occurrence of *grooming self* was found upon relocation to the new enclosure. Together, these results indicated a reduction in the rate of repetition of *grooming self* by the combined focal animals was responsible for the decrease in overall occurrence (Table 3.2). This emphasises the reduction in self-directed behaviour, referred to above, as a consequence of the provision of increased enrichment.

There was no significant difference between the former and new enclosures in the mean bout length of *receiving grooming*. This, in concert with a decline in overall occurrence of *receiving grooming* upon the colony’s relocation, suggests that this “minor” behaviour occurred less repetitively by the combined focal animals in the new enclosure. This supports the contention that male-female pairs groomed more frequently in the former enclosure where rivals could be more clearly and consistently seen. The absence of either a significant difference in either overall occurrence or mean bout length of *grooming other* suggests there was a no change between the enclosures in the degree of repetition of this “minor” behaviour. A decrease in the repetition of *receiving grooming*, together with a similar rate of repetition of *grooming other* between the former and new enclosures, further reinforces the suggestion made above that some of the focal animals may have intensified their grooming of animals additional to their existing harems upon their relocation to the new enclosure.

- “Appeasement” behaviour

As already noted above, there was insufficient data relating to *tactile appeasement* (the only appeasement behaviour recorded in both the former and new enclosures) to allow comparison between enclosures of the mean duration and, therefore, the relative repetition of this “minor” behaviour. This further emphasises the relatively small quantum of “appeasement” behaviours demonstrated by the focal animals.

- “Inactivity” behaviour

The absence of a significant difference in the mean bout length of *sitting* and *resting*, and a decrease in the overall occurrence of these “minor” behaviours upon the colony’s relocation, indicated that the latter occurred because of reduced repetition in the new enclosure (Table 3.2). It would appear that, upon the colony’s relocation, the combined focal animals had fewer opportunities for *sitting* and *resting* throughout the day as a consequence of increased activity, such as *foraging* and “locomotion”.

As no significant differences in either the mean bout length or the overall occurrence of *standing still* were found between the former and new enclosures, no change in the relative repetition of this behaviour could be deduced from the data.

- “Locomotion” behaviour

The increase upon the colony’s relocation in the overall occurrence of *walking*, coupled with no significant difference between the former and new enclosures in mean bout length, indicated that this “minor” behaviour

occurred more frequently in samples from the new enclosure (Table 3.2). This may be attributable to the increase in the overall occurrence of *foraging* and greater opportunities for exploration in the new enclosure, both of which promoted discontinuous *walking*.

By contrast, no significant differences for the combined focal animals between the enclosures in either the mean bout length or the overall occurrence of *running*, suggests that the relative repetition of this “minor” behaviour was similar in the former and new enclosures. This may be a function of energy expenditure. Running consumes considerable energy. This reduces feeding efficiency and also makes it more difficult for the animal to maintain a constant body temperature (Altman, S.A 1974).

There was a significant decline in both the mean bout length and the overall occurrence of *climbing* upon the colony’s relocation. These results indicated that *climbing* may have occurred less repetitively in the new enclosure. Alternatively, the decrease in the mean bout length may have caused the significant reduction in overall occurrence of *climbing* in the new enclosure. Either way, these results indicated that climbing structures were more widely used in the smaller, former enclosure, effectively increasing the available vertical and horizontal space.

Too few occurrences of *jumping* (i.e. single instances in both the former and new enclosures) occurred in data sets for mean bout length analysis to test for a significant difference or determine the relative repetition of this “minor” behaviour between the enclosures. This indicated that the increase in overall occurrence of *jumping* by the combined focal animals was an anomaly in the results, with the single episode in the new enclosure disproportionately longer than the single instance in the former enclosure.

- “Play” behaviour

There was a decline in the overall occurrence and no change in the mean bout length of the two “minor” “play” behaviours common to both enclosures (i.e. *manipulating environment* and *play fighting*). This suggests that there was a decrease in the rate of repetition of these “minor” behaviours by the combined focal animals upon their relocation (Table 3.2).

A reduction in the relative repetition of *manipulating environment* supports the earlier contention that the combined focal animals may have compensated for less variety within the former enclosure by employing objects at their disposal in “abnormal” ways.

Due to the low overall occurrence of *play fighting*, this finding is best explained with reference to the behavioural responses of individual focal animals.

3.7.5 Comparison between the former and new enclosures of overall occurrence of “social” states

Statistically significant changes in the overall occurrence of all three social states, and the determinants of these social states for the combined focal animals, were interrelated. Specifically, the increase in the overall occurrence of the “solitary” state corresponded with a decline in “grouped” and “social” states. This reflects changes in the overall occurrence of “major” and “minor” behaviours due to the colony’s relocation.

The increase in the “solitary” state and the decrease in “grouped” can be largely attributed to the increasing occurrence of “locomotion” and *foraging* behaviours and a decrease in “inactivity” by the combined focal animals. In a similar way, inter-individual spacing alters between these behaviours in free-ranging hamadryas baboons. At rest, hamadryas baboons (specifically females and their harem leaders) in the wild have been found to sit at an average inter-individual distance of 0.65 metres (Kummer and Kurt 1965:68), well within the inter-individual distance for the “grouped” state observed in the current study. When foraging, animals [including male chacma baboons (*Papio cynocephalus ursinus*)] will generally spread out in order to minimise feeding competition (Cowlshaw 1999). Similarly, when wild troops of hamadryas baboons are moving or feeding, the average distance between male unit leaders and their females increases to approximately three metres (Kummer and Kurt 1965:68). This was beyond the “grouped” distance and, therefore, considered as a “solitary” distance in the current study. These results, therefore, support the contention that inter-individual spacing between activities is likely to change (Cowlshaw 1999).

Furthermore, reduced inter-individual distances caused by small enclosures may have a profound effect on the social behaviour of these captive animals (Calhoun 1962, cited in Kummer and Kurt 1965:68). For example, in the former enclosure, the occurrence of *tail holding* behaviour, described above as serving a cohering function within one-male units, was attributed to the close and continuous presence of rival males.

The significant decline in the overall occurrence of the “social” state by the combined focal animals upon their relocation reinforces the observation that captive animals behave socially because, unlike their wild counterparts, their behaviour is not suppressed by activities necessary for survival, such as searching for food (Kummer and Kurt 1965).

Even when housed in appropriate social groupings, non-social activity deprivation may result in captive animals interacting with their companions in atypical ways or to an abnormal extent (Morris 1964). Consequently, the decline in the “social” state may be attributable to the increased foraging variety and exploration enrichment that created more opportunities for the animals in the new enclosure for non-social activity. In a similar way, socially directed behaviour (i.e. “any social behaviors directed at another baboon, the observer, or an unknown source...”) in single-housed olive baboons (*Papio hamadryas anubis* [= *Papio cynocephalus anubis*]) and guinea baboons (*Papio hamadryas papio* [= *Papio cynocephalus papio*]) was found to decrease upon the provision of foraging enrichment (Brent and Long 1995:65).

More activity and increasingly naturalistic behaviour, therefore, may have suppressed the “social” state in the new enclosure relative to the former enclosure. Suppressed activity, more specifically, “abundant food and very little need for physical exercise”, was used to explain the abnormally high percentage of social time spent by the Zurich Zoo hamadryas baboon colony (up to 70 percent) (Kummer 1995:136). This further supports the contention that both the amount and type of food available has a direct effect on both the amount and type of social interaction in monkey groups (Rowell 1972).

The two contentions noted above suggest that feeding opportunities evoke more attention than social interaction (Brent and Long 1995). This effect has been reported in other group-housed primates upon environmental enrichment (Brent and Long 1995).

3.7.6 Comparison of mean bout lengths of “social” states between the former and new enclosures

The significant increase in overall occurrence, and absence of a statistically significant difference in mean bout length, of the “solitary” state by the combined focal animals upon the colony’s relocation indicated an increase in the degree of repetition of this particular social state (Table 3.2).

By contrast, the reduction in the overall occurrence of “grouped” and “social” states, coupled with the absence of a significant difference between the enclosures in the mean bout length of each, indicated that the “grouped” and “social” states occurred less frequently in the new enclosure. This was a favourable outcome of the colony’s relocation to the new enclosure, as the animals would appear to have been engaging in an increasingly naturalistic pattern of behaviour whereby social contact is minimised during the majority of day. This outcome coincided with an increase in the rate of “locomotion” undertaken by the combined focal animals upon relocation. “In hamadryas troops social and non-social behaviour alternate in a daily routine which remains essentially unchanged throughout the year” (Kummer 1968:10). During the long daily procession in the wild, social behaviour is made up of almost completely of “subtle interactions” of spacing (i.e. distance, formation and direction of travel), chasing and copulation virtually cease with grooming and play restricted to the animals’ midday rest (Kummer 1968:33). Resting and social behaviour, including grooming, play, chasing and copulation occur predominantly before the animals depart for their daily journey and, again, upon their return to the ‘waiting area’ in the late afternoon-early evening and decline as it becomes dark (Kummer 1968). These two periods of naturally high socialisation were not included during daily focal sampling due to interruptions caused by daily husbandry and feeding in the morning and the Zoos’ closing in the early evening. The irregular social behaviour by captive baboons relative to their wild counterparts has been attributed previously to differences in their feeding habits (Kummer and Kurt 1965).

CHAPTER 4: RESULTS

PATTERNS OF BEHAVIOUR FOR INDIVIDUAL FOCAL ANIMALS

4.1 EXTENT OF BEHAVIOUR REPERTOIRE

4.1.1 Abu

Each of the nine “major” behavioural categories listed on the combined focal animals’ complete ethogram (Table 2.1) featured in focal samples for Abu. Seven of these “major” behavioural categories, i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity”, “locomotion” and “out of sight”, were common to both the former and the new enclosures. The remaining two behaviours were recorded in samples for Abu exclusively in a single enclosure. These were “play”, recorded exclusively in the former enclosure, and “appeasement”, recorded exclusively in the new enclosure.

Abu’s total repertoire of “minor” behaviours (derived from both enclosures) consisted of 32 behaviours from the possible 44 “minor” behaviours, including “out of sight”, listed in the combined focal animals’ complete ethogram (Table 2.1).

The “minor” behaviours not recorded for Abu in either enclosure were *vocal presentation*, *simulated mating*, and *herded by tail* (“solicitation” behaviours), *reaching out*, *hunting* and *licking* (“feeding activity” behaviours), *vocal appeasement* (“appeasement” behaviour), *jumping* and *relocating object* (“locomotion” behaviours) and *digging*, *play fighting* and *scraping* (“play” behaviours).

11 of the 32 “minor” behaviours recorded in focal samples for Abu were exclusive to a single enclosure. Seven of these, i.e. *visual presentation* and *tail holding* (both “solicitation” behaviours), *visual aggression*, *shaking* and *avoidance* (“agonistic” behaviours), *resting* (“inactivity” behaviour) and *manipulating environment* (“play” behaviour), were recorded only in the former enclosure. The remaining four behaviours, i.e. *relocating food* (“feeding activity” behaviour), *tactile appeasement* (“appeasement” behaviour), and *troop movement* and *troop patrol* (both “locomotion” behaviours), were exclusive to the new enclosure.

The remaining 21 “minor” behaviours, i.e. *receiving visual presentation*, *receiving vocal presentation*, *mating* and *pursuit* (“solicitation” behaviours), *physical aggression*, *vocal aggression*, *supplanting*, *intervention* and *alert* (“agonistic” behaviours), *feeding*, *foraging* and *drinking* (“feeding activity” behaviours), *grooming self*, *receiving grooming* and *grooming other* (“grooming” behaviours), *sitting* and *standing still* (“inactivity” behaviours), *walking*, *running* and *climbing* (“locomotion” behaviours), and *out of sight*, were common to both the former and new enclosures in focal samples for Abu.

4.1.2 Randy

Eight of the nine “major” behavioural categories listed on the combined focal animals’ complete ethogram (Table 2.1), i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “appeasement”, “inactivity”, “locomotion” and “out of sight”, featured in focal samples for Randy. All but one of these (i.e. “appeasement”) was common to both enclosures. “Appeasement” was only recorded in focal samples for Randy prior to his relocation. No instances of “play” behaviour were recorded during focal sampling of Randy in either enclosure.

Randy’s total behavioural repertoire (derived from both enclosures) consisted of 26 of the 44 “minor” behaviours, including *out of sight*, in the combined focal animals’ complete ethogram (Table 2.1).

Those “minor” behaviours that did not occur in either enclosure in the focal samples of Randy were *visual presentation*, *vocal presentation*, and *herded by tail* (“solicitation” behaviours), *shaking*, *supplanting* and *intervention* (“agonistic” behaviours), *reaching out*, *relocating food*, *hunting* and *licking* (“feeding activity” behaviours), *tactile appeasement* (“appeasement” behaviour), *jumping*, *relocating object* and *troop patrol* (“locomotion” behaviours) and *manipulating environment*, *digging*, *play fighting* and *scraping* (“play” behaviours).

Eight of the 26 behaviours recorded in focal samples for Randy were exclusive to a single enclosure. Seven of these, i.e. *tail holding* (“solicitation” behaviour), *vocal aggression* and *alert* (“agonistic” behaviours), *drinking* (“feeding activity” behaviour), *grooming self* (“grooming behaviour”), *vocal appeasement* (“appeasement” behaviour) and *running* (“locomotion” behaviour), were recorded only in the former enclosure. The remaining behaviour, *troop movement* (“locomotion” behaviour), was exclusive to the new enclosure.

The remaining 18 “minor” behaviours were common to both the former and new enclosures in focal samples for Randy. These behaviours were *receiving visual presentation*, *receiving vocal presentation*, *mating*, *simulated mating* and *pursuit* (“solicitation” behaviours), *visual aggression*, *physical aggression* and *avoidance* (“agonistic” behaviours), *feeding* and *foraging* (“feeding activity” behaviour), *receiving grooming* and *grooming other* (“grooming” behaviours), *sitting*, *resting* and *standing still* (“inactivity” behaviours), *walking* and *climbing* (“locomotion” behaviours), and *out of sight*.

4.1.3 Toka

Eight of the nine “major” behavioural categories listed on the combined focal animals’ complete ethogram (Table 2.1), i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity”, “locomotion”, “play” and “out of sight”, featured in focal samples for Toka. Each of these “major” behavioural categories was common to both the former and the new enclosures.

Toka’s total behavioural repertoire (derived from both enclosures) consisted of 36 “minor” behaviours from the possible 44, including *out of sight*, listed in the combined focal animals’ complete ethogram (Table 2.1).

Those “minor” behaviours that did not occur in either enclosure in the focal samples of Toka were *receiving vocal presentation*, *tail holding* and *herded by tail* (“solicitation” behaviours), *visual aggression*, *physical*

aggression and *intervention* (“agonistic” behaviours), *hunting* (“feeding activity” behaviour), and *tactile appeasement* (“appeasement” behaviour).

15 of the 36 “minor” behaviours recorded in focal samples for Toka were exclusive to a single enclosure. Seven of these were recorded only in the former enclosure. These were *receiving visual presentation* and *simulated mating* (both “solicitation” behaviours), *vocal aggression*, *shaking* and *supplanting* (“agonistic” behaviours), *vocal appeasement* (“appeasement” behaviour) and *digging* (“play” behaviour). The remaining eight “minor” behaviours were exclusive to the new enclosure. These were *mating* (“solicitation” behaviour), *drinking* and *licking* (“feeding activity” behaviours), *grooming other* (“grooming” behaviour), *relocating object*, *troop movement* and *troop patrol* (“locomotion” behaviours), and *scraping* (“play” behaviour).

The remaining 21 “minor” behaviours were common to both the former and new enclosures in focal samples for Toka. These behaviours were *visual presentation*, *vocal presentation*, and *pursuit* (“solicitation” behaviours), *avoidance* and *alert* (“agonistic” behaviours), *feeding*, *foraging*, *reaching out* and *relocating food* (“feeding activity” behaviours), *grooming self* and *receiving grooming* (“grooming” behaviours), *sitting*, *resting* and *standing still* (“inactivity” behaviours), *walking*, *running*, *climbing* and *jumping* (“locomotion” behaviours), *manipulating environment* and *play fighting* (“play” behaviours) and *out of sight*.

4.1.4 Tina

Each of the nine “major” behavioural categories listed on the combined focal animals’ complete ethogram (Table 2.1) featured in focal samples for Tina. Of these, two were exclusive to a single enclosure i.e. “appeasement” in the new enclosure and “play” in the former enclosure.

Tina’s total behavioural repertoire consisted of 26 “minor” behaviours from the possible 44, including *out of sight*, in the combined focal animals’ complete ethogram (Table 2.1).

Those “minor” behaviours that did not occur in either enclosure in focal samples for Tina were *receiving visual presentation*, *receiving vocal presentation*, *simulated mating*, *tail holding* and *herded by tail* (all “solicitation” behaviours), *physical aggression*, *vocal aggression*, *shaking*, *supplanting* and *intervention* (“agonistic” behaviours), *licking* (“feeding activity” behaviour), *vocal appeasement* (“appeasement” behaviour), *jumping*, *relocating object* and *troop patrol* (“locomotion” behaviours) and *manipulating environment*, *play fighting* and *scraping* (“play” behaviours).

10 of the 26 “minor” behaviours recorded in focal samples for Tina were exclusive to a single enclosure. Four of these i.e. *visual aggression* (“agonistic” behaviour), *reaching out* (“feeding activity” behaviour), *resting* (“inactivity” behaviour) and *digging* (“play” behaviour), were recorded only in the former enclosure. The remaining six “minor” behaviours were exclusive to the new enclosure. These were *vocal presentation* (“solicitation” behaviour), *hunting* and *drinking* (“feeding activity” behaviours), *tactile appeasement* (“appeasement” behaviour) and *running* and *troop movement* (“locomotion” behaviours).

The remaining 16 “minor” behaviours were common to both the former and new enclosures in focal samples for Tina. These behaviours were *visual presentation*, *mating*, and *pursuit* (“solicitation” behaviours), *avoidance* and

alert (“agonistic” behaviours), *feeding, foraging* and *relocating food* (“feeding activity” behaviours), *grooming self, receiving grooming* and *grooming other* (“grooming” behaviours), *sitting* and *standing still* (“inactivity” behaviours), *walking* and *climbing* (“locomotion” behaviours) and *out of sight*.

4.1.5 Sinead

All of the nine “major” behavioural categories listed on the combined focal animals’ complete ethogram i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “appeasement”, “inactivity”, “locomotion”, “play” and “out of sight” (Table 2.1), featured in focal samples for Sinead. Each of these “major” behavioural categories was common to both the former and the new enclosures.

Sinead’s total behavioural repertoire consisted of 34 “minor” behaviours from the possible 44, including *out of sight*, listed in the combined focal animals’ complete ethogram (Table 2.1).

Those “minor” behaviours that did not occur in either enclosure in focal samples for Sinead were *simulated mating* and *tail holding* (“solicitation” behaviours), *supplanting* and *intervention* (“agonistic” behaviours), *hunting* (“feeding activity” behaviour), *vocal appeasement* (“appeasement” behaviour), *jumping* and *relocating object* (“locomotion” behaviours) and *digging* and *scraping* (“play” behaviours).

13 of the 34 “minor” behaviours recorded in focal samples of Sinead were exclusive to a single enclosure. Seven of these were recorded only in the former enclosure. These seven “minor” behaviours were *receiving vocal presentation, mating* and *herded by tail* (all “solicitation” behaviours), *visual aggression, vocal aggression* and *shaking* (“agonistic” behaviours) and *play fighting* (“play” behaviour). The remaining six “minor” behaviours were exclusive to the new enclosure. These were *reaching out, drinking* and *licking* (“feeding activity” behaviours), *grooming self* (“grooming” behaviour) and *troop movement* and *troop patrol* (“locomotion” behaviours).

The remaining 21 “minor” behaviours were common to both the former and new enclosures. These “minor” behaviours were *visual presentation, receiving visual presentation, vocal presentation* and *pursuit* (“solicitation” behaviours), *physical aggression, avoidance* and *alert* (“agonistic” behaviours), *feeding, foraging* and *relocating food* (“feeding activity” behaviours), *receiving grooming* and *grooming other* (“grooming” behaviours), *tactile appeasement* (“appeasement” behaviour), *sitting, resting* and *standing still* (“inactivity” behaviours), *walking, running* and *climbing* (“locomotion” behaviours), *manipulating environment* (“play” behaviour) and *out of sight*.

4.2 COMPARISON OF THE NUMBER OF “MAJOR” AND “MINOR” BEHAVIOURAL CATEGORIES OCCURRING PER UNIT OF TIME BETWEEN THE FORMER AND NEW ENCLOSURES

Tables 4.1 and 4.2 illustrate the mean number of “major” and “minor” behavioural categories, respectively, occurring per fifteen-minute sample in the former and new enclosures for each of the five focal animals respectively. The tables also include the p-values for statistical tests comparing the odds of each “major” and “minor” behavioural category occurring per sample in the former and new enclosures.

Logit model comparison determined that no statistically significant differences occurred for any of the five focal animals between the former and new enclosures in the odds of each of the “major” behavioural categories occurring per sample (χ^2 test, $p>0.05$).

Likewise, no statistically significant differences occurred for any of the five focal animals between the former and new enclosures in the odds of each of the “minor” behavioural categories occurring per sample (χ^2 test, $p>0.05$).

Table 4.1 Mean number \pm SE and p-value of odds of occurrence of “major” behavioural categories occurring per 15 minute focal sample.

		Abu	Randy	Toka	Tina	Sinead
Former enclosure	No. of samples	11	13	11	11	11
	Mean \pm SE	5.727 \pm 0.226	4.846 \pm 0.341	5.273 \pm 0.26	4.545 \pm 0.298	5.545 \pm 0.298
χ^2 test p-value		0.2071	0.0718	0.5606	0.6583	0.3345
New enclosure	Mean \pm SE	5.071 \pm 0.434	4.357 \pm 0.399	5.214 \pm 0.406	4.5 \pm 0.437	5.231 \pm 0.423
	No. of samples	14	14	14	14	13

Table 4.2 Mean number \pm SE and p-value of odds of occurrence of “minor” behavioural categories occurring per 15 minute focal sample.

		Abu	Randy	Toka	Tina	Sinead
Former enclosure	No. of samples	11	13	11	11	11
	Mean \pm SE	8.909 \pm 0.709	6.462 \pm 0.582	8.636 \pm 0.719	6.636 \pm 0.468	8.818 \pm 0.678
χ^2 test p-value		0.7036	0.5026	0.7684	0.7782	0.8764
New enclosure	Mean \pm SE	8.5 \pm 0.844	6.429 \pm 0.879	8.571 \pm 0.754	6.714 \pm 0.866	8.692 \pm 0.817
	No. of samples	14	14	14	14	13

4.3 COMPARISON OF OVERALL OCCURRENCE OF BEHAVIOURS BETWEEN THE FORMER AND NEW ENCLOSURES

As was the case for the combined focal animals the statistical method used (i.e. chi square tests comparing two log linear models) tested for a significant difference between the former and new enclosures in the overall occurrence of each “major” and “minor” behaviour for each individual focal animal.

4.3.1 Relative occurrence of “major” behaviours

The overall occurrence in the former and new enclosures of each “major” behavioural category for each of the five focal animals is represented in Figures 4.1a to 4.1e. For illustrative purposes, mean percentage time per sample has been used in lieu of overall occurrence. (Precise p-values and degrees of freedom are recorded in Appendix B, Table 6.7.1 to 6.7.5).

4.3.1.1 Abu

Analysis determined statistically significant differences for Abu in the overall occurrence of three of the seven “major” behavioural categories common to both enclosures (Figure 4.1a).

Chi square tests comparing two log linear models determined a significant increase in the overall occurrence of “locomotion” upon Abu’s relocation (χ^2 test, $p = 0.0000$). Conversely, the overall occurrences of “solicitation” and “inactivity” were found to be significantly reduced in the new enclosure (χ^2 test, $p = 0.0000$ and $p = 0.0000$ respectively). No statistically significant differences between the former and new enclosures were found in the overall occurrence of “agonistic”, “feeding activity”, “grooming” or “out of sight” (χ^2 test, $p > 0.05$).

4.3.1.2 Randy

Analysis of data collected for Randy deduced statistically significant differences between the former and new enclosures in the overall occurrence of all of the seven “major” behavioural categories common to both enclosures (Figure 4.1b).

The overall occurrence of “solicitation”, “feeding activity”, “locomotion” and “out of sight” were all found to significantly increase upon Randy’s relocation (χ^2 test, $p = 0.0004$, $p = 0.0000$, $p = 0.0000$ and $p = 0.0000$ respectively). By contrast, the overall occurrence of “agonistic”, “grooming” and “inactivity” were all found to decline significantly (χ^2 test, $p = 0.0430$, $p = 0.0000$ and $p = 0.0000$ respectively).

4.3.1.3 Toka

Statistically significant differences between the former and new enclosures were determined for Toka in the overall occurrence of five of the eight “major” behavioural categories common to both enclosures (Figure 4.1c).

Chi square tests comparing two log linear models determined a statistically significant increase in the overall occurrence of “solicitation”, “agonistic” and “out of sight” (χ^2 test, $p = 0.0038$, $p = 0.0346$, $p = 0.0000$ respectively) upon Toka’s relocation to the new enclosure. By contrast, a statistically significant decrease in the overall occurrence of “grooming” and “play” (χ^2 test, $p = 0.0000$, $p = 0.0000$) occurred upon Toka’s relocation. There was no evidence of a significant difference between the former and new enclosures in overall occurrence for the remaining three behaviours common to both enclosures i.e. “feeding activity”, “inactivity” or “locomotion” (χ^2 test, $p > 0.05$).

4.3.1.4 Tina

Analysis of samples for Tina determined statistically significant differences between the former and new enclosures in the overall occurrence of four of the seven “major” behavioural categories common to both enclosures (Figure 4.1d).

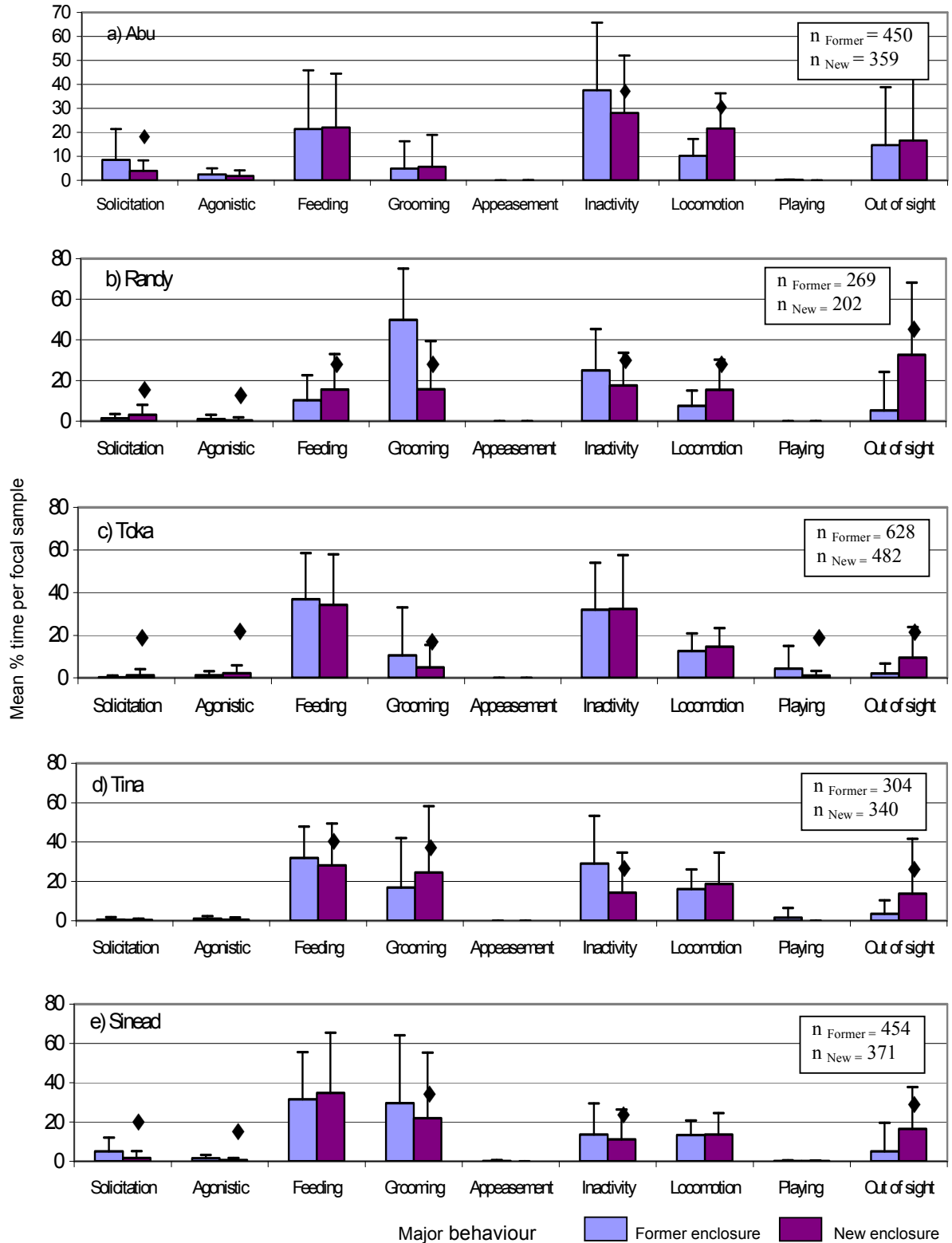
Upon relocation, Tina demonstrated significant increases in overall occurrence of “grooming” and “out of sight” (χ^2 test, $p = 0.0000$, $p = 0.0000$ respectively). Conversely, statistically significant decreases were found in the overall occurrence of “feeding activity” and “inactivity” (χ^2 test, $p = 0.0372$, $p = 0.0000$ respectively).

No statistically significant differences were discernible between the former and new enclosures in the overall occurrence of the remaining “major” behaviours common to both enclosures i.e. “solicitation”, “agonistic”, and “locomotion” (χ^2 test, $p > 0.05$).

4.3.1.5 Sinead

Statistically significant differences in the overall occurrence of five of the nine “major” behavioural categories common to both enclosures were detected upon Sinead’s relocation to the new enclosure (Figure 4.1e).

Analysis showed a significant increase in the overall occurrence of “out of sight” (χ^2 test, $p = 0.0000$). By contrast, the overall occurrence of “solicitation”, “agonistic”, “grooming” and “inactivity” were all found to significantly decline in the new enclosure (χ^2 test, $p = 0.0000$, $p = 0.0255$, $p = 0.0000$, $p = 0.0429$ respectively). No statistically significant differences between the former and new enclosures were found in the overall occurrence of “feeding activity”, “appeasement”, “locomotion”, or “play” (χ^2 test, $p > 0.05$).



Figures 4.1a) to 4.1e). Activity budget for “major” behaviours for individual focal animals, Abu, Randy, Toka, Tina and Sinead respectively. Mean percentage time \pm SD per 10 to 15 minute focal sample for each “major” behaviour are shown. ♦ Indicates “major” behavioural categories with significant differences in overall occurrence between the former and new enclosures, where n = the total number of “major” behaviours sampled.

4.3.2 Relative occurrence of “minor” behaviours

The overall occurrence of each “minor” behaviour in the former and new enclosures for each individual focal animal is represented, for illustrative purposes, as mean percentage time per sample in Figures 4.2a to 4.2e. (Precise p-values and degrees of freedom are recorded in Appendix B, Table 6.8.1 to 6.8.5).

4.3.2.1 Abu

Chi square tests comparing two log linear models were used to determine changes between the former and new enclosures in the overall occurrence of “minor” behaviours. These demonstrated statistically significant differences in five of the 21 “minor” behaviours recorded in focal samples of Abu that were common to both enclosures (Figure 4.2a).

Of these five “minor” behaviours, statistically significant increases were recorded in the overall occurrence of two i.e. *grooming other* (“grooming” behaviour) and *walking* (“locomotion” behaviour) (χ^2 test, $p = 0.0006$, $p = 0.0000$), upon Abu’s relocation to the new enclosure. The overall occurrence of the remaining three “minor” behaviours with significant differences between the enclosures i.e. *receiving vocal presentation* (“solicitation” behaviour), *sitting* (“inactivity” behaviour) and *climbing* (“locomotion” behaviour) was found to decline upon Abu’s relocation to the new enclosure (χ^2 test, $p = 0.0019$, $p = 0.0000$, $p = 0.0014$ respectively).

The remaining 16 “minor” behaviours common to both enclosures were found to have no statistically significant differences in overall occurrence between the former and new enclosures (χ^2 test, $p > 0.05$).

4.3.2.2 Randy

Chi square tests comparing two log linear models determined statistically significant differences in the overall occurrence of eight of the 18 “minor” behaviours common to both enclosures in focal samples for Randy (Figure 4.2b).

Of these eight “minor” behaviours, the overall occurrence of five was found to increase significantly upon Randy’s relocation. These five “minor” behaviours were *receiving vocal presentation* and *pursuit* (“solicitation” behaviours), *foraging* (“feeding activity” behaviour), *walking* (“locomotion” behaviour), and *out of sight* (χ^2 test, $p = 0.0285$, $p = 0.0459$, $p = 0.0000$, $p = 0.0000$, $p = 0.0000$ respectively). The remaining three “minor” behaviours common to both enclosures, for which results indicated a statistically significant difference in overall occurrence i.e. *feeding* (“feeding activity” behaviour), and *receiving grooming* and *grooming other* (“grooming” behaviours), were each found to significantly decline in the new enclosure (χ^2 test, $p = 0.0001$, $p = 0.0000$, $p = 0.0263$).

The other 10 “minor” behaviours common to both enclosures were found to have no statistically significant differences in overall occurrence between the former and new enclosures (χ^2 test, $p > 0.05$).

4.3.2.3 Toka

Statistical tests demonstrated significant differences in 12 of the 21 “minor” behaviours common to both enclosures in focal samples relating to Toka (Figure 4.2c).

Of these 12 “minor” behaviours, statistically significant increases were recorded in the overall occurrence of six i.e. *pursuit* (“solicitation” behaviour), *avoidance* (“agonistic” behaviour), *relocating food* (“feeding activity” behaviour), *sitting* (“inactivity” behaviour), *jumping* (“locomotion” behaviour), and *out of sight* (χ^2 test, $p = 0.0017$, $p = 0.0193$, $p = 0.0009$, $p = 0.0000$, $p = 0.0365$, $p = 0.0000$ respectively), upon Toka’s relocation to the new enclosure. The remaining six “minor” behaviours for which results indicated a statistically significant difference in overall occurrence i.e. *grooming self* and *receiving grooming* (“grooming” behaviours), *resting* (“inactivity” behaviour), *climbing* (“locomotion” behaviour), and *manipulating environment* and *play fighting* (“play” behaviours), were all found to significantly decline upon Toka’s relocation to the new enclosure (χ^2 test, $p = 0.0000$, $p = 0.0000$, $p = 0.0498$, $p = 0.0146$, $p = 0.0174$, $p = 0.0139$ respectively).

The remaining nine “minor” behaviours common to both enclosures were found to have no statistically significant differences in overall occurrence between the former and new enclosures (χ^2 test, $p > 0.05$).

4.3.2.4 Tina

Chi square tests, used to determine changes in the overall occurrence of “minor” behaviours between the former and new enclosures, demonstrated statistically significant differences in seven of the 16 “minor” behaviours common to both enclosures in focal samples relating to Tina (Figure 4.2d).

Of these seven “minor” behaviours, statistically significant increases were recorded in the overall occurrence of four i.e. *grooming other* (“grooming” behaviour), *standing still* (“inactivity” behaviour), *walking* (“locomotion” behaviour) and *out of sight*, upon Tina’s relocation (χ^2 test, $p = 0.0010$, $p = 0.0039$, $p = 0.0120$, $p = 0.0003$ respectively). The remaining three “minor” behaviours common to both enclosures for which results indicated a statistically significant difference in overall occurrence i.e. *foraging* (“feeding activity” behaviour), *grooming self* (“grooming” behaviour) and *sitting* (“inactivity” behaviour), were each found to decline in the new enclosure (χ^2 test, $p = 0.0059$, $p = 0.0014$, $p = 0.0000$).

The remaining nine “minor” behaviours common to both enclosures were found to have no statistically significant differences in overall occurrence between the former and new enclosures (χ^2 test, $p > 0.05$).

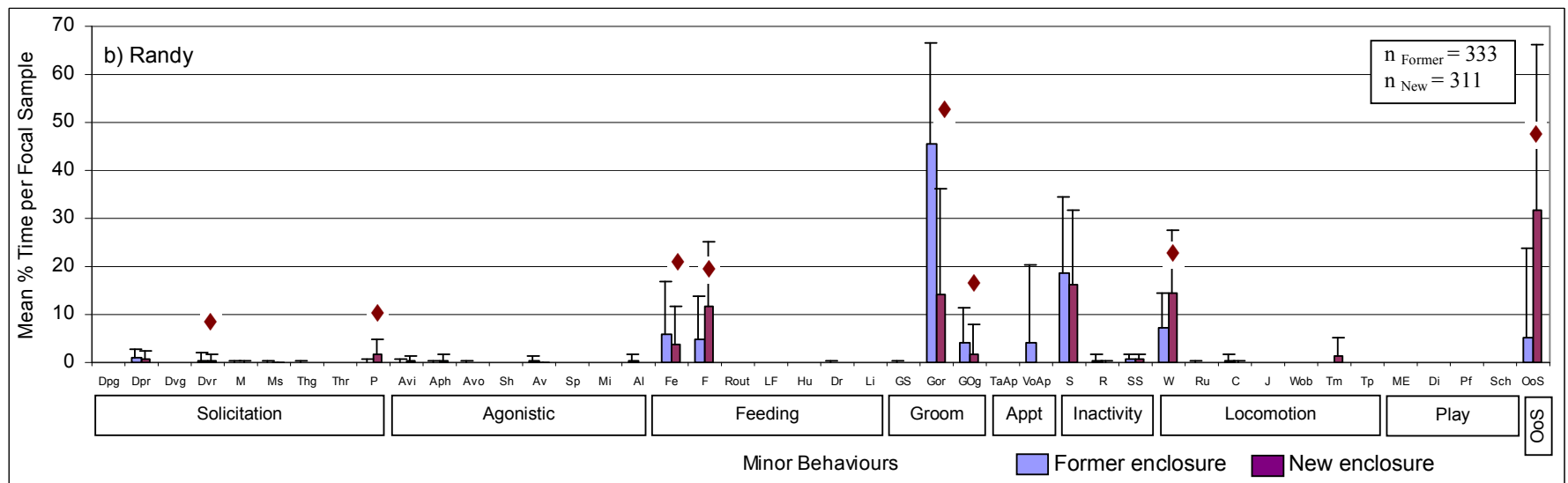
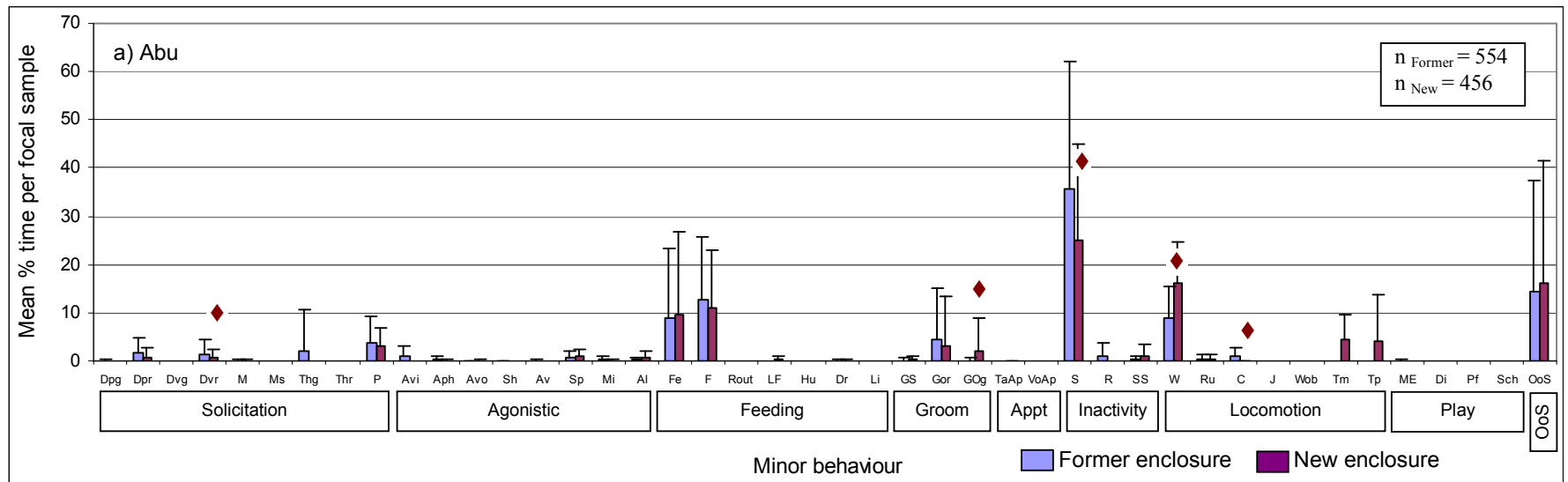
4.3.2.5 Sinead

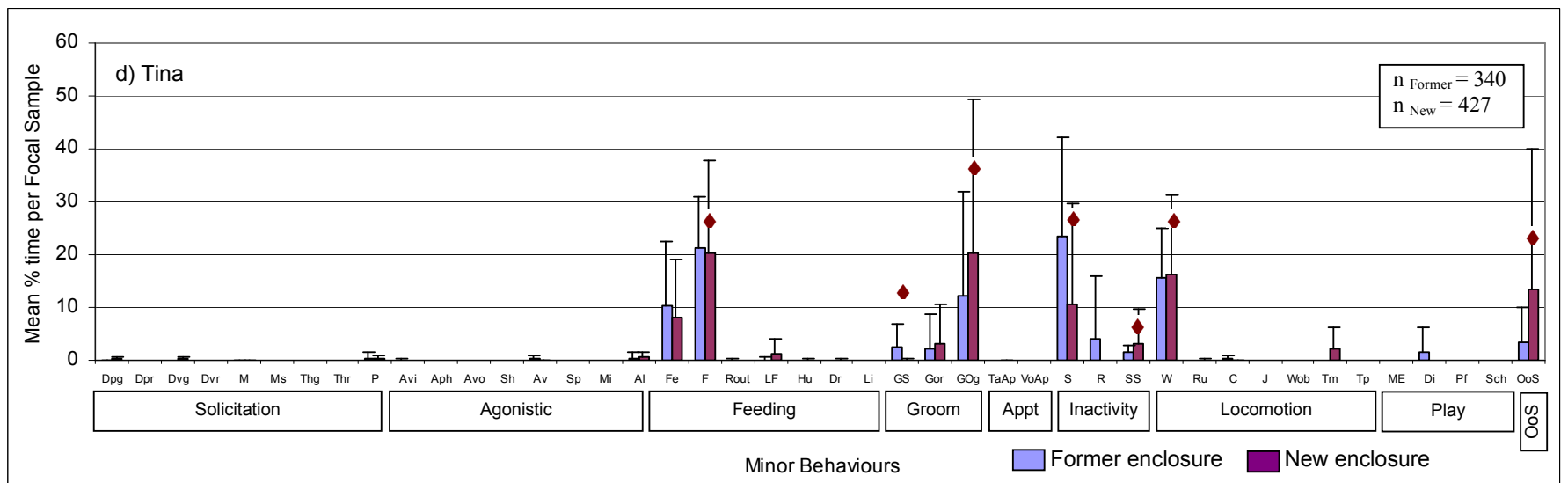
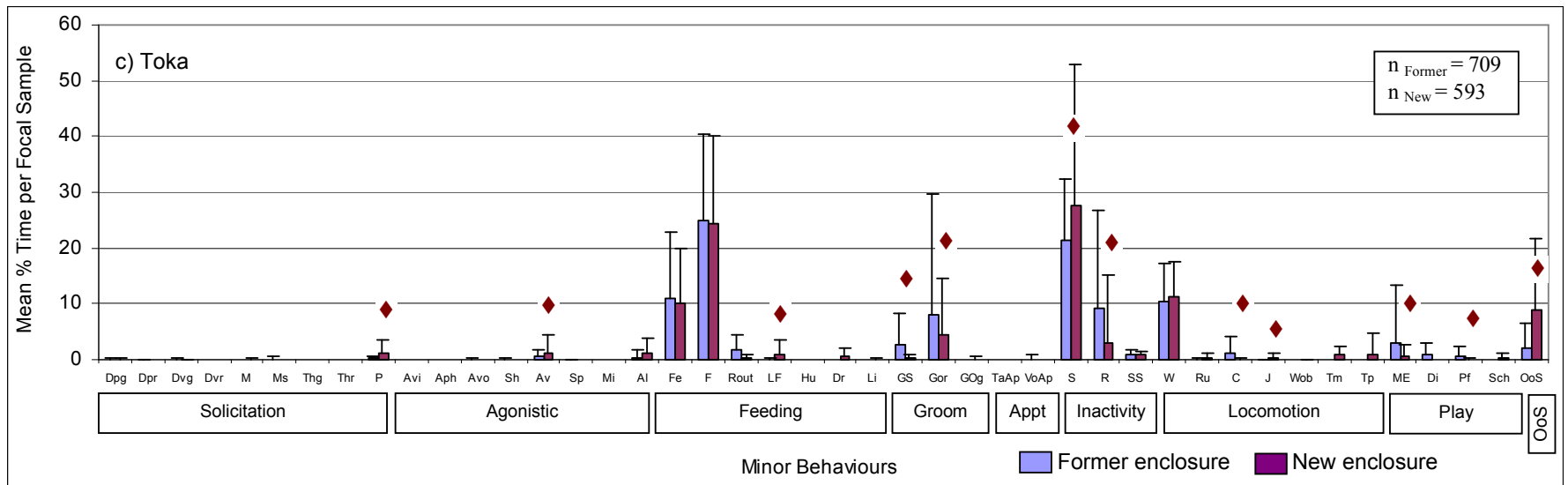
Chi square tests comparing two log linear models demonstrated statistically significant differences in the overall occurrence of nine of the 21 “minor” behaviours common to both enclosures in focal samples of Sinead (Figure 4.2e)

Of these nine “minor” behaviours, statistically significant increases were recorded in the overall occurrence of only two i.e. *feeding* (“feeding activity” behaviour), and *out of sight* (χ^2 test, $p = 0.0003$, $p = 0.0003$

respectively), upon Sinead's relocation to the new enclosure. The remaining seven "minor" behaviours for which results indicated a statistically significant difference in overall occurrence i.e. *pursuit* ("solicitation" behaviour), *foraging* ("feeding activity" behaviour), *receiving grooming* and *grooming other* ("grooming" behaviours), *sitting* and *resting* ("inactivity" behaviours), and *climbing* ("locomotion behaviour), were all found to decline significantly (χ^2 test, $p = 0.0232$, $p = 0.0276$, $p = 0.0003$, $p = 0.0000$, $p = 0.0446$, $p = 0.0055$, $p = 0.0002$ respectively).

The remaining 12 "minor" behaviours common to both enclosure were found to have no statistically significant difference in overall occurrence between the former and new enclosures (χ^2 test, $p > 0.05$).





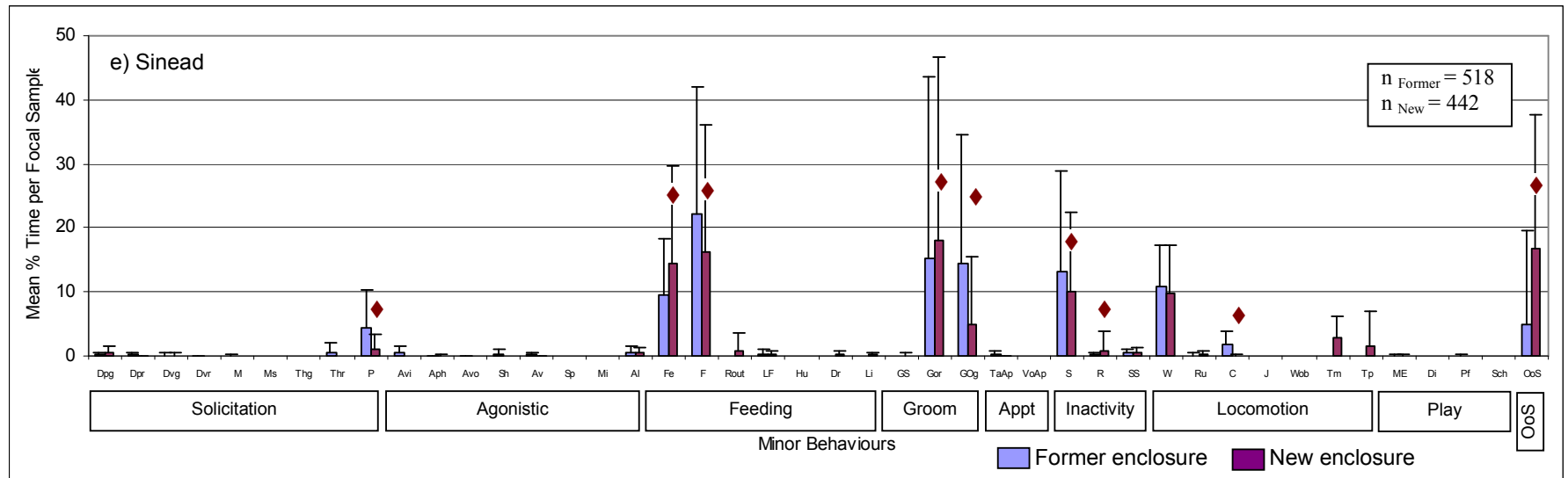


Figure 4.2a) to 4.2e). Activity budget for “minor” behaviours for individual focal animals, Abu, Randy, Toka, Tina and Sinead respectively. Mean percentage time \pm SD per 10 to 15 minute focal sample for each “major” behaviour is shown. ♦ Indicates “minor” behavioural categories with significant differences in overall occurrence between the former and new enclosures, where n = the total number of “minor” behaviours sampled.

4.4 COMPARISON OF MEAN BOUT LENGTHS OF BEHAVIOURS BETWEEN THE FORMER AND NEW ENCLOSURES

4.4.1 Relative bout lengths of “major” behaviours

Figures 4.3a to 4.3e illustrate the distribution of “major” behaviour bout lengths (i.e. duration in seconds) for each individual focal animal in the former and new enclosures. (Precise p-values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.9.1 to 6.9.5).

4.4.1.1 Abu

Analysis of variance determined a statistically significant difference between the former and new enclosures in the mean bout length of one of the seven “major” behaviours common to both enclosures for Abu (Figure 4.3a) i.e. a statistically significant increase in the mean bout length of “locomotion” was found upon Abu’s release into the new enclosure (ANOVA, $p = 0.0407$). No statistically significant differences in mean duration were discernible for the six remaining “major” behaviours common to both enclosures i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity” and “out of sight” (ANOVA, $p > 0.05$).

4.4.1.2 Randy

Analysis of variance deduced a statistically significant difference between the former and new enclosures in the mean bout length of one of the seven “major” behaviours common to both enclosures for Randy (Figure 4.3b) i.e. a statistically significant increase in the mean duration of “feeding activity” was found upon his relocation to the new enclosure (ANOVA, $p = 0.0069$). There was no discernible difference between the enclosures in the mean bout lengths of the remaining “major” behaviours common to both enclosures i.e. “solicitation”, “agonistic”, “grooming”, “inactivity”, “locomotion” and “out of sight” (ANOVA, $p > 0.05$).

4.4.1.3 Toka

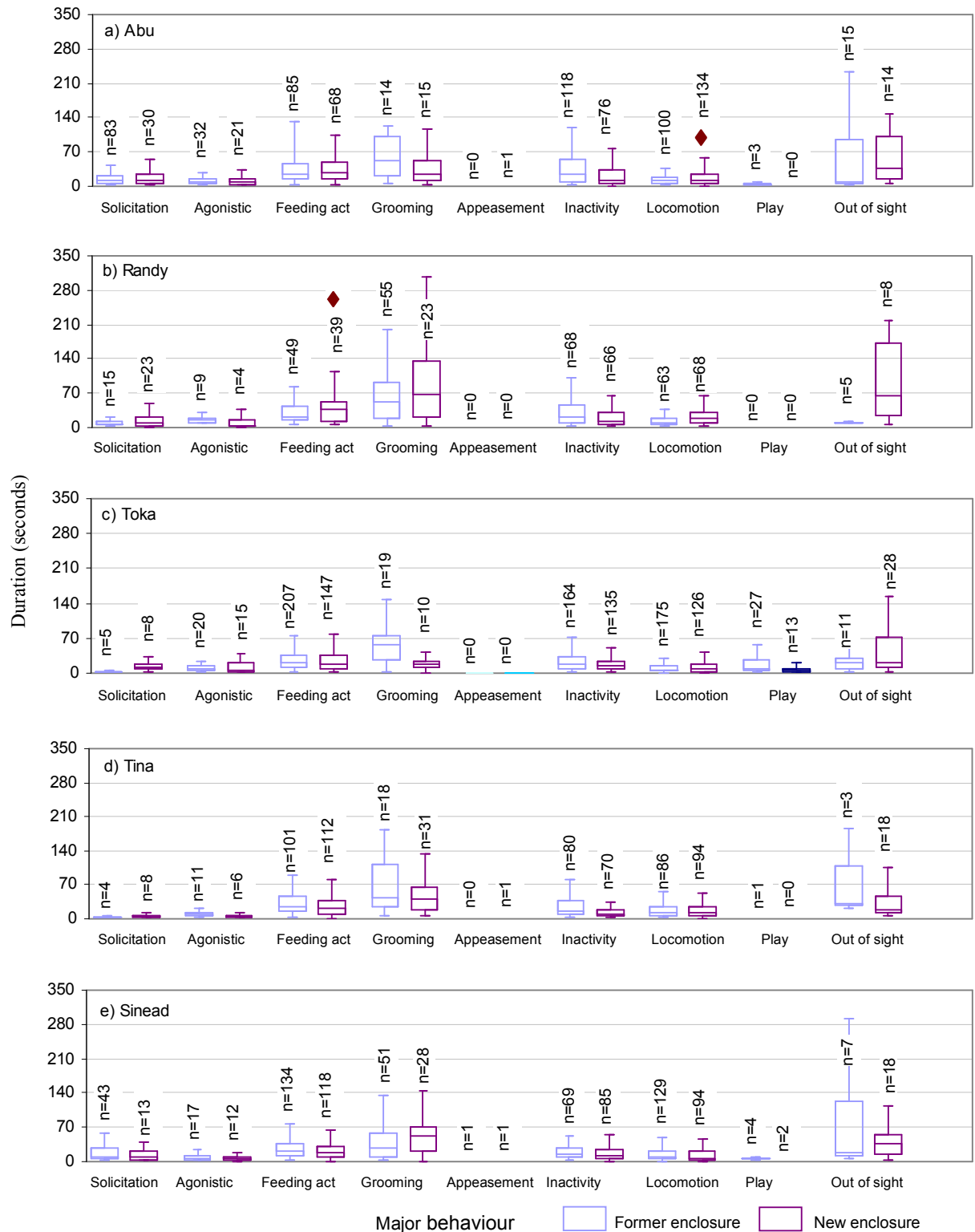
No statistically significant differences between the former and new enclosures were discernible for Toka in the mean bout lengths of the eight “major” behaviours common to both enclosures i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity”, “locomotion”, “play” and “out of sight” (ANOVA, $p > 0.05$) (Figure 4.3c).

4.4.1.4 Tina

Analysis of variance failed to determine statistically significant differences for Tina in the mean duration of the seven “major” behaviours common to both the former and new enclosures i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity”, “locomotion”, and “out of sight” (ANOVA, $p > 0.05$) (Figure 4.3d).

4.4.1.5 Sinead

No statistically significant differences were discernible for Sinead in the mean bout lengths of eight of the nine “major” behaviours common to both the former and new enclosures i.e. “solicitation”, “agonistic”, “feeding activity”, “grooming”, “inactivity”, “locomotion”, “play” and “out of sight” (ANOVA, $p > 0.05$) (Figure 4.3e). There were insufficient instances of the remaining “major” behaviour, i.e. “appeasement” ($n_f = 1$, $n_n = 1$) in both the former and new enclosures for Sinead to compare mean duration.



Figures 4.3a) to 4.3e). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “major” behaviours for individual focal animals (Abu, Randy, Toka, Tina and Sinead respectively) whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. ♦ Indicates significant differences in the mean duration of “major” behaviours between the former and new enclosures, where n = the total number of “major” behaviours sampled.

4.4.2 Relative bout lengths of “minor” behaviours

The distribution of bout lengths (i.e. duration in seconds) of “minor” behaviours for each individual focal animal in the former and new enclosures are illustrated in Figures 4.4a to 4.8h. (Precise p-values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.10.1 to 6.10.5).

4.4.2.1 Abu

Analysis of variance, comparing the mean bout lengths of “minor” behaviours between the former and new enclosures, produced statistically significant results for Abu in two of the 21 “minor” behaviours recorded in both enclosures (Figures 4.4a to 4.4h).

A statistically significant increase in the mean bout length of *walking* (“locomotion” behaviour) was found upon Abu’s relocation (ANOVA, $p = 0.0443$). By contrast, the mean bout length of *climbing* (also a “locomotion” behaviour) for Abu was found to significantly decline upon his relocation to the new enclosure (ANOVA, $p = 0.0327$).

Of these 21 minor behaviours there were too few instances in the former enclosure of *grooming self* ($n_f = 1$) (“grooming” behaviour) to enable a statistical comparison of the mean bout length of this “minor” behaviour between the former and new enclosures. Likewise insufficient instances of *mating* ($n_n = 1$) (“solicitation” behaviour), *physical aggression* ($n_n = 1$), *vocal aggression* ($n_n = 1$) and *intervention* ($n_n = 1$) (“agonistic” behaviours) in focal samples for Abu in the new enclosure prevented a statistical comparison of mean bout length.

4.4.2.2 Randy

Tests comparing the mean bout lengths of “minor” behaviours between the former and new enclosures produced a statistically significant result in one of the 18 “minor” behaviours recorded for Randy in both enclosures (Figures 4.5a to 4.5h).

A statistically significant increase in the mean bout length of *foraging* (“feeding activity” behaviour) was found upon Randy’s relocation to the new enclosure (ANOVA, $p = 0.0363$).

Of these 18 minor behaviours there were too few instances of *receiving vocal presentation* ($n_f = 1$) and *simulated mating* ($n_n = 1$) (both “solicitation” behaviours), *visual aggression* ($n_f = 1$, $n_n = 1$), *physical aggression* ($n_f = 1$) and *avoidance* ($n_n = 1$) (“agonistic” behaviours) and *resting* ($n_n = 1$) (“inactivity” behaviour) in either or both enclosures in focal samples for Randy to make a statistical comparison of mean bout length.

4.4.2.3 Toka

Analysis of variance, comparing the mean bout lengths of “minor” behaviours between the former and new enclosures, produced statistically significant results in one of the 21 “minor” behaviours recorded for Toka in both enclosures (Figure 4.6a to 4.6h).

Results indicated a statistically significant increase in the mean bout length of *running* (“locomotion” behaviour) (ANOVA, $p = 0.0374$).

Of these 21 minor behaviours, there were too few instances of *vocal presentation* ($n_f = 1$, $n_n = 1$) (“solicitation” behaviour), *reaching out* ($n_f = 20$, $n_n = 1$) (“feeding activity” behaviour) and *jumping* ($n_f = 1$, $n_n = 1$) (“locomotion” behaviour) in both enclosures to make a statistical comparison of mean bout length.

4.4.2.4 Tina

Statistically significant differences in mean bout length was found in one of the 16 “minor” behaviours recorded for Tina in both the former and new enclosures (Figure 4.7a to 4.7h).

The mean bout length of *avoidance* (“agonistic” behaviour) was found to significantly decline in the new enclosure (ANOVA, $p = 0.0069$).

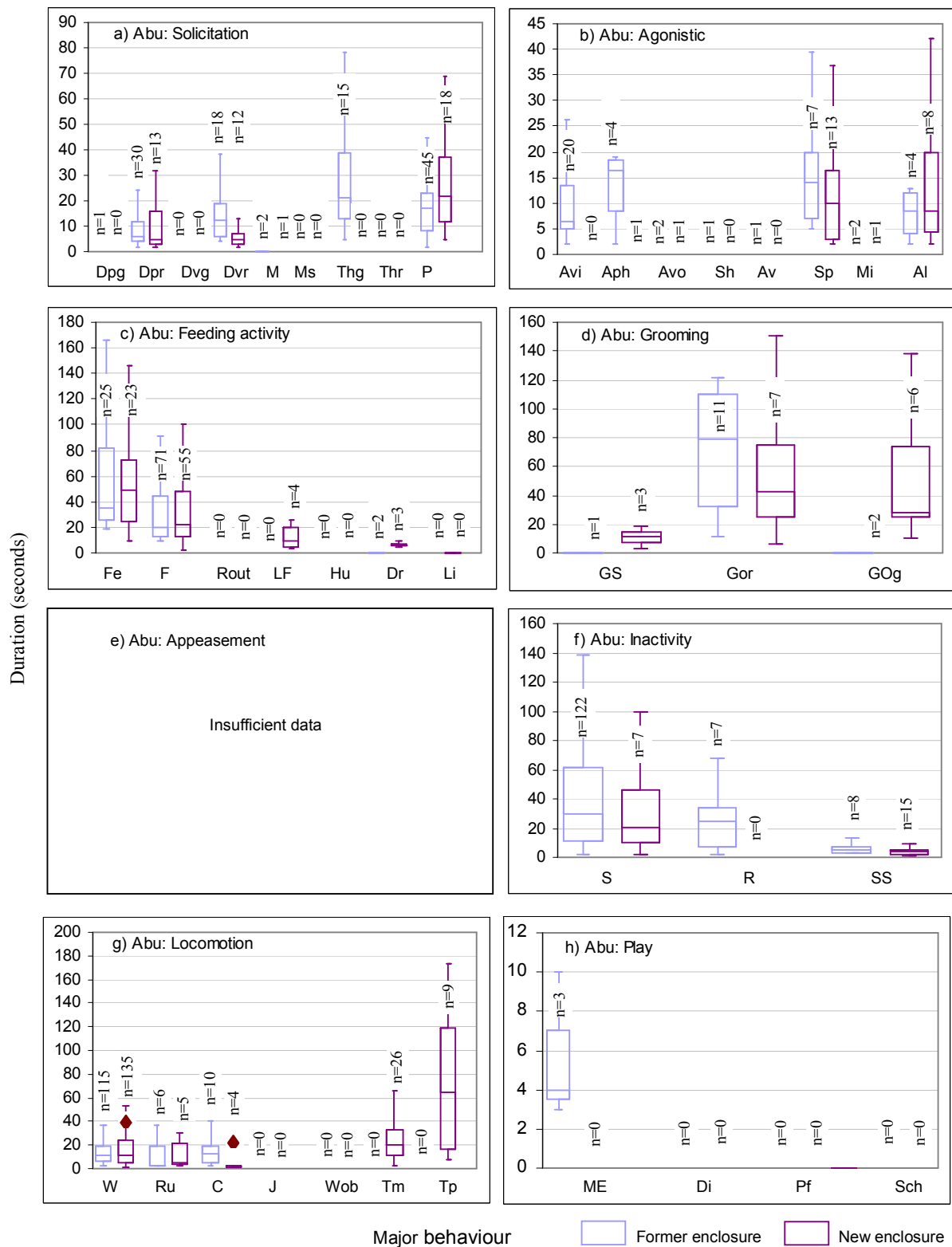
Of these 16 minor behaviours, there were too few instances of *visual presentation* ($n_f = 1$) (“solicitation” behaviour), *grooming self* ($n_n = 1$) (“grooming” behaviour) and *climbing* ($n_n = 1$) (“locomotion” behaviour) in one enclosure to enable a statistical comparison of mean bout length.

4.4.2.5 Sinead

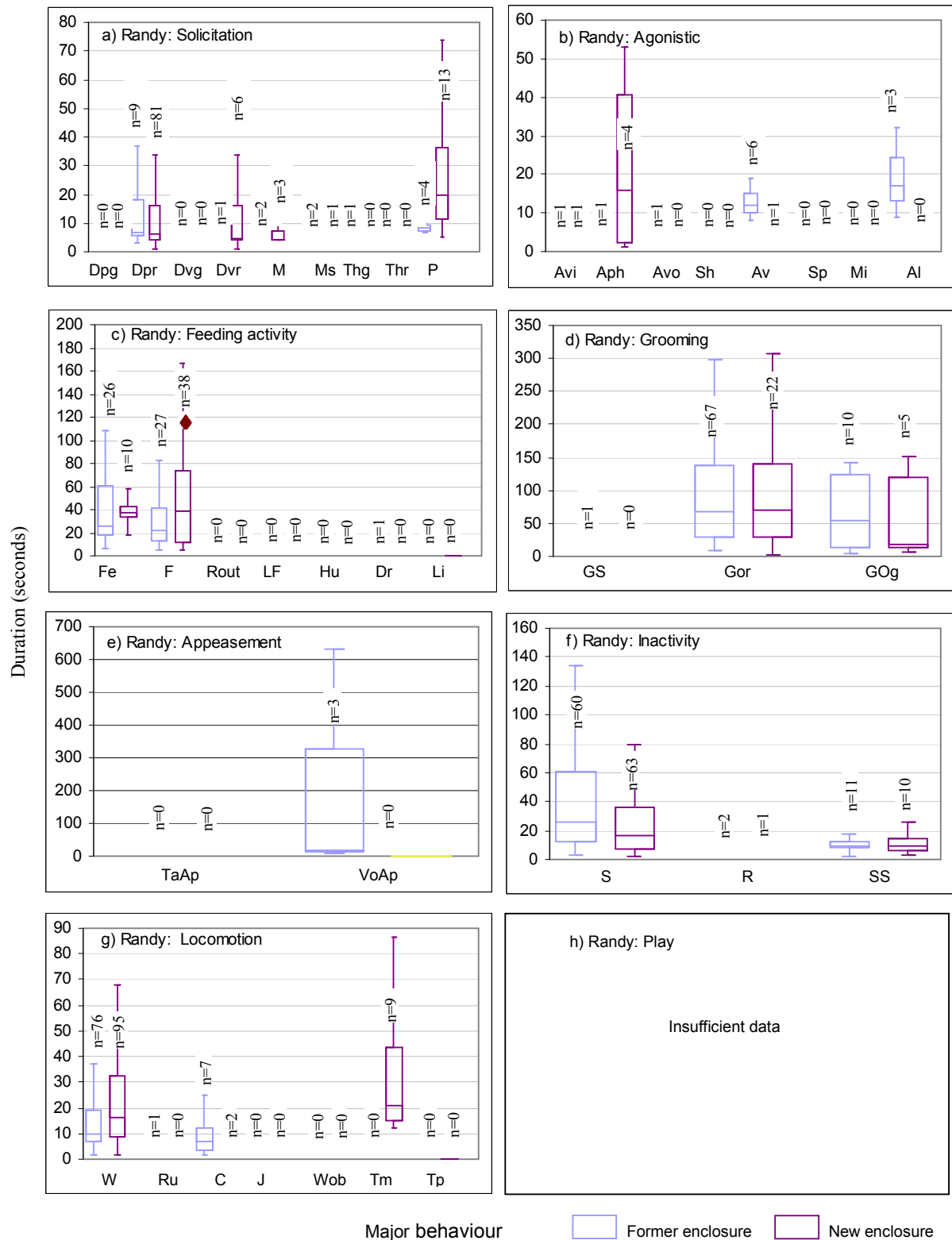
Statistical tests, comparing the mean bout lengths of “minor” behaviours between the former and new enclosures, produced significant results in two of the 21 “minor” behaviours recorded for Sinead in both enclosures (Figure 4.8a to 4.8h).

Statistically significant decreases in the mean bout lengths of *standing still* (“inactivity” behaviour) and *climbing* (“locomotion” behaviour) were found upon Sinead’s relocation (ANOVA, $p = 0.0421$ and $p = 0.0368$ respectively).

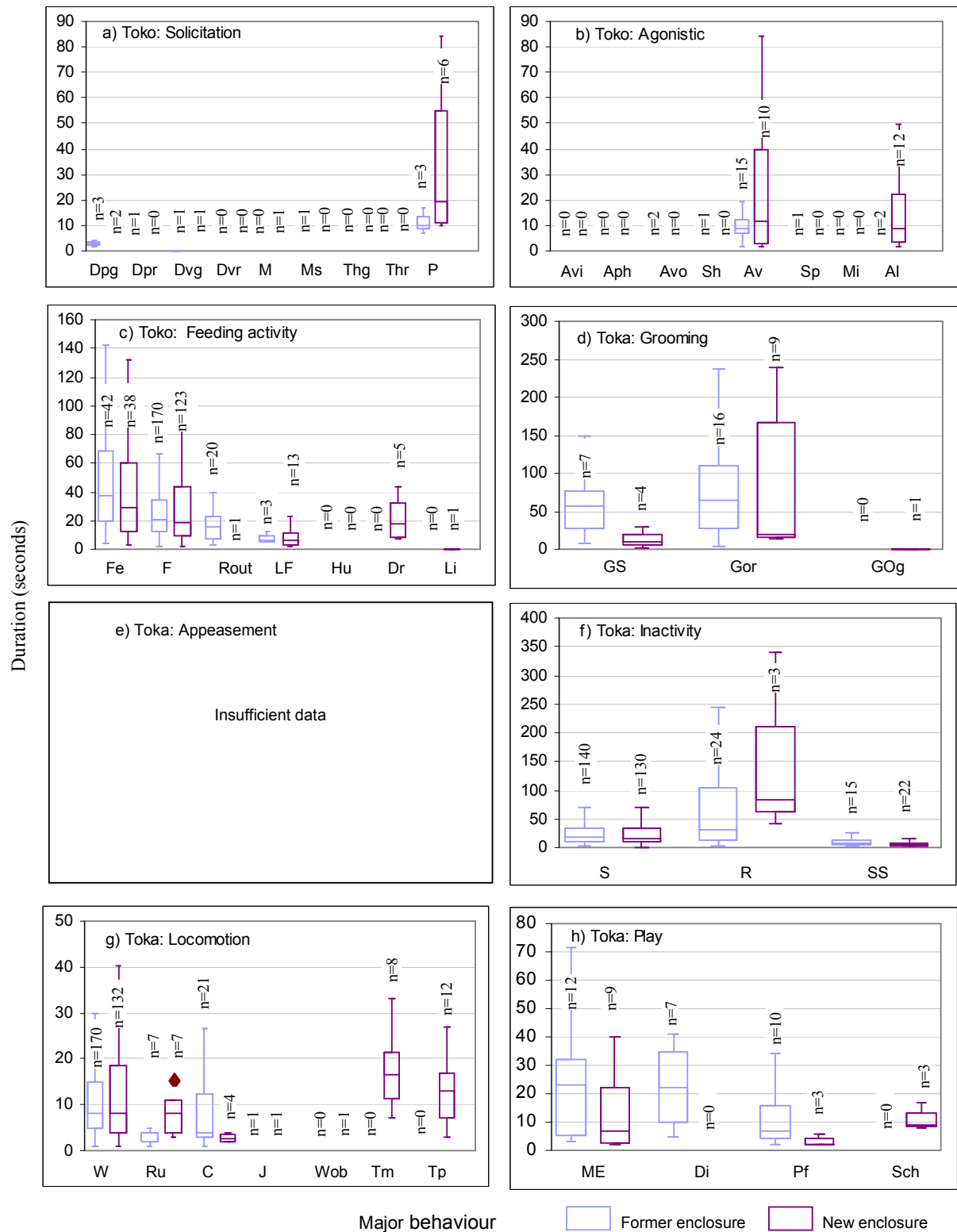
Of these 21 minor behaviours, there were too few instances of *receiving visual presentation* (“solicitation” behaviour) (for which $n_n = 1$ but this instance did not appear in data for mean bout length), *physical aggression* ($n_f = 20$, $n_n = 1$) (“agonistic” behaviour) and *tactile appeasement* ($n_f = 20$, $n_n = 1$) (“appeasement” behaviour) in either or both enclosures to make a statistical comparison of mean bout length.



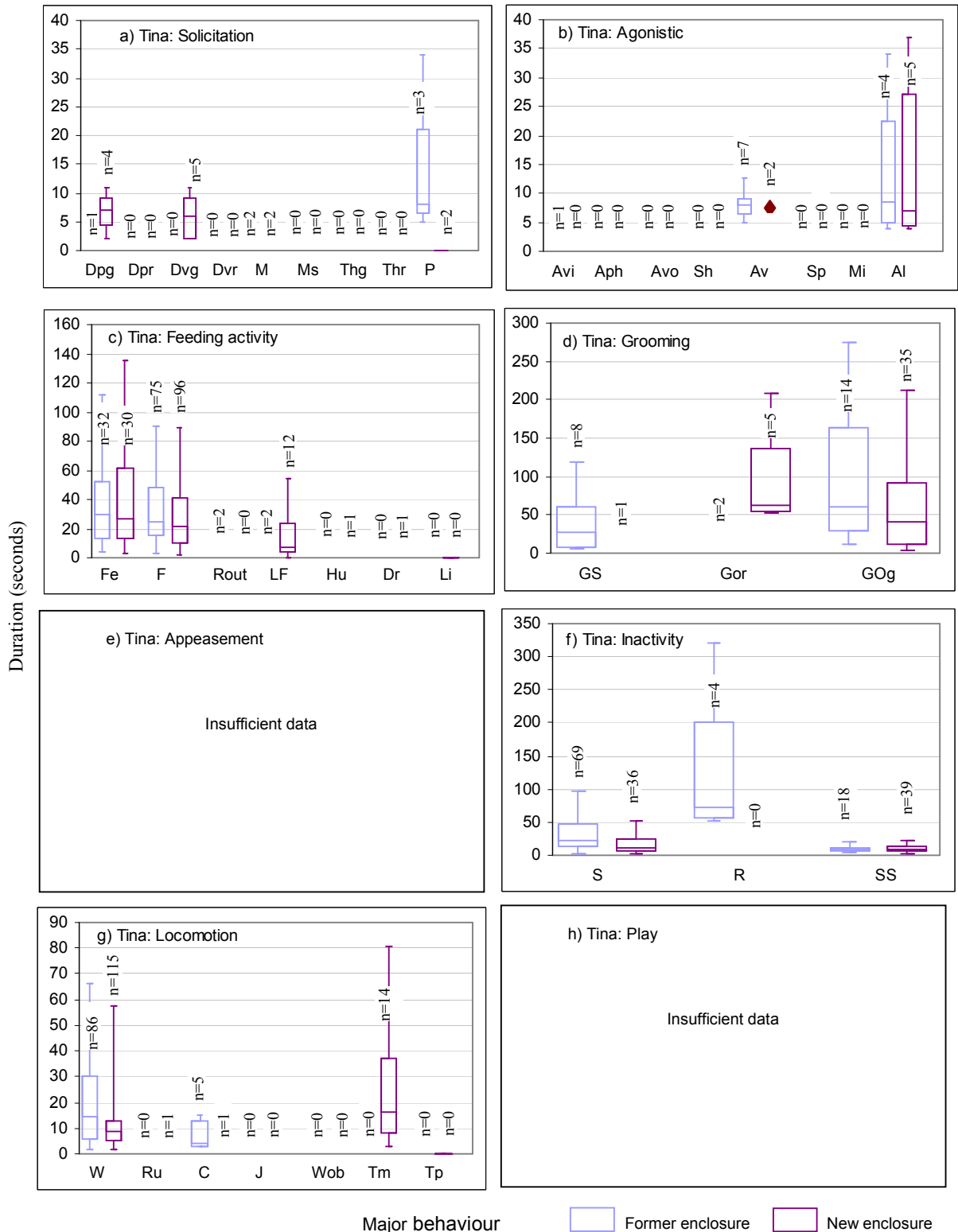
Figures 4.4a) to 4.4h). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for Abu whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.



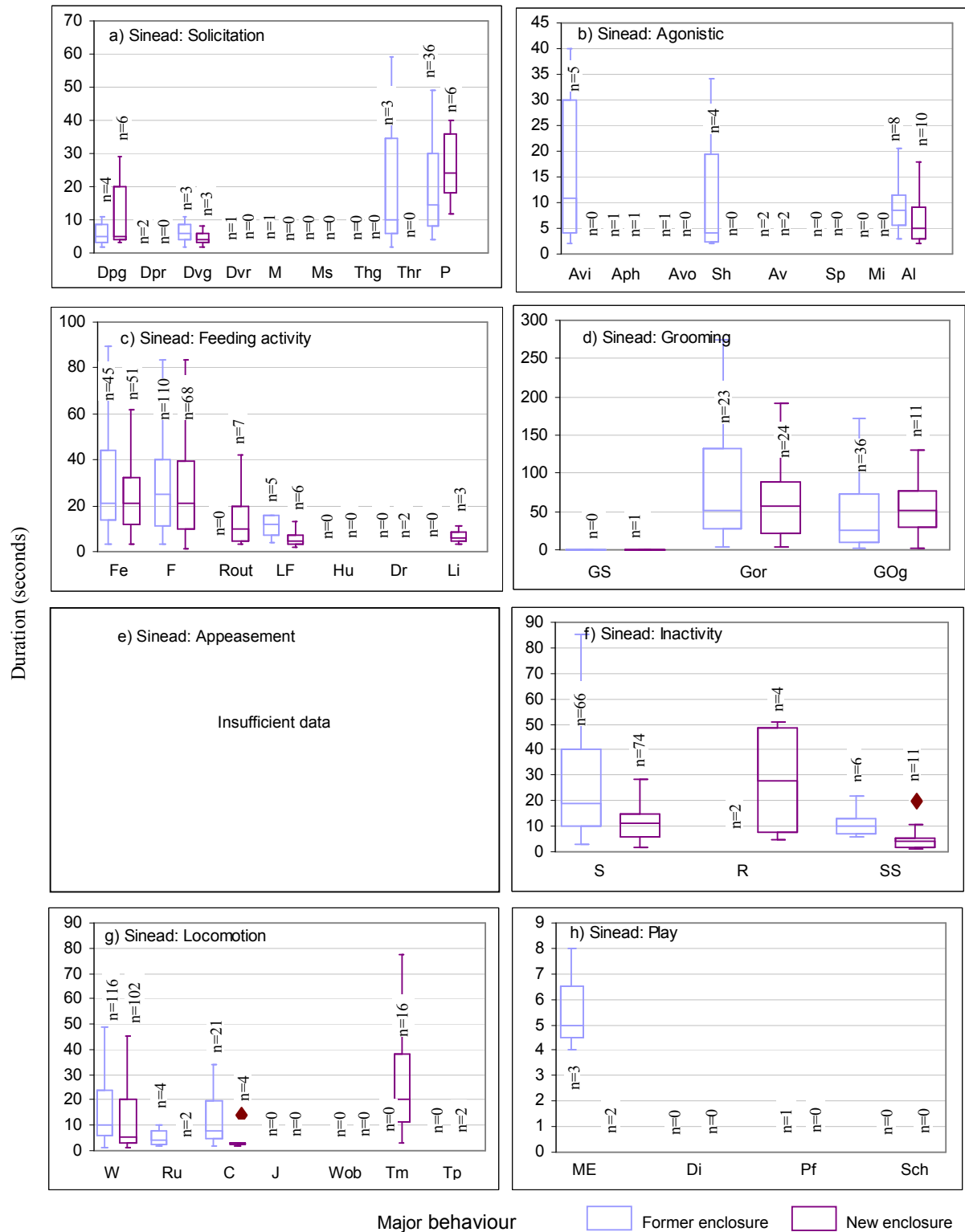
Figures 4.5a) to 4.5h). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for Randy whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.



Figures 4.6a) to 4.6h). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for Toka whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.



Figures 4.7a) to 4.7h). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for Tina whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.



Figures 4.8a) to 4.8h). Modified box-and-whisker plots illustrating the distribution of durations (seconds) of “minor” behaviours for Sinead whereby data points up to 1.5 times the inter-quartile range (from the medians) are shown. Behaviours were only included if their complete duration was visible. “Minor” behaviours are grouped according to “major” behavioural categories. Abbreviations correspond with the ethogram (Table 2.1). ♦ Indicates significant differences in the mean durations of “minor” behaviours between the former and new enclosures, where n = the total number of “minor” behaviours sampled.

4.5 COMPARISON OF OVERALL OCCURRENCE OF SOCIAL STATES BETWEEN THE FORMER AND NEW ENCLOSURES

The overall occurrences of “solitary”, “grouped” and “social” states in the former and new enclosures are represented in Figures 4.9a to 4.9e. These relate to each focal animal, respectively, as mean percentage time per sample in lieu of overall occurrence. (Degrees of freedom are recorded in Appendix B, Table 6.11.1 to 6.11.5).

4.5.1 Abu

Chi square tests comparing two log linear models determined that the overall occurrence of the “solitary” state by Abu significantly increased upon his relocation to the new enclosure (χ^2 test, $p = 0.0000$). By contrast, the overall occurrence of the “grouped” state was found to significantly decline (χ^2 test, $p = 0.0000$). No statistically significant difference was discernible in samples for Abu between the former and new enclosures in the overall occurrence of the “social” state (χ^2 test, $p = 0.3006$) (Figure 4.9a).

4.5.2 Randy

Statistical analysis determined a significant increase in the overall occurrence of both “solitary” and “grouped” states in samples for Randy upon his relocation to the new enclosure (χ^2 test, $p = 0.0000$ and $p = 0.0122$ respectively). Conversely, a statistically significant decrease in the overall occurrence of the “social” state by Randy was determined in the new enclosure (χ^2 test, $p = 0.0000$) (Figure 4.9b).

4.5.3 Toka

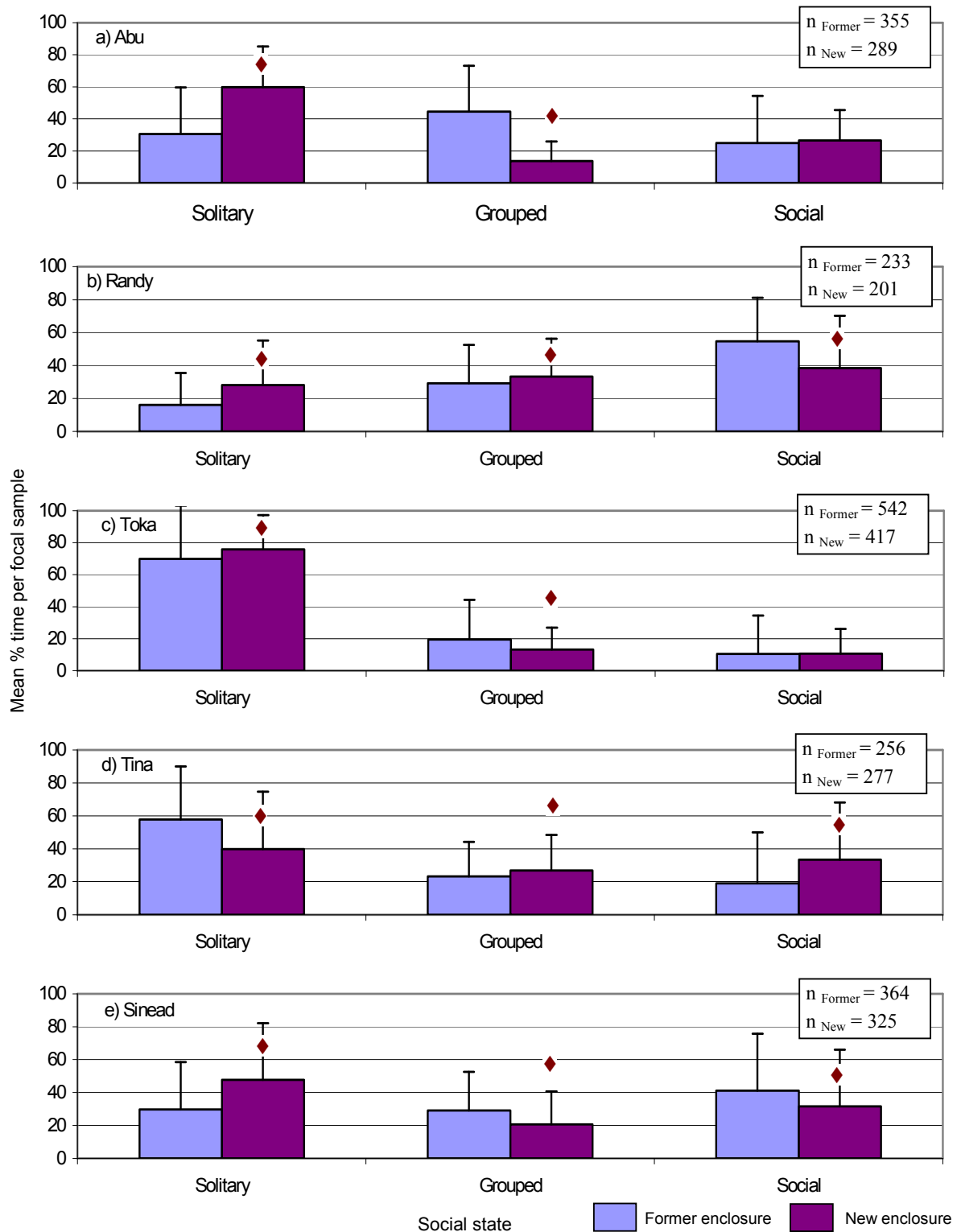
A statistically significant increase in the overall occurrence of the “solitary” state was determined for Toka upon his relocation to the new enclosure (χ^2 test, $p = 0.0000$). By contrast, the overall occurrence of the “grouped” state by Toka was found to significantly decline in the new enclosure (χ^2 test, $p = 0.0000$). No significant difference was discernible between the enclosures in focal samples for Toka in the overall occurrence of the “social” state (χ^2 test, $p = 0.7977$) (Figure 4.9c).

4.5.4 Tina

In contrast to the other animals, the overall occurrence of the “solitary” state was found to significantly decrease upon Tina’s relocation to the new enclosure (χ^2 test, $p = 0.0000$). Conversely, the overall occurrence of both “grouped” and “social” states significantly increased upon her relocation (χ^2 test, $p = 0.0420$ and $p = 0.0000$ respectively) (Figure 4.9d).

4.5.5 Sinead

Statistical testing deduced that the overall occurrence of the “solitary” state by Sinead increased significantly upon her relocation to the new enclosure (χ^2 test, $p = 0.0000$). By contrast, the overall occurrence of the “grouped” and “social” states were found to significantly decrease upon her relocation (χ^2 test, $p = 0.0000$ and $p = 0.0000$ respectively) (Figure 4.9e).

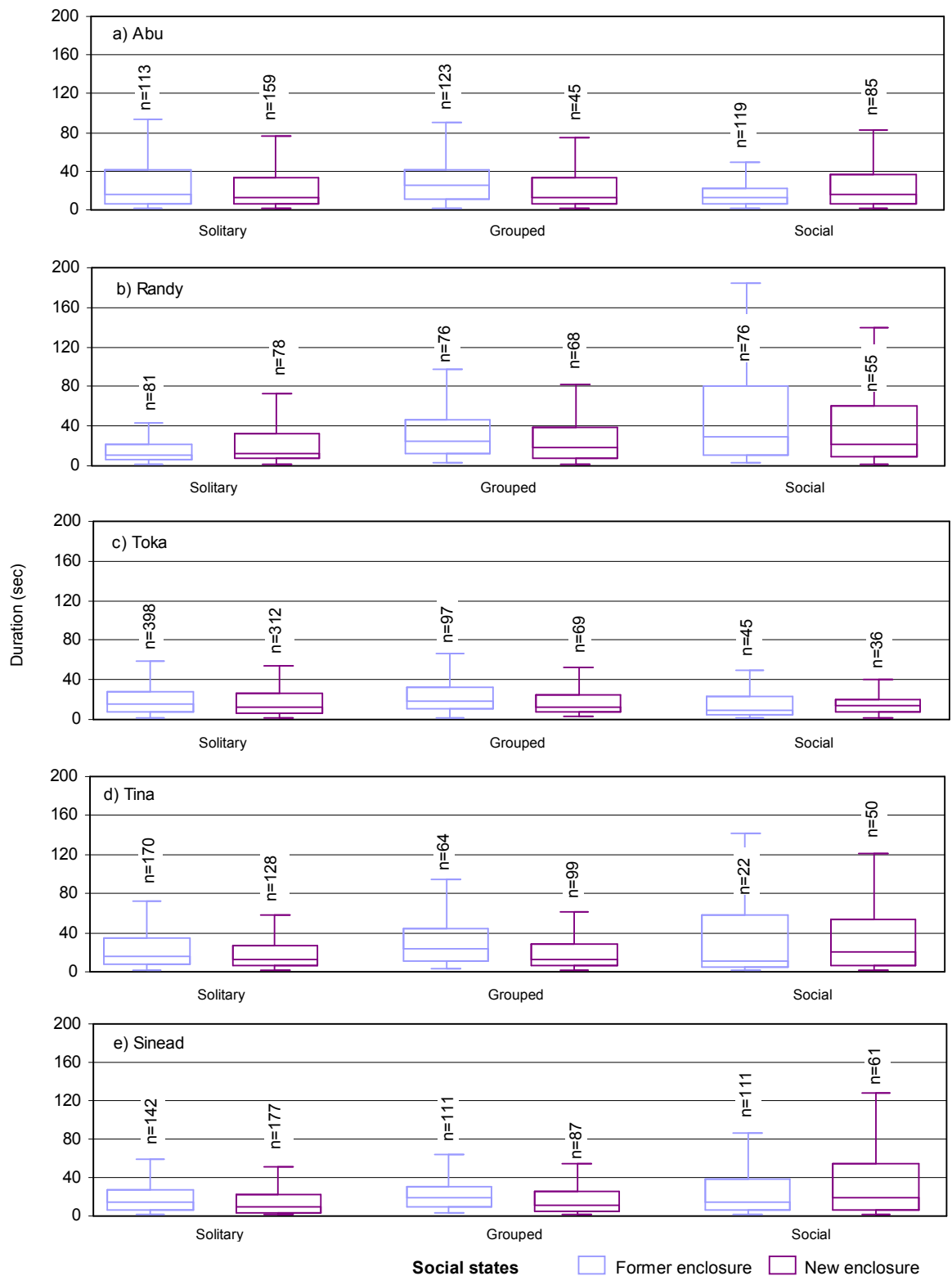


Figures 4.9a) to 4.9e). Activity budget of social states by the individual focal animals., Abu, Randy, Toka, Tina and Sinead respectively. Mean percentage time \pm SD per 10 to 15 minute focal sample for each social state are shown. ♦ Indicates social states with significant differences between the former and new enclosures, where n = the total number of states sampled.

4.6 COMPARISON OF MEAN BOUT LENGTHS OF SOCIAL STATES BETWEEN THE FORMER AND NEW ENCLOSURES

Figures 4.10a to 4.10e illustrate the distribution of bout lengths (i.e. duration in seconds) of “solitary”, “grouped” and “social” states for each focal animal respectively in the former and new enclosures. (Precise p-values, degrees of freedom and the full range of outlying values are recorded in Appendix B, Table 6.12.1 to 6.12.5).

Analysis of variance failed to determine any statistically significant differences between the former and new enclosures in the mean bout lengths of “solitary”, “grouped” or “social” states for any of the five focal animals (ANOVA, $p > 0.05$).



4.7 SUMMARY DISCUSSION ON PATTERNS OF BEHAVIOUR FOR INDIVIDUAL FOCAL ANIMALS

4.7.1 Introduction to individual focal animals


Other researchers have observed differences in the response of individual animals of the same species to environmental enrichment (Brent and Long 1995). Kessel and Brent (1996), for example, found that varying age/sex classes of group-housed baboons showed different use of areas upon the provision of structural enrichment. Such differences have been attributed to variations in body size, level of activity and status (Kessel and Brent 1996).

In order to establish a more detailed understanding of the focal animals' response to relocation, the results of each focal animal were analysed individually. The following summarises interpretations of the results of this analysis. Expanded interpretations for each individual focal animal are appended (Appendix C, 6.3.1 to 6.3.5). These interpretations concentrate primarily on results that deviate from those of the combined focal animals (notwithstanding that each animal's results contributed to this combined response). These deviations are highlighted in tables preceding the summary discussion of each individual focal animal. The tables detail the response of each focal animal to relocation (Tables 4.4 to 4.8) and should be read using the key below (refer Table 4.3).

Interpretations are based on the observer's understanding of each animal's age, relative dominance and social function and the behaviours involved.

Kummer (1995) described his ethogram of the Zurich Zoo hamadryas baboon colony as consisting of behaviours associated with both sexes. By contrast, some behaviours specific to the Wellington Zoo ethogram (such as *herded by tail*, which was undertaken exclusively by male harem leaders) appear to be exclusive to certain situations, including gender. In many instances, absent and infrequent behaviours have best validated a focal animal's individual description. However, it should be noted here that behaviours absent from an individual's focal samples may be a consequence of their extreme infrequency (due to individuality and/or the infrequency of specific situations that would elicit that behaviour) rather than a complete absence of that behaviour from an individual's repertoire.

Table 4.3. Key to tables comparing responses of combined focal animals with those of individual focal animals.

Heading	CFA	Enclosures	Overall occurrence	Mean bout lengths	Repetition	Counts
Definition	Summary of results for combined focal animals	The enclosure/s in which the behaviour was observed	Summary of chi square results comparing overall occurrence between the enclosures	Summary of ANOVA results comparing mean bout length between the enclosures	Summary of relative repetition of behaviours between the enclosures	Summary of logit modelling results that compare the odds of each of the “major” and “minor” behavioural categories occurring per sample in each enclosure
Indicator	Definition					
↑	Increase between the former and new enclosures					
↓	Decrease between the former and new enclosures					
○	No difference between the former and new enclosures					
Too few	Insufficient instances in one or both enclosures to test for a difference upon relocation					
-	Comparison between the enclosures impossible due to absence of behaviour in one or both enclosures					
③	More repetition and/or an increase in mean duration may have caused an increase in overall occurrence (refer Table 3.2)					
⑦	Less repetition and/or a decrease in mean duration may have caused a decrease in overall occurrence (refer Table 3.2)					
	Deviations in the response of the combined focal animals and individual focal animals to relocation					

4.7.2 Preamble to interpretation of male focal animals' responses

Kummer (1995) observed that no discernible rank order was apparent amongst free-ranging male hamadryas baboons and that, if such an order exists, they must disguise it. For example, signs of subordination, including baring teeth, such as those seen amongst other *Papio* subspecies, are never seen in even the most intense fights between male hamadryas baboons (Kummer 1995). In addition, dominance is moderated and restricted by the ‘early bird principle’ (Kummer 1973).

Male hamadryas baboons share multiple bonds, which hold the band together (Kummer 1968). However, the concept of a rank order among these males' of limited value. This is because males can be ranked differently according to specific variables such as the number of females in their units and how influential they are in determining the direction the group will travel (Kummer 1968)

A single rank order was, however, established by Fritz (1979, cited in Kummer 1995:167) for five captive male hamadryas baboons at Munich Zoo.

Kummer (1995) gave no reason as to why this single hierarchical order was determinable in captivity. The observer suggests two possible explanations for this. Firstly, in the constraints of captivity, the animals are prevented from moving between groups. One reason why a single hierarchical order may not exist amongst free-ranging male hamadryas baboons is that the size of the troop is not static. Rather, it is correlated to the availability of ecological resources and, in particular, food density (Kummer 1995). The absence of a rigid rank order amongst male baboons from Ishasha in Uganda was interpreted in this way i.e. the movement of males between troops prevented the formation of a fixed rank order (Rowell 1972). Secondly, some measures of subordination, including submission (Kummer and Kurt 1965), appear to be accentuated in captivity. In Fritz' investigation, instances of 'presenting', which has been found to occur more frequently in captivity than in the wild (Kummer and Kurt 1965), were used to measure subordination (Fritz 1979, cited in Kummer 1995:167). For the purposes of the current investigation, *visual presentation* between males has been described as a 'pseudo-sexual' behaviour.

Within samples of male focal animals in the current investigation, 'presenting' occurred too infrequently to be used as a measure of dominance and subordination, with only four instances recorded in the former enclosure and two in the new enclosure amongst the three focal males.

Instances of *supplanting* and *avoidance* were subsequently deemed to provide the best measure of a rank order among the focal males. Specifically, the animal with the highest incidence of *supplanting* and lowest incidence of *avoidance* was assumed to be the most dominant animal and the animal with the lowest incidence of *supplanting* and highest incidence of *avoidance*, the least dominant. These two particular "minor" behaviours correlate to the approach-retreat interaction described by Rowell (1972) which have also been found to occur more frequently amongst captive hamadryas baboons than their wild counterparts.

The relationship between two monkeys can be influenced by their independent interactions with other conspecifics. It is for this reason that the total number of times that an animal performs a behaviour, independent of partner, can be expected to be a useful measure of the animal's position in its group's social organisation (Rowell 1972).

The supplant-avoidance measure of rank order was especially appropriate for the current investigation because such interactions were seen to occur in both enclosures. Consequently, the same measure could be used to determine if the relative rank of the three focal males remained constant between the enclosures. This is especially significant because hierarchy is not fixed and is "potentially capable of being altered as conditions change" (Rowell 1972:161).

In an effort to find an alternative to hierarchy as a descriptive model for primate social organisation, several workers have attempted to describe the behaviour of monkey groups in terms of social roles [i.e. "a consistent pattern of response shown by particular members of society in specified situations" (Bernstein 1966, cited in Rowell 1972:168)].

Two gradually overlapping roles pertaining to age characterise adult male hamadryas baboons – "that of the young unit leader and breeder, and that of the old troop leader" (Kummer 1968:83). These roles would appear to

correspond to the 'initiator' and 'decider' roles (i.e. "I-role" and "D-role" respectively) described by Kummer (1968). 'Initiator' males propose the course of travel and instigate the group's movement. However, it is typically the older 'decider' male that makes the final verdict in situations including the direction the group will take during its daily march (Kummer 1968).

Due to the infrequency of overt notification, both the occurrence of two-male team behaviour [i.e. "the associations of two units co-ordinated by their leaders" (Kummer 1968:124)] and the role of each of the focal males on the spectrum of unit leader to troop leader could not be clarified given the data available. Notification, a form of presentation, refers to the exchange of gestures thought to indicate the imminent change of the spatial relationship of animals important for the cohesion of the party (Kummer 1968). These gestures can be as inconspicuous as subtle glances or as overt as the presentation of the face or anal field (Kummer 1968). Whether in the two-male team or broader group, the younger unit leader and 'initiator' typically notifies to the older troop leader and 'decider' more often than the other way around (Kummer 1968), providing some index to clarify these roles. Unfortunately, there was also an absence of data on the order of individuals in *troop patrol* and *troop movement* behaviours that may also have shed light onto the specific roles occupied by the focal males. Specifically, 'initiator' males take the lead and 'decider' males take the rear in the procession of two-male teams, and 'initiator' males take the lead and 'decider' males progress in the middle during broader troop movement (Kummer 1968). In the current investigation, the procession of animals during such movement typically went along the enclosures elevated back boundary where the observer could not get an unobstructed view of each of the animal's individually identifying characteristics.

However, in instances of cohesive group movement (specifically, *troop patrol* and *troop movement*), and given the co-ordination role undertaken by adult males under similar situations in the wild, the two adult focal males, i.e. Abu and Randy, could have been expected to fulfil some co-ordination role within the broader colony. This role had an opportunity to develop upon the colony's relocation because, in the former enclosure, cohesive group behaviour beyond the harem was not apparent to the observer.

4.7.2.1 Abu's responses to relocation

Table 4.4. Abu response to relocation including comparison with responses of combined focal animals.

Abu	Enclosures		Overall occurrence		Mean bout lengths		Repetition		Counts	
	CFA	Abu	CFA	Abu	CFA	Abu	CFA	Abu	CFA	Abu
MAJOR BEHAVIOURS									↓	○
Solicitation	Both	Both	↓	↓	○	○	↓	↓		
Agonistic	Both	Both	○	○	○	○	○	○		
Feeding activity	Both	Both	○	○	○	○	○	○		
Grooming	Both	Both	↓	○	○	○	↓	○		
Appeasement	Both	New	○	-	Too few	-	Too few	-		
Inactivity	Both	Both	↓	↓	○	○	↓	↓		
Locomotion	Both	Both	↑	↑	○	↑	↑	③		
Play	Both	Former	↓	-	○	-	↓	-		
Out of Sight	Both	Both	↑	○	○	○	↑	○		
MINOR BEHAVIOURS - SOLICITATION									○	○
Visual presentation	Both	Former	○	-	○	-	○	-		
Receiving visual presentation	Both	Both	○	○	○	○	○	○		
Vocal presentation	Both	Neither	○	-	○	-	○	-		
Receiving vocal presentation	Both	Both	↓	↓	○	○	↓	↓		
Mating	Both	Both	○	○	○	Too few	○	Too few		
Simulated mating	Both	Neither	○	-	Too few	-	Too few	-		
Tail holding	Former	Former	-	-	-	-	-	-		
Herded by tail	Former	Neither	-	-	-	-	-	-		
Pursuit	Both	Both	○	○	↑	○	↓	○		
MINOR BEHAVIOURS - AGONISTIC										
Visual aggression	Both	Former	○	-	Too few	-	Too few	-		
Physical aggression	Both	Both	○	○	○	Too few	○	Too few		
Vocal aggression	Both	Both	○	○	Too few	Too few	Too few	Too few		
Shaking	Former	Former	-	-	-	-	-	-		
Avoidance	Both	Former	○	-	○	-	○	-		
Supplanting	Both	Both	○	○	○	○	○	○		
Intervention	Both	Both	○	○	Too few	Too few	Too few	Too few		
Alert	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS – FEEDING ACTIVITY										
Feeding	Both	Both	○	○	○	○	○	○		
Foraging	Both	Both	↑	○	○	○	↑	○		
Reaching out	Both	Neither	○	-	↑	-	↓	-		
Relocating food	Both	New	↑	-	○	-	↑	-		
Hunting	New	Neither	-	-	-	-	-	-		
Drinking	Both	Both	○	○	○	○	○	○		
Licking	New	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - GROOMING										
Grooming self	Both	Both	↓	○	○	Too few	↓	Too few		
Receiving groomed	Both	Both	↓	○	○	○	↓	○		
Grooming other	Both	Both	○	↑	○	○	○	↑		
MINOR BEHAVIOURS – APPEASEMENT										
Tactile appeasement	Both	New	○	-	Too few	-	Too few	-		
Vocal Appeasement	Former	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - INACTIVITY										
Sitting	Both	Both	↓	↓	○	○	↓	↓		
Resting	Both	Former	↓	-	○	-	↓	-		
Standing still	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS - LOCOMOTION										
Walking	Both	Both	↑	↑	○	↑	↑	③		
Running	Both	Both	○	○	○	○	○	○		
Climbing	Both	Both	↓	↓	↓	↓	②	②		
Jumping	Both	Neither	↑	-	Too few	-	Too few	-		
Relocating object	New	Neither	-	-	-	-	-	-		
Troop movement	New	New	-	-	-	-	-	-		
Troop patrol	New	New	-	-	-	-	-	-		
MINOR BEHAVIOURS - PLAY										
Manipulating environment	Both	Former	↓	-	○	-	↓	-		
Digging	Former	Neither	-	-	-	-	-	-		
Play fighting	Both	Neither	↓	-	○	-	↓	-		
Scraping	New	Neither	-	-	-	-	-	-		
SOCIAL STATES										
Solitary	Both	Both	↑	↑	○	○	↑	↑		
Grouped	Both	Both	↓	↓	○	○	↓	↓		
Social	Both	Both	↓	○	○	○	↓	○		

- Description of first focal male, Abu, and summary of his response to relocation (Note: For a full description of Abu's response to relocation refer Appendix C, 6.3.1).

As a 10.1 year old male when this investigation began, Abu could have been considered a sub-adult or adult male, depending on the classification used. According to the age-sex classes used to classify wild hamadryas baboons developed by Sigg et al. (1982:475), based on his age, Abu fitted into the sub-adult male class (Table 1.1). However, using an alternative age classification developed by Abegglen (in press, cited in Sigg et al. 1982:475), at 10.1 years of age, Abu could have been considered an adult male (Table 1.1). In addition, Abu's physical description more closely resembled that of adult male hamadryas baboons as described by each of the above authors. There is some evidence to suggest that physical development occurs earlier in captivity than in the wild. The final classification represented on Table 1.1 developed by Kummer (1968, cited in Sigg et al. 1982:475) had a footnote indicating that corresponding ages were underestimated based on the author's zoo experience. This is reinforced by the another observation that a difference in weight between males and females was apparent in three-year-old captive baboons, whereas it was not obvious in wild baboons less than five years of age. It was suggested that this difference related to different rates of sexual maturation (Sigg et al. 1982).

All of the above indicated that, when the current investigation began, the most appropriate classification for Abu was adult male.

Using the approach-avoidance criterion outlined above to establish Abu's position in a single male dominance order, Abu was considered to be the highest ranking of the three males for which comparable data was collected. Of these three focal males, Abu demonstrated the least instances of *avoidance* during focal sampling. This occurred in both the former and new enclosures, indicating that his position relative to the other two focal males remained constant in both enclosures. In addition, Abu was seen *supplanting* conspecifics more often than any other focal animal. Abu's relative dominance was seen to be one of a number of influencing variables to his response to relocation as it contrasted with the response of the combined focal animals (Table 4.4).

Abu's most clearly definable role within Wellington Zoo's captive hamadryas baboon colony was that of leader of an established one-male unit (i.e. harem). At the time of this study, Abu's particular unit consisted of himself and two established adult females (i.e. Makele and Sinead, refer Appendix A, Figure 6.1). The composition of this harem was ascertained during the initial observation period.

One characteristic of adult unit leaders is their sexual loyalty towards their harem females (Kummer 1995). [By contrast, during swelling, harem females readily take opportunities to secretly copulate with opportunist juveniles or sub-adults (Kummer 1995)].

Upon entering into a pair bond, the former social attraction amongst sub-adult and adult bachelor males ends (Kummer 1995) as the new leader strives to prevent his unit from mixing with other animals. One way this is achieved is through aggressive herding of unit females by their harem leader (Kummer 1968).

All of the animals in Abu's harem exhibited some degree of naturalistic 'occupational' roles in the former enclosure. These became more apparent upon the animals' relocation to the new enclosure. These more

apparent roles, in turn, further influenced Abu's response to relocation. For example, evidence from his focal samples in the new enclosure showed Abu reasserting his bonds with his females upon the development of these individual 'occupational' roles. These more apparent roles in the new enclosure were also a factor in influencing Abu's limited response to the increased variety of new exploration and foraging opportunities, relative to the other focal animals.

As a harem leader, Abu was naturally protective of his unit (Sigg 1980). This aspect of Abu's harem leadership became more obvious relative to the other focal animals upon the colony's relocation. One indication of this increasingly overt protective behaviour was Abu's response to an increased variety of places to spend time "out of sight" (for privacy and shelter) compared to that of the combined focal animals. In contrast to the latter, Abu remained no less visible upon relocation, accentuating his 'look out' protective function in the new enclosure relative to the combined focal animals.

Abu's exact role beyond his immediate unit could not be fully ascertained. However, as an adult male participating in new cohesive group behaviour (specifically, "minor" "locomotion" behaviours which were only observed in the new enclosure), he may have been required to undertake an increased co-ordination function upon relocation to the new enclosure. This is supported by specific deviations in Abu's response to relocation compared to the combined focal animals. These indicated that Abu's particular co-ordination function was passive (i.e. he was reference point for group behaviour.)

4.7.2.2 Randy's responses to relocation

Table 4.5. Randy's response to relocation including comparison with responses of combined focal animals.

Randy	Enclosures		Overall occurrence		Mean bout lengths		Repetition		Counts	
	CFA	Randy	CFA	Randy	CFA	Randy	CFA	Randy	CFA	Randy
MAJOR BEHAVIOURS										
Solicitation	Both	Both	↓	↑	○	○	↓	↑	↓	○
Agonistic	Both	Both	○	↓	○	○	○	↓		
Feeding activity	Both	Both	○	↑	○	↑	○	3		
Grooming	Both	Both	↓	↓	○	○	↓	↓		
Appeasement	Both	Former	○	-	Too few	-	Too few	-		
Inactivity	Both	Both	↓	↓	○	○	↓	↓		
Locomotion	Both	Both	↑	↑	○	○	↑	↑		
Play	Both	Neither	↓	-	○	-	↓	-		
Out of Sight	Both	Both	↑	↑	○	○	↑	↑		
MINOR BEHAVIOURS - SOLICITATION										
Visual presentation	Both	Neither	○	-	○	-	○	-		
Receiving visual presentation	Both	Both	○	○	○	○	○	○		
Vocal presentation	Both	Neither	○	-	○	-	○	-		
Receiving vocal presentation	Both	Both	↓	↑	○	Too few	↓	Too few		
Mating	Both	Both	○	○	○	○	○	○		
Simulated mating	Both	Both	○	○	Too few	Too few	Too few	Too few		
Tail holding	Former	Former	-	-	-	-	-	-		
Herded by tail	Former	Neither	-	-	-	-	-	-		
Pursuit	Both	Both	○	↑	↑	○	↓	↑		
MINOR BEHAVIOURS - AGONISTIC										
Visual aggression	Both	Both	○	○	Too few	Too few	Too few	Too few		
Physical aggression	Both	Both	○	○	○	Too few	○	Too few		
Vocal aggression	Both	Former	○	-	Too few	-	Too few	-		
Shaking	Former	Neither	-	-	-	-	-	-		
Avoidance	Both	Both	○	○	○	Too few	○	Too few		
Supplanting	Both	Neither	○	-	○	-	○	-		
Intervention	Both	Neither	○	-	Too few	-	Too few	-		
Alert	Both	Former	○	-	○	-	○	-		
MINOR BEHAVIOURS – FEEDING ACTIVITY										
Feeding	Both	Both	○	↓	○	○	○	↓		
Foraging	Both	Both	↑	↑	○	↑	↑	3		
Reaching out	Both	Neither	○	-	↑	-	↓	-		
Relocating food	Both	Neither	↑	-	○	-	↑	-		
Hunting	New	Neither	-	-	-	-	-	-		
Drinking	Both	Former	○	-	○	-	○	-		
Licking	New	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - GROOMING										
Grooming self	Both	Former	↓	-	○	-	↓	-		
Receiving groomed	Both	Both	↓	↓	○	○	↓	↓		
Grooming other	Both	Both	○	↓	○	○	○	↓		
MINOR BEHAVIOURS – APPEASEMENT										
Tactile appeasement	Both	Neither	○	-	Too few	-	Too few	-		
Vocal Appeasement	Former	Former	-	-	-	-	-	-		
MINOR BEHAVIOURS - INACTIVITY										
Sitting	Both	Both	↓	○	○	○	↓	○		
Resting	Both	Both	↓	○	○	Too few	↓	Too few		
Standing still	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS - LOCOMOTION										
Walking	Both	Both	↑	↑	○	○	↑	↑		
Running	Both	Former	○	-	○	-	○	-		
Climbing	Both	Both	↓	○	↓	○	○	○		
Jumping	Both	Neither	↑	-	Too few	-	Too few	-		
Relocating object	New	Neither	-	-	-	-	-	-		
Troop movement	New	New	-	-	-	-	-	-		
Troop patrol	New	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - PLAY										
Manipulating environment	Both	Neither	↓	-	○	-	↓	-		
Digging	Former	Neither	-	-	-	-	-	-		
Play fighting	Both	Neither	↓	-	○	-	↓	-		
Scraping	New	Neither	-	-	-	-	-	-		
SOCIAL STATES										
Solitary	Both	Both	↑	↑	○	○	↑	↑		
Grouped	Both	Both	↓	↑	○	○	↓	↑		
Social	Both	Both	↓	↓	○	○	↓	↓		

- Description of second focal male, Randy, and summary of his response to relocation (Note: For a full description of Randy's response to relocation refer Appendix C, 6.3.2).

As a 19.2-year-old male at the outset of this investigation, Randy could be considered, in wild hamadryas baboon terms, to be an ageing adult male. Free-ranging hamadryas baboons have been estimated to live not much over 20 years (Kummer 1995).

In captivity, hamadryas baboons have survived longer - up to 30 years (Kummer 1995)¹. Randy's old age, and consequent relative inactivity, may provide some indication as to why his complete repertoire of "minor" behaviours (i.e. from both enclosures) consisted of just 26 and, consequently, was much smaller than those of the younger focal animals, in particular Abu, Toka and Sinead, each ten years or more his junior. Age was one variable seen to cause the different use of structural enrichment amongst captive *Papio* baboons in an earlier investigation (Kessel and Brent 1996). One interpretation offered for this, which had also been observed in other captive non-human primates, is higher activity levels of play and locomotion of younger animals (O'Neill et al. 1990, cited in Kessel and Brent 1996:42).

Using the approach-avoidance criterion outlined above, Randy could be considered the second highest ranking of the three focal males i.e. he experienced the second lowest number of instances of *avoidance* of these three animals in both the former and new enclosures. Furthermore, and unlike Abu, at no time was Randy recorded *supplanting* another animal. This indicated that he was not as imposing or threatening. On many occasions (i.e. 85.7 percent) when Randy undertook *avoidance*, Abu supplanted him. This was to be expected because unit leaders, such as Randy and Abu, usually avoid close proximity to each other (Kummer 1968) by keeping at least 1.5 meters apart (Kummer 1995). Such separation is reduced during two types of interaction (Kummer 1968):

- (i) Co-operative interaction in co-ordination of troop movement; and,
- (ii) Aggression.

Of particular interest, on those occasions when Randy exercised *avoidance* behaviour, his actions were often subtle - such as casually turning or lowering his head - rather than pronounced e.g. actively moving away. This subtle behaviour was sufficient to minimise aggression, given that hostility is most imminent when males make eye contact (Kummer 1995). It has also been speculated that responding to conspecifics in such a nonchalant manner is one way in which a male hamadryas baboon maintains his status (Kummer 1968).

Randy was the leader of the other established one-male unit within the Wellington Zoo colony. At the time of this investigation, Randy's unit consisted of long-term bonds with two adult females (i.e. Tina and Jackie – refer Appendix A, Figure 6.1). As a harem leader, Randy could be expected to undertake a protective function similar to Abu, be sexually faithful to his unit, and strive to prevent his females from mixing with other animals. However, Randy had maintained his unit well beyond the estimated age at which unit leaders lose their harems

¹ The oldest baboon within the Wellington Zoo colony at the time of this investigation was a 32.8 year old female.

to younger rivals (i.e. 16 years) (Abegglen in press, cited in Sigg et al. 1982:478). There was evidence in his focal samples to suggest that he was becoming less active in the leadership of his unit. This decline became increasingly apparent upon relocation, especially relative to the response of other focal animals (Table 4.5) and, in particular, Abu, the colony's younger harem leader. This was evident in his limited and declining protective function relative to Abu, whose protective behaviour was accentuated upon relocation.

Despite evidence to suggest that more clearly discernible occupational niches were adopted by Randy's females, in contrast to Abu, these did not appear to limit Randy's response to the increased foraging opportunities offered in the new enclosure. This was one indication of Randy's decreasing level of unit leadership i.e. he was dedicating less time to the protective duties of a harem leader and more time searching for food.

Due to his age, it could be expected that Randy would take the equivalent of a "D-role" (i.e. 'decider' role) in group movement. Old males can maintain this role even after losing their females (Kummer 1995). However, and as was the case with the two other focal males, Randy's exact role beyond his immediate harem could not be fully ascertained due to the absence of overt notification involving Randy and data on the order of individuals during procession. His participation in new cohesive *troop movement* upon relocation to the new enclosure provided some indication that, as an adult male, Randy, like Abu, may also have exercised some co-ordination function. However, unlike Abu, whose response to relocation emphasised an increased co-ordination function, there was no evidence to suggest that Randy responded likewise.

One especially revealing response by Randy to relocation (specifically, an increase in the relative repetition and overall occurrence of "out of sight") corresponded with that of the combined focal animals but deviated from that of the colony's other, younger harem leader, Abu. This deviation in behaviour between Randy and Abu supports the above description of Randy in the following ways:

(i) As a less dominant animal, Randy may have been seeking refuge from social pressure "out of sight" in the greater number of potential hiding places provided in the new enclosure. As an ageing male, Randy had the additional risk of losing his females to younger, stronger rivals. Consequently, the 'early bird principle' may have been insufficient to ensure the coherence of his unit. This lends support to Randy's description as an ageing unit leader.

(ii) It indicated that Randy did not seek out locations with clear views from which to observe and protect his harem. This provided a further indication of his decreasing activity as a unit leader.

(iii) The increased amount of time Randy spent "out of sight" upon relocation indicated that, in contrast to Abu, he did not seek out locations to from which to be seen. This, in turn, indicated that he did not undertake a passive "flag function" (Sigg 1980:274), despite the colony's increased cohesive group behaviour.

4.7.2.3 Toka's responses to relocation

Table 4.6. Toka's response to relocation including comparison with responses of combined focal animals.

Toka	Enclosures		Overall occurrence		Mean bout lengths		Repetition		Counts	
	CFA	Toka	CFA	Toka	CFA	Toka	CFA	Toka	CFA	Toka
MAJOR BEHAVIOURS										
Solicitation	Both	Both	↓	↑	○	○	↓	↑	↓	○
Agonistic	Both	Both	○	↑	○	○	○	↑		
Feeding activity	Both	Both	○	○	○	○	○	○		
Grooming	Both	Both	↓	↓	○	○	↓	↓		
Appeasement	Both	Neither	○	-	Too few	-	Too few	-		
Inactivity	Both	Both	↓	○	○	○	↓	○		
Locomotion	Both	Both	↑	○	○	○	↑	○		
Play	Both	Both	↓	↓	○	○	↓	↓		
Out of Sight	Both	Both	↑	↑	○	○	↑	↑		
MINOR BEHAVIOURS - SOLICITATION										
Visual presentation	Both	Both	○	○	○	○	○	○		
Receiving visual presentation	Both	Former	○	-	○	-	○	-		
Vocal presentation	Both	Both	○	○	○	Too few	○	Too few		
Receiving vocal presentation	Both	Neither	↓	-	○	-	↓	-		
Mating	Both	New	○	-	○	-	○	-		
Simulated mating	Both	Former	○	-	Too few	-	Too few	-		
Tail holding	Former	Neither	-	-	-	-	-	-		
Herded by tail	Former	Neither	-	-	-	-	-	-		
Pursuit	Both	Both	○	↑	↑	○	↓	↑		
MINOR BEHAVIOURS - AGONISTIC										
Visual aggression	Both	Neither	○	-	Too few	-	Too few	-		
Physical aggression	Both	Neither	○	-	○	-	○	-		
Vocal aggression	Both	Former	○	-	Too few	-	Too few	-		
Shaking	Former	Former	-	-	-	-	-	-		
Avoidance	Both	Both	○	↑	○	○	○	↑		
Supplanting	Both	Former	○	-	○	-	○	-		
Intervention	Both	Neither	○	-	Too few	-	Too few	-		
Alert	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS - FEEDING ACTIVITY										
Feeding	Both	Both	○	○	○	○	○	○		
Foraging	Both	Both	↑	○	○	○	↑	○		
Reaching out	Both	Both	○	○	↑	Too few	↓	Too few		
Relocating food	Both	Both	↑	↑	○	○	↑	↑		
Hunting	New	Neither	-	-	-	-	-	-		
Drinking	Both	New	○	-	○	-	○	-		
Licking	New	New	-	-	-	-	-	-		
MINOR BEHAVIOURS - GROOMING										
Grooming self	Both	Both	↓	↓	○	○	↓	↓		
Receiving groomed	Both	Both	↓	↓	○	○	↓	↓		
Grooming other	Both	New	○	-	○	-	○	-		
MINOR BEHAVIOURS - APPEASEMENT										
Tactile appeasement	Both	Neither	○	-	Too few	-	Too few	-		
Vocal Appeasement	Former	Former	-	-	-	-	-	-		
MINOR BEHAVIOURS - INACTIVITY										
Sitting	Both	Both	↓	↑	○	○	↓	↑		
Resting	Both	Both	↓	↓	○	○	↓	↓		
Standing still	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS - LOCOMOTION										
Walking	Both	Both	↑	○	○	○	↑	○		
Running	Both	Both	○	○	○	○	○	○		
Climbing	Both	Both	↓	↓	↓	↑	⊗	↓		
Jumping	Both	Both	↑	↑	Too few	Too few	Too few	Too few		
Relocating object	New	New	-	-	-	-	-	-		
Troop movement	New	New	-	-	-	-	-	-		
Troop patrol	New	New	-	-	-	-	-	-		
MINOR BEHAVIOURS - PLAY										
Manipulating environment	Both	Both	↓	↓	○	○	↓	↓		
Digging	Former	Former	-	-	-	-	-	-		
Play fighting	Both	Both	↓	↓	○	○	↓	↓		
Scrapping	New	New	-	-	-	-	-	-		
SOCIAL STATES										
Solitary	Both	Both	↑	↑	○	○	↑	↑		
Grouped	Both	Both	↓	↓	○	○	↓	↓		
Social	Both	Both	↓	○	○	○	↓	○		

- Description of third focal male, Toka, and summary of his response to relocation (Note: For a full description of Toka's response to relocation refer Appendix C, 6.3.3).

The third and final focal male, Toka, a sub-adult, was 6.6 years old at the start of this investigation.

Whereas no changes in the external appearance of female hamadryas baboons are obvious beyond the juvenile-3 phase, males enter sub-adulthood (Sigg et al. 1982). This lasts approximately five years, during which time the mantle develops and the male almost doubles in weight (Sigg et al. 1982).

Using the approach-avoidance criterion outlined above, Toka could be considered the lowest ranking of the three focal males for which comparable data was collected. In particular, of the three males, Toka had the most instances of *avoidance* in both enclosures. This provided some indication that he maintained the same relative position amongst the three focal males before and after relocation. This lower ranking position was found to be an influential factor in Toka's response to relocation relative to the combined focal animals (Table 4.6).

Unlike Abu and Randy, Toka was too young to have established himself as a unit leader during the course of this investigation. Free-ranging male hamadryas baboons have been seen to establish their first units (i.e. "initial units") with immature females between nine and 11 years of age (Sigg et al. 1982:481). This first pair bond, which in captivity and the wild alike is initially non-sexual (Kummer and Kurt 1965), may be maintained after the females have reached sexual maturity (Sigg et al. 1982). Other males, however, may bypass this "initial unit" stage and form one-male units with adult females (Sigg et al. 1982).

Results for Toka suggested that he occupied a 'follower' position within one of the colony's two established harems before and after the animals' relocation. 'Follower' refers to six to nine year-old bachelor males that join established harems belonging to older males and act in capacities depending on their age (Kummer 1995). Upon establishing their own harems, these males may eventually unite with the male leader of the unit they initially 'followed' to form a two-male team (Kummer 1968).

Confirmation of whether or not Toka was a 'follower' was especially difficult because sub-adult 'followers', unlike adult 'followers', will often separate themselves from their unit and do not maintain a consistent position during the unit's procession (Kummer 1968). While 'followers' seldom "engage in open social contact" within their respective units (Kummer and Kurt 1965:70), sub-adult 'followers' may receive grooming from their unit's adult females (Kummer 1968). In Toka's case, this provided the best indication of his affinity with a single unit. On 56 percent of occasions that Toka was recorded *receiving grooming* during focal sampling, the giver was one or other of the two established females from Randy's one-male unit. The remaining instances were undertaken primarily by other immature males and, on one occasion, an immature female. At no stage did Toka receive grooming from females belonging to Abu's harem.

Consequently, the particular harem to which Toka appeared to be 'affiliated' was that lead by his father, Randy. While it is typical for free-ranging male hamadryas baboons to leave their natal units at two years of age, it is not uncommon for them to return to their natal clans later as 'followers' (Kummer 1995).

Toka's response to relocation relative to other focal animals emphasised his 'follower' position. For example, as a sub-adult 'follower' (and, in contrast to Abu, a harem leader with a pronounced protective function) Toka had time available to explore the varied enrichment of the new enclosure.

The new enclosure also offered Toka the opportunity to develop his position as a sub-adult 'follower' male. This was also reflected in his response to relocation relative to the other focal animals. Whereas independence was difficult in the confines of the former enclosure, the new enclosure afforded Toka the opportunity to distance himself from his unit.

In addition to often separating from his unit (Kummer 1968), as a free-ranging six to eight year old 'follower' male, by definition, Toka would take no part in the leadership of the harem (Kummer 1995). At this stage, the unit leader takes both the "I-role" and "D-role" in the unit's movement with no need for co-ordination between the sub-adult 'follower' and the unit leader (Kummer 1995). It is not until about eight years of age that free-ranging 'followers' begin to take on a protective function within their unit (Kummer 1995) and act as a "second subordinate unit leader" (Kummer 1968:56). If he remains a 'follower', the male's position should become increasingly recognisable as he overtly co-ordinates movement with his unit's adult leader and assumes a consistent position in the unit's processional movement (Kummer 1968).

Just as he had not established a co-operative function within his affiliated unit, Toka was also unlikely to take a co-ordinating role in broader colony behaviour, such as *troop movement*. In the wild, such co-ordination is typically undertaken by "I-role" males and other young adult males (Kummer 1968). This was emphasised upon Toka's relocation where he utilised the increased diversity of spaces as places of refuge "out of sight", rather than remaining visible as a point of reference, like Abu.

4.7.3 Preamble to interpretation of female focal animals' responses

As was the case with the focal males, a single female hierarchical order within the colony was difficult to ascertain for a number of reasons. Firstly, female hamadryas baboons have a preference for associating with offspring or maternal kin. While there is some tendency in hamadryas baboon society (as there is in many other monkey species) to form matriline, this "appears to be overruled by the constraints imposed by the males" (Sigg et al. 1982:486). In addition, hamadryas baboon society is non-female bonded. Rather, "the centripetal tendency of females to remain in large aggregations appears to be based on a general, 'anonymous' attraction among conspecifics, not of specific bonds" (Kummer 1968:152). Consequently, the females do not form "strongly differentiated agonistic and affiliative relationships with one another" (Wrangham 1980; van Schaik 1989, cited in Barton et al. 1996:322) and very rarely show dominance interactions (Sigg 1980) with which to identify a rank order.

Interactions of females beyond their immediate units appear to be limited by their leaders' tolerance. Occasionally, females will, however, groom 'follower' males and females belonging to other units within the

clan (Kummer 1995). Some such social interaction beyond the harem is afforded by one of the relative 'occupational' niches adopted by females within their respective harems. More specifically, female hamadryas baboons have been found to take a 'central' or 'peripheral' role within their unit. In accordance with their different functions, 'central' and 'peripheral' females exhibit different behaviour (Sigg 1980).

The presence of these roles amongst the females within the Wellington Zoo colony became increasingly apparent, and developed, upon their relocation to the new spacious and naturalistic enclosure. The observer contends that this occurred for two reasons:

(i) The harem leaders were able to let their females spread out because rivals were not so closely confined. This allowed for more clearly defined spatial relationships between the harem leaders and each of their females. A similar conjecture was used to explain the absence of a clear differentiation amongst females in a newly formed, artificially combined, one-male unit. In this instance, it was thought that the heavily herded females were unable to maintain a distance from their leader (Sigg 1980);

(ii) Increased opportunities for naturalistic foraging and exploration behaviour in the new enclosure may have provided opportunities for a 'division of labour'.

The relative 'central' or 'peripheral' role of each female within her harem also provided, for the purposes of this investigation, the best indication of each focal female's rank within her unit - with the 'central' female typically younger and more dominant than the older, 'peripheral' female (Kummer 1995). While only one female was sampled from each of the colony's two established harems, the response of each of these focal females to relocation provided many indications of their more clearly discernible roles in their respective units.

4.7.3.1 Tina's responses to relocation

Table 4.7. Tina's response to relocation including comparison with responses of combined focal animals.

Tina	Enclosures		Overall occurrence		Mean bout lengths		Repetition		Counts	
	CFA	Tina	CFA	Tina	CFA	Tina	CFA	Tina	CFA	Tina
MAJOR BEHAVIOURS									↓	○
Solicitation	Both	Both	↓	○	○	○	↓	○		
Agonistic	Both	Both	○	○	○	○	○	○		
Feeding activity	Both	Both	○	↓	○	○	○	↓		
Grooming	Both	Both	↓	↑	○	○	↓	↑		
Appeasement	Both	New	○	-	Too few	-	Too few	-		
Inactivity	Both	Both	↓	↓	○	○	↓	↓		
Locomotion	Both	Both	↑	○	○	○	↑	○		
Play	Both	Former	↓	-	○	-	↓	-		
Out of Sight	Both	Both	↑	↑	○	○	↑	↑		
MINOR BEHAVIOURS - SOLICITATION									○	○
Visual presentation	Both	Both	○	○	○	Too few	○	Too few		
Receiving visual presentation	Both	Neither	○	-	○	-	○	-		
Vocal presentation	Both	New	○	-	○	-	○	-		
Receiving vocal presentation	Both	Neither	↓	-	○	-	↓	-		
Mating	Both	Both	○	○	○	○	○	○		
Simulated mating	Both	Neither	○	-	Too few	-	Too few	-		
Tail holding	Former	Neither	-	-	-	-	-	-		
Herded by tail	Former	Neither	-	-	-	-	-	-		
Pursuit	Both	Both	○	○	↑	○	↓	○		
MINOR BEHAVIOURS - AGONISTIC										
Visual aggression	Both	Former	○	-	Too few	-	Too few	-		
Physical aggression	Both	Neither	○	-	○	-	○	-		
Vocal aggression	Both	Neither	○	-	Too few	-	Too few	-		
Shaking	Former	Neither	-	-	-	-	-	-		
Avoidance	Both	Both	○	○	○	↓	○	↑		
Supplanting	Both	Neither	○	-	○	-	○	-		
Intervention	Both	Neither	○	-	Too few	-	Too few	-		
Alert	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS – FEEDING ACTIVITY										
Feeding	Both	Both	○	○	○	○	○	○		
Foraging	Both	Both	↑	↓	○	○	↑	↓		
Reaching out	Both	Former	○	-	↑	-	↓	-		
Relocating food	Both	Both	↑	○	○	○	↑	○		
Hunting	New	New	-	-	-	-	-	-		
Drinking	Both	New	○	-	○	-	○	-		
Licking	New	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - GROOMING										
Grooming self	Both	Both	↓	↓	○	Too few	↓	Too few		
Receiving groomed	Both	Both	↓	○	○	○	↓	○		
Grooming other	Both	Both	○	↑	○	○	○	↑		
MINOR BEHAVIOURS – APPEASEMENT										
Tactile appeasement	Both	New	○	-	Too few	-	Too few	-		
Vocal Appeasement	Former	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - INACTIVITY										
Sitting	Both	Both	↓	↓	○	○	↓	↓		
Resting	Both	Former	↓	-	○	-	↓	-		
Standing still	Both	Both	○	↑	○	○	○	↑		
MINOR BEHAVIOURS - LOCOMOTION										
Walking	Both	Both	↑	↑	○	○	↑	↑		
Running	Both	New	○	-	○	-	○	-		
Climbing	Both	Both	↓	○	↓	Too few	○	Too few		
Jumping	Both	Neither	↑	-	Too few	-	Too few	-		
Relocating object	New	Neither	-	-	-	-	-	-		
Troop movement	New	New	-	-	-	-	-	-		
Troop patrol	New	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - PLAY										
Manipulating environment	Both	Neither	↓	-	○	-	↓	-		
Digging	Former	Former	-	-	-	-	-	-		
Play fighting	Both	Neither	↓	-	○	-	↓	-		
Scraping	New	Neither	-	-	-	-	-	-		
SOCIAL STATES										
Solitary	Both	Both	↑	↓	○	○	↑	↓		
Grouped	Both	Both	↓	↑	○	○	↓	↑		
Social	Both	Both	↓	↑	○	○	↓	↑		

- Description of first focal female, Tina, and summary of her response to relocation (Note: For a full description of Tina's response to relocation refer Appendix C, 6.3.4).

At the outset of data collection, Tina was a 13.1 year old, sexually mature, adult female.

In hamadryas baboon society, females are always integrated into one-male units (Sigg et al. 1982). They experience greatest freedom as juveniles within their parental unit, at which time sexual activity with other adolescents has few repercussions (Kummer 1995). This type of freedom comes to an abrupt end at three to five years of age when the females are sequestered by their first male (Kummer 1995), who acts to forcefully maintain the integrity of his unit (Kummer 1968).

At the time of this investigation, Tina was established in Randy's harem, despite her leader being beyond the average age at which males have been estimated to lose their harems. While female hamadryas baboons may change units two or three times during their lifetimes (Sigg et al. 1982), the inclination to remain in a harem is thought to be reinforced by (Sigg 1980:298):

- (i) Knowledge of other group members, which enables individuals to optimise their own behaviour in relation to their partners;
- (ii) Individuals working most successfully as a unit through role-differentiation;
- (iii) Knowledge and use of areas frequently utilised by particular units for foraging; and,
- (iv) Security of infants in their natal units.

Focal samples indicated that Tina undertook some behaviour characteristic of 'central' females prior to relocation. Her results, and especially those that deviated from the combined focal animals (Table 4.7), indicated her more clearly discernible position as the dominant 'central' female within her respective harem upon the colony's relocation. This was emphasised by her relative lack of interest in the new opportunities for exploration and environmental matters, typical of 'central' females (Kummer 1995).

Rather than be concerned with ecological matters, the function of 'central' females is social bonding (Sigg 1980), through the extension of social effort within and beyond their immediate units (Kummer 1995). Tina's increasingly discernible 'central' position upon relocation was especially evident in deviations in her social behaviour upon relocation relative to the combined focal animals. In particular, a reduction in "solitary" behaviour and increase in "grouped" and "social" behaviour further indicated her increasingly social function.

This 'central' position affords these females closer proximity to their harem leaders relative to 'peripheral' females (Sigg 1980). Remaining close to the adult male leader provides 'central' females with benefits, including increased security compared to more distant positions (Sigg 1980). It is this security that, in part, enables 'central' females the opportunity to devote attention to the social sphere (Sigg 1980). There was also some evidence in Tina's response to relocation, relative to the combined focal animals, that her 'central'

position, and consequent proximity to her harem leader, also afforded her access to areas of high food concentration.

Competition with the other female in her harem over access to their mate was another noticeable aspect of Tina's developing 'central' position within her harem. There is some evidence in literature to suggest that harem females prefer the 'central' position. There is also a view that this preference is a cause of competition among females (Sigg 1980). Experimentation has shown that, when the 'central' female is unable to intervene, the 'peripheral' female comes significantly closer to the male, engages in more bodily contact with him and undertakes the same activity as her leader more often (Sigg 1980).

4.7.3.2 Sinead's responses to relocation

Table 4.8. Sinead's response to relocation including comparison with responses of combined focal animals.

Sinead	Enclosures		Overall occurrence		Mean bout lengths		Repetition		Counts	
	CFA	Sinead	CFA	Sinead	CFA	Sinead	CFA	Sinead	CFA	Sinead
MAJOR BEHAVIOURS										
Solicitation	Both	Both	↓	↓	○	○	↓	↓	↓	○
Agonistic	Both	Both	○	↓	○	○	○	↓		
Feeding activity	Both	Both	○	○	○	○	○	○		
Grooming	Both	Both	↓	↓	○	○	↓	↓		
Appeasement	Both	Both	○	○	Too few	Too few	Too few	Too few		
Inactivity	Both	Both	↓	↓	○	○	↓	↓		
Locomotion	Both	Both	↑	○	○	○	↑	○		
Play	Both	Both	↓	○	○	○	↓	○		
Out of Sight	Both	Both	↑	↑	○	○	↑	↑		
MINOR BEHAVIOURS - SOLICITATION									○	○
Visual presentation	Both	Both	○	○	○	○	○	○		
Receiving visual presentation	Both	Both	○	○	○	Too few	○	Too few		
Vocal presentation	Both	Both	○	○	○	○	○	○		
Receiving vocal presentation	Both	Former	↓	-	○	-	↓	-		
Mating	Both	Former	○	-	○	-	○	-		
Simulated mating	Both	Neither	○	-	Too few	-	Too few	-		
Tail holding	Former	Neither	-	-	-	-	-	-		
Herded by tail	Former	Former	-	-	-	-	-	-		
Pursuit	Both	Both	○	↓	↑	○	↓	↓		
MINOR BEHAVIOURS - AGONISTIC										
Visual aggression	Both	Former	○	-	Too few	-	Too few	-		
Physical aggression	Both	Both	○	○	○	Too few	○	Too few		
Vocal aggression	Both	Former	○	-	Too few	-	Too few	-		
Shaking	Former	Former	-	-	-	-	-	-		
Avoidance	Both	Both	○	○	○	○	○	○		
Supplanting	Both	Neither	○	-	○	-	○	-		
Intervention	Both	Neither	○	-	Too few	-	Too few	-		
Alert	Both	Both	○	○	○	○	○	○		
MINOR BEHAVIOURS - FEEDING ACTIVITY										
Feeding	Both	Both	○	↑	○	○	○	↑		
Foraging	Both	Both	↑	↓	○	○	↑	↓		
Reaching out	Both	New	○	-	↑	-	↓	-		
Relocating food	Both	Both	↑	○	○	○	↑	○		
Hunting	New	Neither	-	-	-	-	-	-		
Drinking	Both	New	○	-	○	-	○	-		
Licking	New	New	-	-	-	-	-	-		
MINOR BEHAVIOURS - GROOMING										
Grooming self	Both	New	↓	-	○	-	↓	-		
Receiving groomed	Both	Both	↓	↓	○	○	↓	↓		
Grooming other	Both	Both	○	↓	○	○	○	↓		
MINOR BEHAVIOURS - APPEASEMENT										
Tactile appeasement	Both	Both	○	○	Too few	Too few	Too few	Too few		
Vocal Appeasement	Former	Neither	-	-	-	-	-	-		
MINOR BEHAVIOURS - INACTIVITY										
Sitting	Both	Both	↓	↓	○	○	↓	↓		
Resting	Both	Both	↓	↓	○	○	↓	↓		
Standing still	Both	Both	○	○	○	↓	○	↑		
MINOR BEHAVIOURS - LOCOMOTION										
Walking	Both	Both	↑	○	○	○	↑	○		
Running	Both	Both	○	○	○	○	○	○		
Climbing	Both	Both	↓	↓	↓	↓	⑦	⑦		
Jumping	Both	Neither	↑	-	Too few	-	Too few	-		
Relocating object	New	Neither	-	-	-	-	-	-		
Troop movement	New	New	-	-	-	-	-	-		
Troop patrol	New	New	-	-	-	-	-	-		
MINOR BEHAVIOURS - PLAY										
Manipulating environment	Both	Both	↓	○	○	○	↓	○		
Digging	Former	Neither	-	-	-	-	-	-		
Play fighting	Both	Former	↓	-	○	-	↓	-		
Scrapping	New	Neither	-	-	-	-	-	-		
SOCIAL STATES										
Solitary	Both	Both	↑	↑	○	○	↑	↑		
Grouped	Both	Both	↓	↓	○	○	↓	↓		
Social	Both	Both	↓	↓	○	○	↓	↓		

- Description of second focal female, Sinead, and summary of her response to relocation (Note: For a full description of Sinead's response to relocation refer Appendix C, 6.3.5).

At 9.1 years of age at the outset of data collection, Sinead was the younger of the two focal females.

As was the case with Tina, as an adult female, Sinead was integrated into a one-male unit - in this instance belonging to Abu. There was some evidence in focal samples for Sinead that she also occupied a more clearly defined occupational niche (specifically, a 'peripheral' position) upon relocation. This position was in keeping with her relative age, Sinead being the older of the two sexually mature and established females in Abu's harem.

As a 'peripheral' female, Sinead was likely to have been lower in rank than the 'central' female within her unit. This was emphasised upon the colony's relocation when there was some evidence to suggest that Sinead was displaced from areas of high food concentration. "More independent behaviour, separate spatial position, and reduced access to food resources" are thought to necessitate extensive searches for food by these females, with less time available for social activity (Sigg 1980:278).

There has been some suggestion that age furthers the emotional ability of 'peripheral' females to cope with the environment with greater independence (Sigg 1980). However, in captivity, where food is provided in easy view of the colony, the low ranking 'peripheral' female loses the benefits of her particular skills (Kummer 1995). In captivity, only the 'central' position is rewarding. This is because food is in full view and, as a result, the 'peripheral' female cannot use her greater ecological knowledge to turn her position to advantage (Kummer 1995). Consequently, the energy levels of 'peripheral' females are relatively poor because, at feeding sites, they are displaced by dominant 'central' females that are advantaged by sitting close to unit leaders who monopolise feeding sites (Zinner 1993, cited in Kummer 1995:129).

Upon the colony's relocation to the new and greatly enriched enclosure, there was more evidence of Sinead's interest in, and knowledge of, ecological matters, which is typical of 'peripheral' females (Kummer 1995). This was reflected in her response to relocation, and the consequent provision of greater opportunities for exploration and reconnaissance, relative to other focal animals (Table 4.8).

Sinead's response to relocation also indicated her increased independence from her harem, as exemplified by her increasingly solitary behaviour. One indication of this was the infrequency with which she participated directly in her unit's new in-line processional behaviour, specifically *troop patrol*, around the spacious new enclosure. In keeping with her increasingly discernible 'peripheral' role, Sinead's separation from her harem on such occasions was thought to indicate her developing function as a 'scout' for her unit in keeping with her increasingly 'peripheral' position (Kummer 1995:130).

CHAPTER 5: SUMMARY DISCUSSION

5.1 SUMMARY OF FINDINGS

Although there has been some debate over criteria for the improvement of the welfare of non-human primates, it is generally accepted that the following are beneficial (Brent and Long 1995:68):

- (i) A reduction in abnormal behaviours thought to be related to distress and possibly detrimental to physical health [(such as self-mutilation and a restricted behavioural repertoire (Duncan and Poole 1990)]; and,
- (ii) An increase in species-typical behaviour.

It has been acknowledged in the past that identifying abnormal behaviour is difficult because the cause of such behaviour is not always easy to interpret (Bostock 1993). In addition, some abnormal behaviours do not necessarily indicate physical or even mental suffering, rather may give the animals satisfaction through the release of endorphins (Bostock 1993). However, according to the second criterion above, the well-being of the five focal animals within the Wellington Zoo hamadryas baboon colony was considered to have improved upon relocation to the new enclosure as they were seen to undertake more species-typical behaviour of wild hamadryas baboons. This included more clearly discernible roles within one-male units by the focal animals, as well as reduced “inactivity” associated with increasingly naturalistic levels of *foraging* and “locomotion”. The observer acknowledges that differences in the behaviour exhibited by animals between environments may be, in some instances, more illustrative of how adaptable animals are rather than an indication of the state of the animals’ welfare (Duncan and Poole 1990).

Tables 5.1 and 5.2 summarise the main responses of the combined and individual focal animals to relocation relative to the hypotheses, respectively.

Table 5.1. Summary of the main responses of the combined focal animals relative to this study's hypotheses.

Ho: There is no change in the combined focal animals' behaviour between the former and new enclosures.	
Alternative hypothesis	Summary of key findings associated with the corresponding hypothesis
Ha: There is a difference in the behaviour of the combined focal animals between the former and new enclosures.	<p>Results indicated that there were numerous differences in the combined focal animals' behaviour between the former and new enclosures including differences in:</p> <ul style="list-style-type: none"> - The overall occurrence of six "major" behaviours and 13 "minor" behaviours; - The mean bout length of three "minor" behaviours; - The relative repetition of six "major" and 13 "minor" behaviours.
Ha ₁ : Upon relocation to the new, more expansive and naturalistic enclosure, the combined focal animals demonstrate a broader repertoire of species-typical behaviour.	<p>Upon relocation, the combined focal animals undertook new, naturalistic, exploration-type behaviours, specifically:</p> <ul style="list-style-type: none"> - <i>Licking</i> and <i>scraping</i>, associated with the provision of unique surfaces; and, - New cohesive group behaviour i.e. <i>troop movement</i> and <i>troop patrol</i>, associated with increased space. <p>Analysis also revealed an absence of vestigial <i>digging</i> (this was attributed to increased opportunities for foraging) and vacuum <i>shaking</i> (attributed to an expansive and unobstructed view beyond the new enclosure) in the combined focal animals behavioural repertoire upon relocation.</p>
Ha ₂ : The provision of more space and areas of privacy in the new enclosure reduce the incidence of aggression and, consequently, the need for appeasement behaviour.	<p>No change was found between the former and new enclosures for the combined focal animals in "agonistic" or non-grooming "appeasement" behaviour. Low levels of aggression and, consequently, "appeasement" behaviour were associated with the appropriateness of the focal animals' social setting and the placement of adjacent enclosures, as well as the provision of some foraging enrichment in each enclosure.</p> <p>There was some evidence to suggest that aggressive interaction by the focal animals towards the viewing public decreased upon the colony's relocation to the new enclosure because:</p> <ul style="list-style-type: none"> - There was less need for the animals to generate external environmental variation; - There was room for the animals to distance themselves from the public; and, - The public acted in a less hostile manner towards the animals.
Ha ₃ : The provision of increased space, and the greater variety of environmental enrichment, in the new enclosure impact upon levels of social interaction.	<p>The different variety and amount of activity undertaken by the combined focal animals upon relocation impacted directly on inter-individual distances within the colony. This caused a difference between the former and new enclosures in the occurrence and repetition of the three social states.</p> <p>A reduction in "social" interaction by the combined focal animals upon relocation, consistent with more naturalistic behaviour, was also attributable to increased opportunities for non-social activity in the new enclosure that suppressing the "social" state.</p>

Table 5.2. Summary of the main responses of the individual focal animals relative to this study's hypotheses.

Ho: There is no difference in the responses of individual focal animals to relocation.	
Alternative hypothesis	Summary of key findings associated with the corresponding hypothesis
Ha: There is a difference in the response of the individual focal animals to relocation.	Data analysis revealed numerous variations in the responses of individual focal animals to relocation. These were exemplified in the many deviations of each animal's response relative to that of the combined focal animals (Tables 4.4 – 4.8).
<p>Ha₁: Gender plays a part in the different responses of the individual focal animals.</p> <p>Ha₂: Age plays a part in the different responses of the individual focal animals.</p>	<p>Analysis revealed that a combination of gender and age influenced each focal animal's relative authority and position within their respective harem as well as the colony as a whole.</p> <p>Relocation to the new enclosure accentuated each animal's relative authority and position and provided conditions that enabled them to develop more naturalistic behaviours consistent with these characteristics</p> <p>The increased space and greater opportunities for naturalistic foraging and exploration contributed to the development of more naturalistic behaviours. These particular variables in the new enclosure:</p> <ul style="list-style-type: none"> - Enabled increasingly naturalistic spatial relationships within harems; - Encouraged increased cohesive group behaviour; and; - Provided increased opportunities for non-social activity. <p>These all contributed to the adoption of more clearly defined and naturalistic occupational niches by the five focal animals consistent with each animal's age and gender.</p>

5.2 LIMITATIONS AND PROBLEMS ENCOUNTERED

This study offered a unique opportunity to investigate the behavioural response of a single captive colony of hamadryas baboons to relocation to a new enclosure that differed vastly in degrees of environmental enrichment from their former enclosure.

However, unlike other studies concerning baboons in which enrichment variables or devices may be introduced into the captive environment gradually, the Wellington Zoo colony was released into an entirely new, structurally and physically complex enclosure, enriched in a broad variety of ways. As such, variations in the behaviour of the focal animals between the former and new enclosures could not be attributed to specific enrichment items, such as the provision of a foraging board. Rather, they were attributable to enrichment categories, such as foraging enrichment. Fortunately, research on hamadryas baboons by previous authors provided valuable insights into the responses of the Wellington Zoo focal animals to their new surroundings.

The use of video recorded samples, and suitable ethogram detail, increased the accuracy of the data collected. The use of the video camera, however, meant that focal sampling could not be undertaken in the rain. This biased the results towards daily sample periods during dry weather. The absence of wet weather data was particularly relevant because fine weather has been interpreted as causing increased motivation towards exploration in hamadryas baboons (Sigg and Stolba 1981).

The sampling method employed enabled the accurate recording of all the actions of, and discernible interactions involving, individual focal animals during 10 to 15 minute observation periods. However, focal sampling may not have recorded all of the acts (i.e. social interactions), such as silent threats, or notification in the form of subtle glances, directed at the focal animals by other members of the colony, that may have motivated the behaviour of focal animals (Altman, J 1974). This may have further biased the results.

By only sampling the behaviour of sub-adult and adult animals, the results of this study are not representative of the entire colony's response to relocation.

During the preliminary observations without the video camera, the degree of public interaction with the baboons was observed to be greater than when the animals were being filmed. Anecdotal observations suggested that, during filming, the public were less inclined to aggravate the animals. This observer effect may have biased the results by reducing the amount of aggression sampled at each of the enclosures to levels below those typical on a normal day. Direct human interference with sampling equipment also caused premature termination of numerous samples.

Expert advice was sought to determine the best methods of data analysis for this investigation. As such, statistical problems were minimised. However, due to the infrequent occurrence of some of the "major" and "minor" behaviours, statistical comparisons between the former and new enclosures could not always be undertaken.

In addition, due to the length of the focal samples and the number of samples collected, data transfer from video to spreadsheet took an extremely long time. Consequently, minor inconsistencies that required time-consuming amendments occurred during data entry.

5.3 IMPLICATIONS OF THIS STUDY

5.3.1 Implications for management of captive hamadryas baboons

According to UFAW (1988, cited in Duncan and Poole 1990:223), zoos have three main functions – research, conservation and education. The current study satisfies the first of these. The findings of this research have implications for the remaining two main functions i.e. improving conservation of hamadryas baboons in captivity and increasing the educational value of hamadryas baboon enclosures.

5.3.1.1 Implication in relation to Wellington Zoo

The current investigation emphasised ways in which additional management practices could increase the behavioural benefits and educational value of the new, enriched and naturalistic hamadryas baboon enclosure at Wellington Zoo. Specifically:

(i) In the new enclosure, reduced “inactivity” by the combined focal animals was attributed to increased foraging opportunities. However, “inactivity” was considered unlikely to reach naturally low levels given the current feeding regime by keepers, as this discourages reconnaissance and time spent on other “feeding activity” behaviours. This implies that variation in the temporal and spatial provision of some major food items, with consideration to the animals’ natural feeding ecology, offers the potential to encourage greater time spent searching for food and, consequently, increasingly naturalistic levels of activity. Such variation may increase the complexity of the new enclosure, further reduce environmental predictability and provide stimulus for ‘new’ behaviours, thereby encouraging a broader behavioural repertoire. As animals can consume different food in different ways, temporal and spatial feeding variation may be of additional educational value in that it could give the public opportunities to view natural variations in feeding behaviour (Hutchins et al. 1984). There are, of course, significant benefits in regularly attracting the animals to one place, such as for administering veterinary treatment (Cowlshaw 1999). Consequently, and notwithstanding the above, it may be necessary to continue to provide some incentives at an easily accessible location. The following are examples of temporal and spatial variation in the provision of food that could be experimented with in the new enclosure at Wellington Zoo:

- a) In the wild, eating and drinking change according to the season (Kummer 1968). Consequently, the temporal and, specifically, seasonal variation in both food type and quantity could be investigated as an additional means of reducing environmental predictability;
- b) Spatial variation could be enhanced by burying major food items, thus providing stimuli to encourage species-typical digging. In such cases, food items that can be consumed entirely could be selected in order to minimise

food remnants and, therefore, keeper workload. There may also be additional benefits to providing this form of variation. Experimentation has found that ‘control’ of food by dominant captive stump-tail macaques (*Macaca arctoides*) could be reduced by partitioning their enclosure or burying food items (Chamove et al. 1982). The advantages of these initiatives were improved food distribution and a reduction in aggression. These benefits were enhanced when the food was frozen (Chamove et al. 1982).

c) In the wild, adult male hamadryas baboons are prevented from dominating food from fruit-bearing trees due to their weight. At such sites it is only the lighter females and juveniles that can reach fruit from weaker, outer branches (Kummer 1995). It may be possible to create additional variation by replicating this and, therefore, an increasingly natural environment by varying the placement of food within the enclosure.

(ii) A reduction in the frequency of socialisation by the combined focal animals during the middle of the day (when their wild counterparts would be undertaking a long daily journey with limited social contact) was partially attributable to an increase in the overall occurrence of *foraging* by the combined focal animals upon their relocation. This implies that the feeding habits of the hamadryas baboons at Wellington Zoo could be further ‘manipulated’ in order to encourage increasingly naturalistic behaviour and, specifically, patterns of social interaction. Such ‘manipulation’ could be achieved through the alteration of daily husbandry and feeding times.

Captive baboons have been seen to participate in a morning social period lasting until 10:00 a.m. This period of socialisation is comparable to that of wild hamadryas baboons before the troop’s daily march (Kummer and Kurt 1965). In the wild, feeding is completely absent during morning socialisation and commences when the troop departs on its daily journey (Kummer 1968).

The implication of the above is that daily husbandry and feeding of the Wellington Zoo colony before 10:00 a.m. may be interrupting this initial period of socialisation. Delaying the provision of the animals’ main daily feed until later in the morning (i.e. after 10:00 a.m.) may encourage a more naturalistic routine, including morning socialisation before exploration in search of food.

(iii) The results of this investigation illustrate that special consideration should be given to vestigial behaviours by Wellington Zoo’s hamadryas baboons as they arise. This study indicated that vestigial behaviour may illustrate the absence of environmental stimuli, which could be easily provided to generate functional responses. Vestigial *digging*, for example, which occurred exclusively in the former enclosure, was attributed to a lack of foraging opportunities. It was subsequently eliminated from samples upon the animals’ relocation to the new enclosure that provided an increased variety of foraging enrichment.

5.3.1.2 Implications for other zoos

Increased space in the new hamadryas baboon enclosure at Wellington Zoo was especially beneficial in allowing for increased environmental complexity. Some benefits attributable to the opportunities afforded by this space included an increase in the combined focal animals’ repertoire of exploratory behaviours and a decrease in “inactivity”. Wellington Zoo is fortunate in having sufficient land to allow for the design of such an expansive enclosure with as many and varied opportunities for exploration. Other Zoos may be less fortunate. However,

and notwithstanding the above, Wilson (1972, cited in Kessel and Brent 1996:41) concluded that “the structures or objects present in the non-human primates’ environment are much more important than the size of the enclosure”.

The current study emphasised ways in which enclosures of any size can be managed to optimal effect in order to improve the welfare of captive *Papio* baboons, by encouraging neophilic tendencies and alleviating monotony and errant behaviours.

Implications for other zoos from the current study relate to physical characteristics of, and variability within, enclosures.

- Physical characteristics

(i) In the new enclosure, a favourable decrease in *visual* and *vocal aggression* by the combined focal animals was attributed, in part, to an increase in time spent “out of sight” from the observer and, by inference, one another. The ramification of this finding is that captive hamadryas baboons benefit from a diversity of spaces which provide areas of refuge and privacy.

(ii) The findings of the current study emphasised the Wellington Zoo focal animals’ preference for shade cover or shelter. Furthermore, baboons actively seek [and require (Altman, S.A 1974)] shady resting sites in the wild (Sigg and Stolba 1981). The implication of these two observations is that shade cover should be provided for baboons in captivity. In addition, for the animals to best exercise this preference, enough shady resting sites should be provided for each one-male unit within a captive colony [just as in the wild, where each unit will usually shelter under a different tree (Kummer 1968)].

(iii) In the current study, the combined focal animals were found to spend more time *climbing* in the smaller, former enclosure than in the new, enlarged enclosure. This prompted the suggestion that the presence of structural enrichment contributed to the absence of behavioural abnormalities associated with stress, especially prior to the colony’s relocation where such structural enrichment is thought to have provided escape routes and areas of refuge. The implication of this is that the provision of climbing structures in small enclosures can minimise unfavourable self-directed behaviours, including food regurgitation, seen in other captive *Papio* species (Brent and Belik 1996) but noticeably missing during the course of the current investigation. A greater amount of *climbing* in the former enclosure emphasises the importance of such structures, especially as vantage points for observation (Maple 1979, cited in Kessel and Brent 1996:38) as well as a means of increasing inter-individual distances, thereby reducing the physical restrictions of smaller enclosures.

- Enclosure variability

(i) The results of this investigation have emphasised the importance of providing spatial variation [i.e. “multi-dimensional surfaces of different materials such as rocks, soil, water and vegetation” (Hutchins et al. 1984:29)] for captive hamadryas baboons. For example, a reduction in *visual* and *vocal aggression* by the combined focal animals upon their relocation to the new enclosure, which was seen to corresponded, in part, with fewer interactions with the viewing public, was partially attributed to enhanced environmental variation that provided

the animals with the necessary environmental stimulation within their enclosure. The significance of this is that varieties of surfaces should be experimented with in order to satisfy neophilic tendencies. (As an aside, anecdotal evidence from the months of observation associated with the current study suggested that some members of the viewing public used objects surrounding the enclosures [such as stones or bark-chip] in an attempt to attract the animals' attention and, thereby, generating an aggressive response. The implication of this is that such objects surrounding the enclosure should be kept to an absolute minimum).

(ii) In a similar way, the provision of periodic environmental enrichment may provide further behavioural opportunities. Exposure to new and unique enrichment items and surfaces in the new enclosure led to a favourable increase in the combined focal animals' repertoire of exploratory behaviours. The implication from the current study, therefore, is that exposure to a variety of new environmental enrichment can have a positive impact on the behavioural repertoire of captive hamadryas baboons.

5.3.1.3 Implications for new enclosures at other zoos

The findings of the current study have generated further implications, in addition to those above, that may aid in the design, and increase the benefits of, new *Papio* baboon enclosures.

(i) The current study exemplified the behavioural benefits of increased natural environmental variability. The implication of these benefits is that new enclosures should be designed with consideration to not only ease of daily husbandry, hygiene and the regular addition of enrichment material but also increased environmental variation by incorporating into the design naturally occurring factors. By encouraging natural environmental variation, it is possible to increase enclosure complexity and enhance behavioural opportunities for the animals. In the baboon's new enclosure at Wellington Zoo, for example, the favourable increase in overall occurrence of *foraging* was partially attributable to additional foraging opportunities afforded by natural leaf litter and patchy erosion of the grassy bank.

(ii) Enclosures designed with flexibility in mind provide for increased spatial and temporal variation. For example, enclosures could incorporate physical structures that could be changed or rearranged periodically (Hutchins et al. 1984). Such flexibility may further reduce the predictability of the captive environment. This, in turn, could encourage a more extensive behavioural repertoire and behavioural flexibility such as employed by wild animals to cope with the variety and unpredictability of wild habitats (Hutchins et al. 1984). An implication drawn from the current study is that enclosure flexibility may allow for the preferences and/or needs of the animals as these manifest (for example, the provision of appropriate stimuli to generate functional forms of vestigial behaviours).

(iii) The low overall occurrence of "agonistic" behaviour within the Wellington Zoo combined focal group in both the former and new enclosures was considered to be partially attributable to both enclosures' isolation from other animals. One "minor" "agonistic" behaviour observed during focal sampling in the former enclosure was *shaking*. This was attributed to the obstructed visibility from the former enclosure due, in part, to an adjacent enclosure that remained empty for the duration of this investigation. The implication of this is that the appropriateness of adjacent species, and the positioning of surrounding exhibits, are other variables that should

be considered in new enclosure design in order to minimise animal frustration and associated abhorrent behaviours.

(iv) The current study also emphasised the extent to which the use of appropriate, natural enrichment materials can impact upon the behaviour of captive hamadryas baboons. For example, upon the focal animals' relocation to the new enclosure, which was enriched with naturalistic rather than mechanistic enrichment, neophilic exploration tendencies increased in overall occurrence and form. In addition, a reduction in socialisation was partially related to increased opportunities for non-social activity. The significance of these two positive findings for enclosure design is also relevant in relation to public education. The use of natural enrichment materials is deemed especially important for authenticity and aesthetics (Hutchins et al. 1984).

5.4 RELEVANCE OF THIS STUDY

The findings of the current study are of particular relevance because they add to the limited pool of empirical information currently available for the effects of enclosure enrichment for captive (and, especially, group-housed) baboons (Brent and Belik 1997). This study provided information on both combined and individual responses of group-housed hamadryas baboons to a new, spacious and naturalistic enclosure. Whereas many enrichment techniques for captive baboons have been borrowed from studies of other species, the current study has species-specific information and implications on which to base decisions regarding environmental improvements for hamadryas baboons at Wellington Zoo and in captivity elsewhere. In addition, the findings of this study are especially relevant because enhancing the environment of captive primates is of increasing concern to those responsible for their welfare and management (Brent and Long 1995).

Perhaps the most directly beneficial implications for the welfare of captive baboons from the current study are those pertaining to improved management, which are applicable to any hamadryas baboon enclosure, irrespective of size. In recognising that not all zoological facilities have the means to create spacious, purpose-designed enclosures, the current study is particularly relevant as it has implications, as discussed above, that can benefit animals in all manner of enclosures.

The current study is also relevant to other facilities considering enclosure redesign for *Papio* species as it describes the types of behavioural responses to enclosure enrichment that may be anticipated. In so doing, it provided insights and implications, as discussed above, on which to base decisions regarding enclosure design.

This study has additional relevance as a baseline for future studies. The methodology employed, the flexible ethogram developed for the study, the descriptions of individually identifying features for each colony member and the additional information recorded but not used for this investigation (such as space use data), all promote the use of this study as a point of comparison for follow-up studies and other investigations.

5.5 FUTURE STUDIES

5.5.1 Using current data as a baseline

This investigation was designed with follow-up studies at Wellington Zoo in mind. Such studies would be useful from a management perspective, because they could provide information regarding the long-term use of enrichment variables in the new enclosure (Kessel and Brent 1996).

In addition, other topics of investigation at Wellington Zoo could employ the results of this study as a baseline for comparison. For example, as breeding is a desired outcome of the new enclosure, there is special scope to investigate the influence of infants on the colony's behaviour. Information from such an investigation could be especially revealing as the last baboon birth at Wellington Zoo prior to this investigation was in 1995. Such a study would also be beneficial in clarifying age-related distinctions in relation to enrichment use.

As the colony expands, through breeding and the introduction of animals from co-operative zoos, there is the further potential to investigate the effect of increasing group size on enrichment use, whereby the current study could act as a baseline. The added advantage of such investigation at Wellington Zoo is that it would allow for the comparison of results of a single population as it expands.

5.5.2 Ideas for further studies

In the new enclosure, there are further opportunities to investigate ways of encouraging more naturalistic behaviour and provide further empirical data on enrichment.

Consideration of the space use data collected during the current investigation at the former and new enclosures, which was not analysed due to time restrictions, provides further opportunities to study the animals' response upon their relocation to the new enclosure. Specifically, this data could be used to ascertain the colony's use of space in order to provide information on the preferences and use of structural enrichment by group-housed baboons. This is a particular area of study for which information is currently lacking but which has value in the design of effective enclosures (Kessel and Brent 1996).

An investigation into the colony's daily behavioural routine may provide insights into ways of manipulating the animals' activity so that their daily activity regime more closely resembles that of their wild counterparts. For example, by experimenting with the spatial and temporal provision of food, it may be possible to discourage the animals from anticipating the regular provision of food by their keepers. In so doing, it may be also possible to encourage the animals to undertake exploratory marches in search of food as they would in the wild. This, in turn, has the potential to broaden their repertoire of "feeding activity" behaviours.

Findings from the current study indicated that there is value in investigating the direct influence of abiotic variables on the colony's behaviour. Such a study could prove invaluable in further highlighting the animals' preferences, for example, for shade cover or shelter from the wind. Suggestions derived and implemented from such an investigation have the potential to increase the wellbeing of captive baboons and could be applied in such a way as to increase viewing opportunities for the public.

An investigation into the causes and effects of public interaction with the animals could be of direct value to the well-being of captive baboons in the public eye. Such an investigation would provide valuable insights into how negative interactions could be minimised in order to provide more satisfactory captive environments for the animals. Anecdotal observations from the current study suggested that the baboons' smell, in particular, caused a negative reaction by some members of the public who, in turn, aggravated the animals. This was particularly evident in the former enclosure where the animals, and their waste, were confined to a much smaller area in close proximity to the public.

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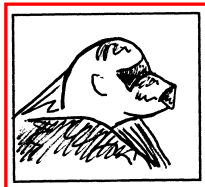
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CHAPTER 6: APPENDICES

6.1 APPENDIX A

Figure 6.1 Individually identifying features and age of each member of the Wellington Zoo hamadryas baboon colony, at onset of investigation. Age/sex classes based on estimates and corresponding physical descriptions by Sigg et al (1982: 475) and Abegglen (in press, cited in Sigg et al 1992:475). Focal animals feature red border.



Randy
19.2 years, adult male.
Considerable hair loss on face and scalp.



Tina
13.1 years, adult female.
Heavy brow line. Light coloured hair around face, on chest and tail. Tip of nose pointed.



Jackie
20.6 years, adult female.
Similar looking to Tina with light coloured hair on face, chest and tail. Tip of nose small and rounded.



Abu
10.1 years, adult male.
Largest animal within colony. Hair on top of head white with a dark parting.



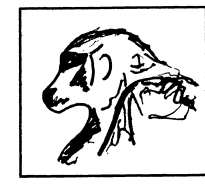
Makele
6.8 years, adult female.
Very fine hair, especially across shoulders. Square ears. Distinctive dimples in cheeks.



Sinead
9.1 years, adult female.
Dark face. Receding hair line, leaving extended bare forehead. Hair on head is short and lies flat.



Toka
6.6 years, sub-adult male.
Maturing mantle. Hair on top of head dark.



Anubis
5.1 years, castrated male.
Coat remains brown. Larger than juvenile 2 males. Bridge of nose long and unwrinkled.



Albert
6.1 years, juvenile 3 male.
Short grey-flecked cape.



Suzy
32.8 years, adult female.
Elderly, arthritic and crouched over. Hair receding around face, especially above ears.



Beth
5.5 years, juvenile 3 female.
Small patches of hair missing from tail.



Zara
5.2 years, juvenile 3 female.
Similar looking to Makele, with thicker hair over shoulders. Small notch out of left hand side ear.



Ramses
4.4 years, juvenile 2 male.
Brown hair. Shorter wrinkled muzzle. Rounded ears.



Pharaoh
4.1 years, juvenile 2 male.
Brown fur. Shorter wrinkled muzzle. Pointed, triangular shared ears.

6.2 APPENDIX B

6.2.1 Results for the combined focal animals

CHI-SQUARED TESTS

Table 6.1. Test comparing the overall occurrence of “major” behaviours between the former and new enclosures.

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 2105	New enclosure n = 1754			
Solicitation	3.235 \pm 7.389	2.046 \pm 3.753	19.0883	1	0.0000
Agonistic	1.454 \pm 2.024	1.172 \pm 2.237	1.7915	1	0.1807
Feeding activity	26.108 \pm 22.282	26.982 \pm 24.119	0.7886	1	0.3745
Grooming	22.286 \pm 29.112	14.263 \pm 25.237	206.9617	1	0.0000
Appeasement	0.027 \pm 0.245	0.011 \pm 0.056	0.6301	1	0.4273
Inactivity	27.714 \pm 23.389	20.893 \pm 21.768	88.5321	1	0.0000
Locomotion	11.650 \pm 8.215	16.687 \pm 13.245	77.8880	1	0.0000
Play	1.270 \pm 5.660	0.251 \pm 1.065	55.5666	1	0.0000
Out of Sight	6.206 \pm 16.233	17.695 \pm 26.430	543.3043	1	0.0000

Table 6.2. Tests comparing the overall occurrence of “minor” behaviours between the former and new enclosures.

Minor Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 2454	New enclosure n = 2229			
Dpg	0.045 \pm 0.2	0.13 \pm 0.524	2.1597	1	0.1417
Dpr	0.6 \pm 1.772	0.322 \pm 1.213	0.1936	1	0.6599
Dvg	0.03 \pm 0.185	0.057 \pm 0.266	0.1556	1	0.6932
Dvr	0.418 \pm 1.739	0.248 \pm 1.029	14.3915	1	0.0001
M	0.042 \pm 0.159	0.051 \pm 0.19	0.1469	1	0.7015
Ms	0.038 \pm 0.245	0.003 \pm 0.022	0.1856	1	0.6666
Thg	0.46 \pm 4.002				
Thr	0.078 \pm 0.712				
P	1.802 \pm 4.111	1.422 \pm 2.926	0.0402	1	0.8411
Avi	0.384 \pm 1.103	0.06 \pm 0.515	0.4892	1	0.4843
Aph	0.081 \pm 0.355	0.132 \pm 0.62	0.6885	1	0.4067
Avo	0.032 \pm 0.133	0.008 \pm 0.067	0.3577	1	0.5498
Sh	0.064 \pm 0.386				
Av	0.371 \pm 0.787	0.301 \pm 1.516	1.0167	1	0.3133
Sp	0.133 \pm 0.654	0.215 \pm 0.791	0.7120	1	0.3988
Mi	0.051 \pm 0.329	0.016 \pm 0.136	0.3315	1	0.5648
Al	0.378 \pm 1.15	0.614 \pm 1.476	0.6935	1	0.4050
Fe	9.121 \pm 11.953	9.215 \pm 13.006	1.3340	1	0.2481
F	16.979 \pm 16.008	16.752 \pm 16.716	4.7452	1	0.0294
Rout	0.409 \pm 1.56	0.193 \pm 1.316	0.1716	1	0.6787
LF	0.105 \pm 0.379	0.565 \pm 1.772	6.6744	1	0.0098
Hu		0.014 \pm 0.12			
Dr	0.018 \pm 0.12	0.219 \pm 0.717	0.0000	1	1.0000
Li		0.04 \pm 0.245			
GS	1.023 \pm 3.431	0.137 \pm 0.491	39.8600	1	0.0000
Gor	15.841 \pm 25.46	8.464 \pm 18.603	43.3676	1	0.0000

GOg	5.389 ± 13.376	5.533 ± 15.905	0.2146	1	0.6432
TaAp	0.026 ± 0.237	0.01 ± 0.052	2.0191	1	0.1553
VoAp	0.891 ± 7.803				
S	22.568 ± 19.618	18.189 ± 20.523	13.7640	1	0.0002
R	3.141 ± 10.43	0.854 ± 5.849	5.6773	1	0.0172
SS	0.697 ± 1.051	1.217 ± 3.238	2.8235	1	0.0929
W	10.24 ± 7.613	13.479 ± 10.911		1	0.0000
Ru	0.132 ± 0.472	0.18 ± 0.603	2.4421	1	0.1181
C	0.989 ± 2.013	0.053 ± 0.132		1	0.0000
J	0.003 ± 0.029	0.055 ± 0.471	4.3734	1	0.0365
Wob		0.003 ± 0.026			
Tm		2.359 ± 3.896			
Tp		1.334 ± 5.473			
ME	0.756 ± 5.2	0.174 ± 0.93	5.1841	1	0.0228
Di	0.399 ± 2.116				
Pf	0.154 ± 0.953	0.012 ± 0.062	6.0547	1	0.0139
Sch		0.051 ± 0.434			

ANALYSES OF VARIANCE

Table 6.3. Tests comparing the mean bout length of “major” behaviours between the former and new enclosures.

Major Behaviour	Former enclosure			New enclosure			F Value	d. f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	150	15 \pm 15	42, 43, 45, 45, 46, 47, 49, 56, 59, 81, 81, 90	82	16 \pm 16	53, 55, 57, 64, 69	0.19	1	0.6651
Agonistic	89	12 \pm 10	32, 34, 34, 37, 40, 58	58	11 \pm 13	40, 42, 53, 64	0.57	1	0.4540
Feeding activity	576	33 \pm 35	85, 85, 86, 86, 96, 97, 98, 99, 108, 108, 111, 113, 114, 115, 117, 118, 119, 122, 123, 132, 132, 135, 136, 137, 140, 141, 142, 142, 149, 163, 169, 170, 172, 173, 174, 182, 186, 200, 219, 303	484	35 \pm 49	92, 96, 97, 99, 99, 100, 101, 101, 103, 108, 110, 111, 112, 114, 116, 130, 141, 144, 146, 149, 151, 153, 167, 176, 188, 196, 204, 215, 252, 263, 265, 289, 304, 305, 520	2.08	1	0.1521
Grooming	157	66 \pm 72	194, 209, 214, 218, 230, 231, 247, 274, 420, 454	107	67 \pm 82	165, 208, 218, 234, 263, 334, 368, 406, 409	0.09	1	0.7640
Appeasement	1	27 \pm 0		3	3 \pm 1				
Inactivity	498	33 \pm 46	88, 91, 92, 92, 95, 96, 99, 99, 103, 103, 104, 106, 107, 107, 108, 108, 110, 112, 114, 114, 115, 117, 118, 119, 132, 132, 135, 136, 137, 142, 145, 148, 151, 157, 165, 170, 175, 222, 264, 322, 634	432	27 \pm 58	55, 60, 60, 61, 61, 62, 63, 67, 72, 73, 76, 78, 78, 83, 89, 96, 100, 112, 112, 117, 125, 126, 142, 154, 163, 166, 166, 181, 315, 348, 441, 444, 454, 456, 534	0.12	1	0.7306
Locomotion	553	15 \pm 18	42, 42, 42, 43, 43, 45, 45, 45, 45, 46, 47, 48, 48, 48, 49, 49, 49, 50, 51, 53, 53, 56, 59, 60, 61, 62, 82, 116, 118, 119, 136, 163, 172	516	19 \pm 28	50, 51, 51, 52, 52, 52, 53, 55, 55, 56, 57, 58, 63, 64, 69, 69, 75, 77, 78, 83, 85, 86, 86, 91, 91, 95, 97, 101, 103, 108, 137, 142, 151, 174, 196, 204, 215, 252	2.21	1	0.1396
Play	35	20 \pm 35	72, 200	31	42 \pm 74	159, 283, 302	1.46	1	0.2440
Out of Sight	41	66 \pm 119	186, 188, 364, 375, 563	86	57 \pm 67	174, 179, 192, 219, 237, 283, 302	0.53	1	0.4691

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

Table 6.4. Tests comparing the mean bout length of “minor” behaviours between the former and new enclosures.

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Dpg	9	4 \pm 3		12	9 \pm 8	20, 29	4.24	1	0.0735
Dpr	42	12 \pm 14	30, 56, 81	24	11 \pm 12	25, 25, 32, 53	0.39	1	0.5359
Dvg	6	5 \pm 3		9	5 \pm 3		0.27	1	0.6331
Dvr	20	17 \pm 17	81	18	11 \pm 18	16, 53, 69	3.09	1	0.1008
M	7	5 \pm 3		7	6 \pm 3		1.09	1	0.3277
Ms	3	8 \pm 5		1	2 \pm 0				
Thg	16	30 \pm 24	81, 90	0					
Thr	3	24 \pm 25		0					
P	91	18 \pm 12	46, 47, 49, 57	45	26 \pm 18	84	9.85	1	0.0032
Avi	27	12 \pm 10	37, 40	1	53 \pm 0				
Aph	6	11 \pm 7		6	18 \pm 18		0.51	1	0.4971
Avo	6	5 \pm 3		1	6 \pm 0				
Sh	6	9 \pm 11	34	0					
Av	31	11 \pm 5	23, 26	15	17 \pm 25	68, 84	0.19	1	0.6683
Sp	8	15 \pm 13	44	13	13 \pm 16	64	0.01	1	0.9317
Mi	2	20 \pm 1		1	13 \pm 0				
Al	21	14 \pm 13	58	35	13 \pm 14	42, 68	0.51	1	0.4801
Fe	170	45 \pm 44	122, 132, 137, 140, 149, 169, 170, 173, 182, 219, 303	152	46 \pm 59	116, 120, 126, 130, 135, 176, 188, 255, 263, 288, 289, 304, 305	0.08	1	0.7832
F	453	33 \pm 34	85, 85, 89, 92, 92, 98, 99, 108, 108, 111, 114, 117, 118, 119, 123, 132, 136, 141, 142, 142, 162, 163, 170, 171, 172, 174, 186, 200, 303	380	35 \pm 39	97, 97, 99, 99, 100, 101, 103, 108, 111, 112, 114, 115, 130, 141, 144, 146, 149, 151, 151, 153, 167, 190, 196, 204, 215, 252, 265	0.96	1	0.33
Rout	22	15 \pm 9		8	19 \pm 16		9.09	1	0.0236
LF	10	10 \pm 4		35	12 \pm 16	36, 48, 83	0.42	1	0.5237
Hu	0			1	11 \pm 0				
Dr	3	5 \pm 3		11	15 \pm 11	44	0.08	1	0.7929
Li	0			4	8 \pm 3				
GS	17	49 \pm 54	218	9	12 \pm 8		4.43	1	0.0553

Gor	119	103 ± 113	295, 318, 327, 338, 382, 420, 487, 496, 657	67	90 ± 99	263, 368, 406, 409, 420	1.42	1	0.2381
GOg	62	71 ± 86	257, 258, 275, 454	58	70 ± 87	218, 225, 334, 498	0.5	1	0.4861
TaAp	1	27 ± 0		3	3 ± 1				
VoAp	4	171 ± 267		0					
S	457	40 ± 54	103, 103, 104, 106, 107, 107, 108, 108, 110, 112, 114, 114, 115, 116, 117, 118, 132, 136, 137, 141, 142, 145, 146, 157, 157, 165, 170, 173, 175, 178, 179, 215, 222, 241, 243, 252, 264, 322, 345, 469, 486	377	34 ± 63	76, 78, 89, 93, 96, 96, 98, 100, 112, 117, 125, 126, 142, 149, 152, 154, 155, 163, 166, 166, 181, 188, 206, 264, 309, 315, 347, 348, 441, 444, 454, 456	0.16	1	0.6884
R	39	60 ± 76	248, 287, 320	8	74 ± 104	340	0	1	0.9918
SS	58	10 ± 6	24, 25, 29, 31	97	10 ± 14	21, 22, 23, 28, 33, 33, 41, 78, 112	0.01	1	0.9317
W	563	16 ± 18	39, 39, 39, 40, 40, 42, 42, 42, 43, 43, 44, 45, 45, 45, 45, 46, 46, 47, 48, 48, 48, 49, 49, 49, 50, 51, 53, 53, 55, 56, 57, 59, 60, 60, 61, 62, 82, 89, 118, 119, 136, 163, 172	579	19 ± 26	51, 51, 52, 52, 52, 54, 55, 55, 56, 57, 63, 64, 69, 69, 70, 71, 74, 75, 77, 78, 79, 79, 84, 85, 86, 91, 91, 93, 95, 97, 103, 108, 115, 151, 196, 204, 215, 252	1.5	1	0.2227
Ru	18	6 ± 8	10, 19, 37	15	9 ± 7	30	0.09	1	0.7684
C	64	12 ± 16	57, 116	15	3 ± 2	8	12.78	1	0.0009
J	1	3 ± 0		1	40 ± 0				
Wob	0			1	2 ± 0				
Tm	0			73	25 ± 20	78, 79, 93, 95			
Tp	0			23	45 ± 50	174			
ME	18	33 ± 75	72, 333	11	11 ± 12	29, 40	0.72	1	0.413
Di	8	45 ± 60	200	0					
Pf	11	10 ± 9	36	3	3 ± 2		1.45	1	0.2734
Sch	0			3	11 ± 4				

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

CHI-SQUARED TESTS

Table 6.5. Tests comparing the overall occurrence of social states between the former and new enclosures.

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 1750	New enclosure n = 1509			
Solitary	40.604 \pm 34.800	51.137 \pm 32.725	195.8860	1	0.0000
Grouped	29.308 \pm 25.646	21.218 \pm 19.518	133.0357	1	0.0000
Social	30.088 \pm 32.736	27.645 \pm 28.939	12.8029	1	0.0003

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Table 6.6. Tests comparing the mean bout length of social states between the former and new enclosures.

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	904	27 \pm 40	103, 104, 106, 107, 107, 108, 108, 108, 110, 111, 113, 114, 114, 115, 115, 116, 117, 118, 118, 119, 119, 119, 122, 132, 132, 132, 136, 136, 137, 140, 142, 142, 145, 148, 151, 157, 165, 169, 170, 172, 174, 182, 200, 218, 219, 264, 303, 634	854	26 \pm 48	61, 61, 63, 65, 66, 66, 67, 67, 68, 68, 69, 69, 69, 70, 71, 72, 72, 73, 73, 73, 74, 74, 74, 74, 75, 75, 77, 78, 78, 81, 81, 81, 83, 83, 83, 84, 89, 91, 91, 92, 96, 97, 99, 99, 100, 101, 103, 108, 110, 111, 112, 114, 116, 117, 125, 126, 130, 141, 142, 146, 149, 151, 153, 154, 163, 167, 176, 181, 188, 204, 215, 265, 304, 305, 315, 348, 444, 454, 520, 534	0.95	1	0.3318
Grouped	471	32 \pm 34	91, 92, 94, 97, 99, 103, 108, 112, 114, 117, 123, 132, 135, 137, 141, 142, 149, 163, 170, 171, 173, 175, 186, 222, 322	368	26 \pm 46	72, 73, 74, 76, 77, 78, 82, 85, 86, 88, 89, 96, 100, 112, 112, 144, 166, 166, 196, 252, 263, 289, 441, 456	0.17	1	0.6807
Social	373	34 \pm 53	81, 81, 83, 85, 89, 90, 90, 90, 90, 92, 102, 106, 112, 113, 114, 114, 116, 118, 121, 122, 122, 124, 129, 133, 137, 137, 144, 163, 164, 171, 181, 183, 183, 194, 209, 214, 230, 231, 247, 274, 420, 454	287	38 \pm 58	116, 122, 126, 130, 137, 138, 141, 141, 142, 151, 152, 162, 165, 174, 208, 218, 234, 263, 334, 368, 406, 409	0.2	1	0.8910

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

6.2.2 Results for individual focal animals

CHI-SQUARED TESTS

6.2.2.1 Tests comparing the overall occurrence of “major” behaviours between the former and new enclosures.

Table 6.7.1. Abu

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 450	New enclosure n = 359			
Solicitation	8.623 \pm 12.780	4.039 \pm 4.319	29.3154	1	0.0000
Agonistic	2.423 \pm 2.593	1.936 \pm 2.274	0.9106	1	0.3400
Feeding activity	21.470 \pm 24.440	22.037 \pm 22.377	0.1546	1	0.6942
Grooming	4.971 \pm 11.360	5.591 \pm 13.325	0.6311	1	0.4270
Appeasement		0.027 \pm 0.103			
Inactivity	37.503 \pm 28.214	28.160 \pm 23.878	32.3950	1	0.0000
Locomotion	10.247 \pm 7.097	21.641 \pm 14.693	81.5026	1	0.0000
Play	0.093 \pm 0.303	0.000 \pm 0.000	2.0204	1	0.1552
Out of Sight	14.670 \pm 24.141	16.569 \pm 26.421	2.2420	1	0.1343

Table 6.7.2. Randy

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 269	New enclosure n = 202			
Solicitation	1.272 \pm 2.232	3.033 \pm 4.940	12.5478	1	0.0004
Agonistic	0.957 \pm 2.129	0.385 \pm 1.349	4.0956	1	0.0430
Feeding activity	10.229 \pm 12.346	15.482 \pm 17.534	20.3924	1	0.0000
Grooming	49.755 \pm 25.325	15.718 \pm 23.578	442.9473	1	0.0000
Appeasement					
Inactivity	24.964 \pm 20.329	17.426 \pm 16.279	27.8422	1	0.0000
Locomotion	7.587 \pm 7.378	15.360 \pm 14.800	50.0039	1	0.0000
Play					
Out of Sight	5.236 \pm 18.972	32.595 \pm 35.531	444.8232	1	0.0000

Table 6.7.3. Toka

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 628	New enclosure n = 482			
Solicitation	0.369 \pm 0.719	1.194 \pm 2.831	8.3930	1	0.0038
Agonistic	1.302 \pm 1.773	2.224 \pm 3.658	4.4628	1	0.0346
Feeding activity	36.851 \pm 21.596	34.184 \pm 23.791	2.7604	1	0.0966
Grooming	10.653 \pm 22.322	4.938 \pm 10.487	40.7673	1	0.0000
Appeasement					
Inactivity	31.940 \pm 22.009	32.332 \pm 25.291	0.0628	1	0.8021
Locomotion	12.537 \pm 8.294	14.614 \pm 8.785	3.2794	1	0.0702
Play	4.281 \pm 10.601	1.093 \pm 2.139	36.0606	1	0.0000
Out of Sight	2.068 \pm 4.595	9.421 \pm 14.334	98.0644	1	0.0000

Table 6.7.4. Tina

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 304	New enclosure n = 340			
Solicitation	0.460 \pm 1.361	0.318 \pm 0.733	0.3423	1	0.5585
Agonistic	0.975 \pm 1.276	0.546 \pm 1.071	1.6112	1	0.2043
Feeding activity	31.859 \pm 15.980	28.106 \pm 21.233	4.3403	1	0.0372
Grooming	16.845 \pm 25.046	24.554 \pm 33.528	23.4168	1	0.0000
Appeasement		0.014 \pm 0.053			
Inactivity	29.026 \pm 24.122	14.166 \pm 20.444	86.2337	1	0.0000
Locomotion	16.033 \pm 9.911	18.602 \pm 16.053	2.9765	1	0.0845
Play	1.417 \pm 4.909				
Out of Sight	3.384 \pm 6.852	13.694 \pm 27.961	92.3581	1	0.0000

Table 6.7.5. Sinead

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 454	New enclosure n = 371			
Solicitation	5.043 \pm 7.020	1.588 \pm 3.602	30.2193	1	0.0000
Agonistic	1.472 \pm 1.758	0.659 \pm 0.912	4.9899	1	0.0255
Feeding activity	31.447 \pm 24.090	34.697 \pm 30.813	3.5036	1	0.0612
Grooming	29.486 \pm 34.649	21.819 \pm 33.498	24.3351	1	0.0000
Appeasement	0.141 \pm 0.563	0.013 \pm 0.052	1.8877	1	0.1695
Inactivity	13.531 \pm 15.884	11.171 \pm 15.181	4.0981	1	0.0429
Locomotion	13.403 \pm 7.319	13.485 \pm 11.072	0.0015	1	0.9691
Play	0.150 \pm 0.281	0.088 \pm 0.242	0.2516	1	0.6160
Out of Sight	5.066 \pm 14.517	16.479 \pm 21.227	109.9673	1	0.0000

6.2.2.2 Tests comparing the overall occurrence of “minor” behaviours between the former and new enclosures.

Table 6.8.1. Abu.

Minor Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure N = 554	New enclosure n = 456			
Dpg	0.036 \pm 0.146				
Dpr	1.802 \pm 2.968	0.815 \pm 2.059	0.8367	1	0.3603
Dvg					
Dvr	1.503 \pm 3.055	0.722 \pm 1.792	9.6194	1	0.0019
M	0.061 \pm 0.184	0.062 \pm 0.232	0.1542	1	0.6946
Ms					
Thg	2.049 \pm 8.448				
Thr					
P	3.868 \pm 5.245	2.986 \pm 3.959	0.0725	1	0.7877
Avi	1.152 \pm 1.801				
Aph	0.316 \pm 0.69	0.079 \pm 0.295	0.0193	1	0.8895
Avo	0.019 \pm 0.054	0.039 \pm 0.146	0.3577	1	0.5498
Sh	0.013 \pm 0.055				
Av	0.073 \pm 0.301				
Sp	0.613 \pm 1.305	1.061 \pm 1.479	0.712	1	0.3988
Mi	0.24 \pm 0.679	0.079 \pm 0.295	0.3315	1	0.5648
Al	0.186 \pm 0.562	0.676 \pm 1.404	0.1043	1	0.7467
Fe	8.881 \pm 14.376	9.643 \pm 17.071	3.0201	1	0.0822
F	12.648 \pm 13.157	11.123 \pm 12.016	0.1891	1	0.6637

Rout					
LF		0.289 ± 0.753			
Hu					
Dr	0.035 ± 0.146	0.125 ± 0.263	0	1	1
Li					
GS	0.136 ± 0.56	0.247 ± 0.755	0.0919	1	0.7618
Gor	4.53 ± 10.415	3.095 ± 10.264	0.7452	1	0.388
GOg	0.152 ± 0.625	1.954 ± 7.073	11.686	1	0.0006
TaAp		0.024 ± 0.091			
VoAp					
S	35.601 ± 26.385	24.899 ± 20.089		1	0
R	1.01 ± 2.903				
SS	0.343 ± 0.786	0.985 ± 2.486	1.6763	1	0.1954
W	8.993 ± 6.46	15.967 ± 8.611		1	0
Ru	0.334 ± 0.873	0.347 ± 0.889	0.0882	1	0.7665
C	0.905 ± 1.789	0.05 ± 0.102	10.2246	1	0.0014
J					
Wob					
Tm		4.458 ± 5.127			
Tp		4.149 ± 9.688			
ME	0.089 ± 0.28				
Di					
Pf					
Sch					

Table 6.8.2. Randy

Minor Behaviour	Mean per sample ± SD		Chi-square	d.f	p-value
	Former enclosure N = 333	New enclosure n = 311			
Dpg					
Dpr	0.871 ± 1.824	0.75 ± 1.515	0.376	1	0.5398
Dvg					
Dvr	0.43 ± 1.774	0.503 ± 1.242	4.7948	1	0.0285
M	0.046 ± 0.134	0.124 ± 0.299	0.0897	1	0.7646
Ms	0.056 ± 0.168	0.013 ± 0.048	0.1855	1	0.6667
Thg	0.1 ± 0.411				
Thr					
P	0.162 ± 0.521	1.761 ± 3.061	3.9844	1	0.0459
Avi	0.144 ± 0.595	0.297 ± 1.113	0.4892	1	0.4843
Aph	0.045 ± 0.187	0.513 ± 1.254	1.2547	1	0.2627
Avo	0.045 ± 0.187				
Sh					
Av	0.442 ± 0.873	0.017 ± 0.063	2.0556	1	0.1516
Sp					
Mi					
Al	0.329 ± 1.358				
Fe	5.954 ± 11.108	3.944 ± 7.864	15.0234	1	0.0001
F	4.969 ± 8.779	11.707 ± 13.329		1	0
Rout					
LF					
Hu					
Dr	0.051 ± 0.209				
Li					
GS	0.071 ± 0.291				
Gor	45.452 ± 21.188	14.07 ± 22.069		1	0

GOg	4.023 ± 7.196	1.797 ± 6.175	4.9367	1	0.0263
TaAp					
VoAp	3.996 ± 16.475				
S	18.767 ± 15.655	16.16 ± 15.539	0.8535	1	0.3556
R	0.395 ± 1.283	0.089 ± 0.333	1.3266	1	0.2494
SS	0.71 ± 0.946	0.677 ± 0.917	0.0602	1	0.8062
W	7.176 ± 7.146	14.318 ± 13.17		1	0
Ru	0.057 ± 0.234				
C	0.47 ± 1.171	0.057 ± 0.171	2.9806	1	0.0843
J					
Wob					
Tm		1.495 ± 3.829			
Tp					
ME					
Di					
Pf					
Sch					

Table 6.8.3. Toka

Minor Behaviour	Mean per sample ± SD		Chi-square	d.f	p-value
	Former enclosure N = 709	New enclosure n = 593			
Dpg	0.04 ± 0.175	0.064 ± 0.198	0.0611	1	0.8048
Dpr	0.008 ± 0.035				
Dvg	0.04 ± 0.175	0.013 ± 0.052	0.3141	1	0.5752
Dvr					
M		0.035 ± 0.134			
Ms	0.107 ± 0.468				
Thg					
Thr					
P	0.199 ± 0.527	1.053 ± 2.635	9.8208	1	0.0017
Avi					
Aph					
Avo	0.06 ± 0.183				
Sh	0.034 ± 0.146				
Av	0.713 ± 1.095	1.33 ± 3.043	5.4761	1	0.0193
Sp	0.009 ± 0.039				
Mi					
Al	0.422 ± 1.388	1.261 ± 2.459	0.5765	1	0.4477
Fe	11.074 ± 11.781	10.017 ± 9.766	2.5481	1	0.1104
F	24.948 ± 15.399	24.308 ± 15.851	0.3999	1	0.5271
Rout	1.661 ± 2.847	0.21 ± 0.814	0.1716	1	0.6787
LF	0.109 ± 0.294	0.893 ± 2.579	11.1154	1	0.0009
Hu					
Dr		0.634 ± 1.297			
Li		0.069 ± 0.266			
GS	2.597 ± 5.662	0.268 ± 0.595		1	0
Gor	8.052 ± 21.76	4.508 ± 10.193		1	0
GOg		0.118 ± 0.457			
TaAp					
VoAp	0.144 ± 0.629				
S	21.336 ± 10.974	27.626 ± 25.246		1	0
R	9.327 ± 17.486	3.088 ± 11.962	3.8485	1	0.0498
SS	0.777 ± 1.066	0.904 ± 0.633	0.6518	1	0.4195
W	10.39 ± 6.901	11.228 ± 6.186	3.6096	1	0.0574

Ru	0.108 ± 0.264	0.336 ± 0.725	2.9393	1	0.0864
C	1.334 ± 2.817	0.066 ± 0.161	5.9657	1	0.0146
J	0.013 ± 0.058	0.255 ± 0.987	4.3734	1	0.0365
Wob		0.014 ± 0.053			
Tm		0.863 ± 1.47			
Tp		0.964 ± 3.735			
ME	3.01 ± 10.334	0.721 ± 1.887	5.6575	1	0.0174
Di	0.826 ± 2.081				
Pf	0.616 ± 1.875	0.055 ± 0.125	6.0547	1	0.0139
Sch		0.235 ± 0.91			

Table 6.8.4. Tina

Minor Behaviour	Mean per sample ± SD		Chi-square	d.f	p-value
	Former enclosure n = 340	New enclosure n = 427			
Dpg	0.017 ± 0.056	0.171 ± 0.459	0.9	1	0.3428
Dpr					
Dvg		0.177 ± 0.48			
Dvr					
M	0.048 ± 0.107	0.033 ± 0.086	0.0144	1	0.9045
Ms					
Thg					
Thr					
P	0.396 ± 1.313	0.211 ± 0.582	2.8047	1	0.094
Avi	0.108 ± 0.359				
Aph					
Avo					
Sh					
Av	0.422 ± 0.637	0.027 ± 0.066	2.2512	1	0.1335
Sp					
Mi					
Al	0.447 ± 1.116	0.493 ± 0.983	0.0204	1	0.8864
Fe	10.417 ± 12.18	8.223 ± 10.881	0.0035	1	0.9528
F	21.299 ± 9.758	20.158 ± 17.635	7.5844	1	0.0059
Rout	0.091 ± 0.303				
LF	0.125 ± 0.416	1.405 ± 2.623	2.4384	1	0.1184
Hu		0.074 ± 0.268			
Dr		0.041 ± 0.149			
Li					
GS	2.522 ± 4.251	0.036 ± 0.131	10.2379	1	0.0014
Gor	2.056 ± 6.819	3.038 ± 7.451	0.539	1	0.4628
GOg	12.267 ± 19.755	20.274 ± 29.163	10.8018	1	0.001
TaAp		0.014 ± 0.051			
VoAp					
S	23.46 ± 18.707	10.602 ± 19.235		1	0
R	4.149 ± 11.902				
SS	1.42 ± 1.463	3.154 ± 6.464	8.3118	1	0.0039
W	15.658 ± 9.373	16.2 ± 15.121	6.3096	1	0.012
Ru		0.036 ± 0.131			
C	0.297 ± 0.576	0.012 ± 0.044	0.7552	1	0.3848
J					
Wob					
Tm		2.273 ± 3.871			
Tp					
ME					

Di	1.417 ± 4.7				
Pf					
Sch					

Table 6.8.5. *Sinead*

Minor Behaviour	Mean per sample ± SD		Chi-square	d.f	p-value
	Former enclosure n = 518	New enclosure n = 442			
Dpg	0.133 ± 0.367	0.445 ± 1.026	2.0581	1	0.1514
Dpr	0.134 ± 0.438	0.024 ± 0.086	0.5217	1	0.4701
Dvg	0.11 ± 0.363	0.108 ± 0.339	0.0221	1	0.8818
Dvr	0.022 ± 0.085				
M	0.065 ± 0.251				
Ms					
Thg					
Thr	0.41 ± 1.588				
P	4.38 ± 6.055	1.017 ± 2.372	5.1505	1	0.0232
Avi	0.475 ± 1.125				
Aph	0.019 ± 0.075	0.063 ± 0.226	0.2786	1	0.5976
Avo	0.019 ± 0.075				
Sh	0.28 ± 0.833				
Av	0.159 ± 0.437	0.027 ± 0.099	0.641	1	0.4233
Sp					
Mi					
Al	0.543 ± 1.045	0.586 ± 0.79	0.7576	1	0.3841
Fe	9.542 ± 8.748	14.477 ± 15.128	13.1177	1	0.0003
F	22.163 ± 19.812	16.144 ± 19.883	4.8517	1	0.0276
Rout		0.781 ± 2.817			
LF	0.32 ± 0.669	0.251 ± 0.403	0.8302	1	0.3622
Hu					
Dr		0.257 ± 0.639			
Li		0.131 ± 0.472			
GS		0.118 ± 0.424			
Gor	15.327 ± 28.29	18.155 ± 28.54	13.1005	1	0.0003
GOg	14.396 ± 20.05	4.816 ± 10.582	20.8467	1	0
TaAp	0.137 ± 0.529	0.013 ± 0.047	2.0191	1	0.1553
VoAp					
S	13.051 ± 15.755	9.974 ± 12.545	4.0346	1	0.0446
R	0.14 ± 0.378	0.889 ± 3.054	7.7166	1	0.0055
SS	0.44 ± 0.68	0.464 ± 0.923	0.2286	1	0.6326
W	10.841 ± 6.308	9.768 ± 7.568	0.1348	1	0.7135
Ru	0.117 ± 0.313	0.162 ± 0.584	0.7903	1	0.374
C	1.754 ± 2.135	0.079 ± 0.127	13.6953	1	0.0002
J					
Wob					
Tm		2.829 ± 3.253			
Tp		1.506 ± 5.428			
ME	0.105 ± 0.235	0.094 ± 0.24	0.0181	1	0.893
Di					
Pf	0.04 ± 0.156				

ANALYSES OF VARIANCE

6.2.2.3 Tests comparing the mean bout length of “major” behaviours between the former and new enclosures.

Table 6.9.1. *Abu*

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	83	16 \pm 15	46, 56, 81, 90	30	19 \pm 19	57, 64, 69	1.63	1	0.2140
Agonistic	32	11 \pm 8	37	21	13 \pm 15	42, 64	0.06	1	0.8062
Feeding activity	85	38 \pm 40	97, 137, 142, 149, 170, 182, 186	68	42 \pm 49	110, 153, 176, 188, 289	0.26	1	0.6129
Grooming	14	60 \pm 44		15	52 \pm 69	138, 263	0.81	1	0.3849
Appeasement	0			1	4 \pm 0				
Inactivity	118	41 \pm 47	165, 170, 222, 322	76	40 \pm 83	96, 100, 112, 125, 126, 154, 181, 444, 534	0.94	1	0.3408
Locomotion	100	14 \pm 11	37, 37, 37, 45, 48, 56, 62	134	21 \pm 26	64, 69, 75, 78, 91, 95, 103, 142, 174	4.62	1	0.0407
Play	3	6 \pm 4		0					
Out of Sight	15	90 \pm 165	375, 563	14	56 \pm 51		0.65	1	0.4360

Table 6.9.2. Randy

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	15	13 \pm 19	81	23	15 \pm 15	53	0.03	1	0.8578
Agonistic	9	16 \pm 8		4	15 \pm 25	53	0.03	1	0.8807
Feeding activity	49	32 \pm 29	86, 163	39	53 \pm 67	252, 263, 265	9.32	1	0.0069
Grooming	55	72 \pm 73	209, 230, 420	23	87 \pm 82	368	1.00	1	0.3294
Appeasement	0			0					
Inactivity	68	43 \pm 82	103, 112, 117, 136, 142, 145, 148, 634	66	24 \pm 31	76, 89, 163, 166	2.84	1	0.1035
Locomotion	63	17 \pm 23	42, 51, 82, 163	68	26 \pm 34	77, 85, 108, 252	0.70	1	0.4116
Play	0			0					
Out of Sight	5	15 \pm 12	37	8	93 \pm 83		1.39	1	0.2770

Table 6.9.3. Toka

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	5	6 \pm 6	17	8	16 \pm 17	55	1.24	1	0.3159
Agonistic	20	13 \pm 13	26, 58	15	13 \pm 12		0.20	1	0.6593
Feeding activity	207	30 \pm 32	78, 81, 83, 96, 99, 108, 108, 114, 115, 117, 122, 123, 132, 303	147	30 \pm 38	81, 83, 84, 92, 111, 114, 130, 141, 146, 149, 305	0.08	1	0.7786
Grooming	19	65 \pm 56	183, 218	10	38 \pm 69	234	0.53	1	0.4812
Appeasement	0			0					
Inactivity	164	28 \pm 31	74, 81, 91, 92, 104, 108, 114, 119, 132, 132, 135, 151, 175	135	29 \pm 57	52, 52, 55, 63, 72, 78, 83, 112, 117, 142, 315, 348, 441	0.35	1	0.5612
Locomotion	175	12 \pm 13	33, 48, 49, 49, 53, 60, 116	126	13 \pm 14	45, 48, 48, 48, 51, 52, 52, 55, 69	0.02	1	0.8767
Play	27	17 \pm 16	72	13	8 \pm 10	40	1.65	1	0.2276
Out of Sight	11	35 \pm 54	67, 188	28	43 \pm 45		0.02	1	0.8847

Table 6.9.4. Tina

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	4	3 \pm 1		8	5 \pm 3		2.14	1	0.2394
Agonistic	11	11 \pm 8	34	6	6 \pm 6	17	1.19	1	0.3036
Feeding activity	101	37 \pm 40	113, 118, 119, 136, 140, 172, 200, 219	112	34 \pm 40	81, 82, 83, 86, 88, 89, 96, 97, 112, 151, 196, 204, 215	0.00	1	0.9894
Grooming	18	66 \pm 58		31	63 \pm 74	162, 208, 218, 334	0.16	1	0.6987
Appeasement	0			1	2 \pm 0				
Inactivity	80	28 \pm 28	82, 84, 86, 92, 95, 96, 157	70	26 \pm 75	41, 48, 78, 454, 456	0.10	1	0.7558
Locomotion	86	22 \pm 30	59, 61, 118, 119, 136, 172	94	25 \pm 40	63, 83, 86, 97, 151, 196, 204, 215	0.00	1	0.9469
Play	1	200 \pm 0		0					
Out of Sight	3	80 \pm 92		18	53 \pm 72	179, 192, 237	0.43	1	0.5291

Table 6.9.5. Sinead

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solicitation	43	18 \pm 15		13	14 \pm 13		1.58	1	0.2310
Agonistic	17	11 \pm 11	34, 40	12	8 \pm 7	20, 21	1.72	1	0.2104
Feeding activity	134	33 \pm 35	83, 85, 98, 111, 132, 135, 141, 142, 169, 173, 174	118	33 \pm 59	70, 73, 91, 99, 100, 101, 116, 144, 167, 304, 520	0.96	1	0.3367
Grooming	51	60 \pm 87	181, 214, 231, 247, 274, 454	28	73 \pm 99	406, 409	0.30	1	0.5886
Appeasement	1	27 \pm 0		1	2 \pm 0				
Inactivity	69	29 \pm 39	56, 56, 58, 58, 58, 67, 99, 114, 137, 264	85	15 \pm 21	29, 29, 30, 30, 33, 34, 41, 43, 43, 46, 51, 60, 62, 166	3.56	1	0.0695
Locomotion	129	15 \pm 12		94	16 \pm 23	46, 55, 58, 86, 91, 101, 137	0.84	1	0.3686
Play	4	6 \pm 2		2	7 \pm 2		0.23	1	0.6590
Out of Sight	7	94 \pm 130	364	18	66 \pm 90	159, 283, 302	0.46	1	0.5086

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

6.2.2.4 Tests comparing the mean bout length of “minor” behaviours between the former and new enclosures.

Table 6.10.1. *Abu*

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOV A p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Dpg	1	6 \pm 0		0					
Dpr	30	10 \pm 11	30, 56	13	10 \pm 10		0.23	1	0.6373
Dvg	0			0					
Dvr	18	14 \pm 9	42	12	10 \pm 18	69	1.02	1	0.3340
M	2	7 \pm 3		1	10 \pm 0				
Ms	0			0					
Thg	15	30 \pm 25	81, 90	0					
Thr	0			0					
P	45	18 \pm 11	46, 57	18	27 \pm 20		2.67	1	0.1216
Avi	20	11 \pm 9	27, 37	0					
Aph	4	14 \pm 7		1	13 \pm 0				
Avo	2	2 \pm 0		1	6 \pm 0				
Sh	1	2 \pm 0		0					
Av	1	17 \pm 0		0					
Sp	7	17 \pm 13	44	13	13 \pm 16	64	0.43	1	0.5244
Mi	2	20 \pm 1		1	13 \pm 0				
Al	4	8 \pm 4		8	14 \pm 13		0.24	1	0.6429
Fe	25	60 \pm 49	170, 182	23	68 \pm 67	176, 188, 289	1.04	1	0.3273
F	71	33 \pm 33	92, 142, 162, 186	55	33 \pm 29	103, 153	0.89	1	0.3551
Rout	0			0					
LF	0			4	12 \pm 9				
Hu	0			0					
Dr	2	3 \pm 0		3	7 \pm 2		2.33	1	0.2667
Li	0			0					
GS	1	22 \pm 0		3	11 \pm 7				
Gor	11	72 \pm 40		7	73 \pm 82	263	0.19	1	0.6731
GOg	2	14 \pm 9		6	51 \pm 44		0.23	1	0.7137
TaAp	0			1	4 \pm 0				

VoAp	0			0					
S	122	51 ± 67	146, 157, 165, 170, 222, 241, 252, 322, 486	74	47 ± 72	125, 126, 149, 154, 181, 264, 309, 444	0.86	1	0.3614
R	7	25 ± 21		0					
SS	8	8 ± 6	24	15	11 ± 27	112	0.01	1	0.9317
W	115	15 ± 13	44, 45, 46, 48, 56, 57, 60, 62	135	19 ± 19	54, 57, 64, 69, 71, 75, 78, 91, 103	4.41	1	0.0443
Ru	6	11 ± 13		5	11 ± 10		0.25	1	0.6371
C	10	16 ± 15	57	4	2 ± 1		7.63	1	0.0327
J	0			0					
Wob	0			0					
Tm	0			26	25 ± 19	78			
Tp	0			9	73 ± 55				
ME	3	6 ± 3		0					
Di	0			0					
Pf	0			0					
Sch	0			0					

Table 6.10.2. Randy

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average ± SD (sec)	*Additional data points (sec)	n	Average ± SD (sec)	*Additional data points (sec)			
Dpg	0			0					
Dpr	9	18 ± 23	81	10	12 ± 15	53	0.21	1	0.6567
Dvg	0			0					
Dvr	1	81 ± 0		6	14 ± 18	53			
M	2	4 ± 1		3	6 ± 3		0.57	1	0.5067
Ms	2	5 ± 2		1	2 ± 0				
Thg	1	22 ± 0		0					
Thr	0			0					
P	4	9 ± 1		13	22 ± 14		1.69	1	0.2412
Avi	1	25 ± 0		1	53 ± 0				
Aph	1	10 ± 0		4	22 ± 21				
Avo	1	10 ± 0		0					

Sh	0			0					
Av	6	13 ± 4		1	3 ± 0				
Sp	0			0					
Mi	0			0					
Al	3	19 ± 10							
Fe	26	39 ± 30		10	59 ± 70	77, 263	0.83	1	0.3832
F	27	33 ± 32	83, 163	38	51 ± 58	252, 265	5.22	1	0.0363
Rout	0			0					
LF	0			0					
Hu	0			0					
Dr	1	9 ± 0		0					
Li	0			0					
GS	1	10 ± 0		0					
Gor	67	114 ± 131	318, 327, 338, 420, 487, 496, 657	22	90 ± 80	368	1.77	1	0.1974
GOg	10	66 ± 50		5	57 ± 55		1.74	1	0.2357
TaAp	0			0					
VoAp	3	220 ± 293		0					
S	60	51 ± 65	136, 142, 145, 173, 215, 243, 345	63	38 ± 59	89, 152, 155, 163, 166, 206, 347	1.34	1	0.2564
R	2	32 ± 17		1	12 ± 0				
SS	11	11 ± 6	25	10	11 ± 8	28	0.00	1	0.9517
W	76	16 ± 21	42, 51, 82, 163	95	25 ± 33	77, 79, 85, 93, 108, 115, 252	1.25	1	0.2725
Ru	1	8 ± 0		0					
C	7	10 ± 9	30	2	5 ± 3		1.12	1	0.3504
J	0			0					
Wob	0			0					
Tm	0			9	32 ± 25	93			
Tp	0			0					
ME	0			0					
Di	0			0					
Pf	0			0					
Sch	0			0					

Table 6.10.3. Toka

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Dpg	3	3 \pm 1		2	6 \pm 4		0.17	1	0.7510
Dpr	1	2 \pm 0		0					
Dvg	1	3 \pm 0		1	2 \pm 0				
Dvr	0			0					
M	0			1	5 \pm 0				
Ms	1	15 \pm 0		0					
Thg	0			0					
Thr	0			0					
P	3	11 \pm 4		6	33 \pm 27		2.93	1	0.1623
Avi	0			0					
Aph	0			0					
Avo	2	6 \pm 1		0					
Sh	1	6 \pm 0		0					
Av	15	10 \pm 7	23, 26	10	25 \pm 28		1.22	1	0.2914
Sp	1	2 \pm 0		0					
Mi	0			0					
Al	2	41 \pm 18		12	17 \pm 18	68	3.64	1	0.0979
Fe	42	54 \pm 52	303	38	44 \pm 54	305	0.02	1	0.8792
F	170	30 \pm 33	78, 81, 83, 92, 99, 108, 108, 114, 117, 123, 170, 303	123	32 \pm 34	97, 111, 114, 130, 141, 146, 149, 151	0.18	1	0.6770
Rout	20	16 \pm 9		1	34 \pm 0				
LF	3	8 \pm 3		13	11 \pm 14	36, 48	0.78	1	0.4275
Hu	0			0					
Dr	0			5	20 \pm 13				
Li	0			1	10 \pm 0				
GS	7	70 \pm 66	218	4	13 \pm 10		3.04	1	0.1249
Gor	16	93 \pm 95	382	9	79 \pm 88		0.13	1	0.7304
GOg	0			1	25 \pm 0				
TaAp	0			0					
VoAp	1	24 \pm 0		0					

S	140	29 ± 31	70, 74, 81, 92, 104, 108, 114, 132, 141, 175, 178	130	33 ± 59	72, 78, 93, 96, 112, 117, 142, 188, 315, 348, 441	0.87	1	0.3578
R	24	66 ± 76	248, 287	3	155 ± 132		0.02	1	0.8914
SS	15	10 ± 7	31	22	6 ± 4		3.43	1	0.0798
W	170	12 ± 10	31, 31, 33, 36, 48, 49, 49, 53, 60	132	14 ± 15	45, 48, 48, 50, 51, 52, 52, 55, 69, 84	1.06	1	0.3118
Ru	7	3 ± 1		7	7 ± 3		7.91	1	0.0374
C	21	12 ± 24	116	4	3 ± 1		1.57	1	0.2340
J	1	3 ± 0		1	40 ± 0				
Wob	0			1	2 ± 0				
Tm	0			8	17 ± 8				
Tp	0			12	13 ± 7				
ME	12	47 ± 88	72, 333	9	12 ± 13		0.75	1	0.4107
Di	7	22 ± 13		0					
Pf	10	11 ± 10	36	3	3 ± 2		1.45	1	0.2734
Sch	0			3	11 ± 4				

Table 6.10.4. Tina

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	N	Average ± SD (sec)	*Additional data points (sec)	n	Average ± SD (sec)	*Additional data points (sec)			
Dpg	1	2 ± 0		4	7 ± 3				
Dpr	0			0					
Dvg	0			5	6 ± 3				
Dvr	0			0					
M	2	3 ± 0		2	3 ± 1		1.00	1	0.4226
Ms	0			0					
Thg	0			0					
Thr	0			0					
P	3	16 ± 13		2	20 ± 12		0.04	1	0.8692
Avi	1	13 ± 0		0					
Aph	0			0					
Avo	0			0					
Sh	0			0					

Av	7	8 ± 3	13	2	3 ± 1		26.10	1	0.0069
Sp	0			0					
Mi	0			0					
Al	4	14 ± 12		5	14 ± 12		0.24	1	0.6432
Fe	32	43 ± 45	113, 117, 140, 219	30	39 ± 33		0.67	1	0.4274
F	75	38 ± 36	118, 119, 136, 172, 200	96	36 ± 41	96, 97, 112, 151, 196, 204, 215	0.00	1	0.9816
Rout	2	6 ± 3		0					
LF	2	11 ± 3		12	17 ± 22	83	0.33	1	0.6071
Hu	0			1	11 ± 0				
Dr	0			1	6 ± 0				
Li	0			0					
GS	8	40 ± 40		1	6 ± 0				
Gor	2	122 ± 61		5	89 ± 60		0.18	1	0.7455
GOg	14	108 ± 93		35	80 ± 104	218, 225, 334, 498	0.00	1	0.9950
TaAp	0			1	2 ± 0				
VoAp	0			0					
S	69	41 ± 62	157, 179, 469	36	40 ± 102	68, 454, 456	0.27	1	0.6099
R	4	129 ± 111		0					
SS	18	10 ± 6	29	39	12 ± 13	33, 41, 78	0.14	1	0.7134
W	86	25 ± 30	89, 118, 119, 136, 172	115	24 ± 37	63, 74, 86, 95, 97, 151, 196, 204, 215	0.43	1	0.5198
Ru	0			1	6 ± 0				
C	5	7 ± 5		1	2 ± 0				
J	0			0					
Wob	0			0					
Tm	0			14	25 ± 24	95			
Tp	0			0					
ME	0			0					
Di	1	200 ± 0		0					
Pf	0			0					
Sch	0			0					

Table 6.10.5. Sinead

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOV A p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Dpg	4	6 \pm 3		6	11 \pm 10		1.98	1	0.2323
Dpr	2	11 \pm 7		0					
Dvg	3	6 \pm 4		3	5 \pm 2		0.11	1	0.7744
Dvr	1	4 \pm 0		0					
M	1	9 \pm 0		0					
Ms	0			0					
Thg	0			0					
Thr	3	24 \pm 25		0					
P	36	19 \pm 14		6	26 \pm 10		2.56	1	0.1438
Avi	5	16 \pm 14		0					
Aph	1	3 \pm 0		1	8 \pm 0				
Avo	1	3 \pm 0		0					
Sh	4	11 \pm 13		0					
Av	2	11 \pm 2		2	2 \pm 1		10.70	1	0.1888
Sp	0			0					
Mi	0			0					
Al	8	10 \pm 6	23	10	8 \pm 7	20, 21	0.04	1	0.8428
Fe	45	34 \pm 35	169, 173	51	41 \pm 64	65, 70, 99, 116, 255, 288, 304	0.00	1	0.9837
F	110	34 \pm 34	85, 98, 111, 132, 141, 142, 171, 174	68	33 \pm 37	91, 99, 100, 144, 167, 190	0.74	1	0.3971
Rout	0			7	16 \pm 16	53			
LF	5	11 \pm 4		6	6 \pm 4	15	1.49	1	0.2621
Hu	0			0					
Dr	0			2	19 \pm 4				
Li	0			3	7 \pm 3				
GS	0			1	15 \pm 0				
Gor	23	90 \pm 85		24	99 \pm 126	224, 406, 409, 420	0.07	1	0.8029
Gog	36	61 \pm 89	181, 214, 231, 454	11	58 \pm 41		0.42	1	0.5310
TaAp	1	27 \pm 0		1	2 \pm 0				
VoAp	0			0					
S	66	31 \pm 39	99, 114, 137, 264	74	18 \pm 24	29, 29, 30, 30, 34, 41, 43, 43,	3.35	1	0.0788

						54, 60, 62, 66, 98, 166			
R	2	11 ± 1		4	28 ± 21		12.00	1	0.1789
SS	6	12 ± 6	23	11	6 ± 9	33	5.28	1	0.0421
W	116	15 ± 12		102	14 ± 17	46, 55, 70, 79, 91	0.31	1	0.5825
Ru	4	5 ± 3		2	12 ± 8		16.33	1	0.1544
C	21	13 ± 10		4	3 ± 0		5.64	1	0.0368
J	0			0					
Wob	0			0					
Tm	0			16	26 ± 20	79			
Tp	0			2	112 ± 26				
ME	3	6 ± 2		2	7 ± 2		0.19	1	0.6925
Di	0			0					
Pf	1	6 ± 0		0					
Sch	0			0					

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

CHI-SQUARED TESTS

6.2.2.5 Tests comparing the occurrence of social states between the former and new enclosures.

Table 6.11.1. Abu

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 355	New enclosure n = 289			
Solitary	30.650 \pm 28.904	59.820 \pm 25.384	274.5411	1	0.0000
Grouped	44.482 \pm 28.730	13.674 \pm 12.079	370.4040	1	0.0000
Social	24.868 \pm 29.486	26.506 \pm 18.966	1.0714	1	0.3006

Table 6.11.2. Randy

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 233	New enclosure n = 201			
Solitary	16.119 \pm 19.292	28.258 \pm 27.016	69.2250	1	0.0000
Grouped	29.209 \pm 23.422	33.340 \pm 22.918	6.2807	1	0.0122
Social	54.671 \pm 26.482	38.402 \pm 31.882	84.8107	1	0.0000

Table 6.11.3. Toka

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 542	New enclosure n = 417			
Solitary	69.932 \pm 33.349	75.979 \pm 21.299	16.4570	1	0.0000
Grouped	19.576 \pm 24.777	13.264 \pm 13.719	25.7907	1	0.0000
Social	10.492 \pm 24.174	10.757 \pm 15.499	0.0657	1	0.7977

Table 6.11.4. Tina

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 256	New enclosure n = 277			
Solitary	57.756 \pm 32.130	39.762 \pm 34.957	81.3183	1	0.0000
Grouped	23.237 \pm 20.961	26.761 \pm 21.601	4.1336	1	0.0420
Social	19.007 \pm 30.980	33.477 \pm 34.763	68.0139	1	0.0000

Table 6.11.5. Sinead

Major Behaviour	Mean per sample \pm SD		Chi-square	d.f	p-value
	Former enclosure n = 364	New enclosure n = 325			
Solitary	29.825 \pm 28.676	47.745 \pm 34.427	105.5399	1	0.0000
Grouped	29.064 \pm 23.458	20.628 \pm 20.054	29.5842	1	0.0000
Social	41.111 \pm 34.753	31.627 \pm 34.417	30.1345	1	0.0000

ANALYSES OF VARIANCE

6.2.2.6 Tests comparing the mean bout length of social states between the former and new enclosures.

Table 6.12.1. *Abu*

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	113	33 \pm 41	99, 106, 107, 107, 108, 110, 115, 118, 137, 142, 165, 170, 182	159	32 \pm 63	81, 91, 103, 110, 125, 126, 153, 154, 176, 181, 188, 444, 534	1.11	1	0.3015
Grouped	123	36 \pm 44	97, 103, 149, 170, 186, 222, 322	45	31 \pm 48	96, 100, 112, 289	0.01	1	0.9192
Social	119	20 \pm 24	56, 66, 79, 81, 90, 90, 106, 114, 116, 122	85	30 \pm 41	86, 95, 138, 142, 174, 263	0.48	1	0.4935

Table 6.12.2. *Randy*

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	81	28 \pm 74	60, 61, 63, 78, 103, 136, 145, 148, 634	78	27 \pm 39	74, 77, 99, 101, 108, 163, 265	0.07	1	0.7969
Grouped	76	35 \pm 32	112, 117, 142, 163	68	32 \pm 47	85, 89, 166, 252, 263	0.00	1	0.9667
Social	76	57 \pm 69	194, 209, 230, 420	55	48 \pm 64	141, 141, 151, 152, 165, 368	0.38	1	0.5414

Table 6.12.3. *Toka*

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	398	24 \pm 31	60, 63, 64, 65, 65, 65, 67, 69, 70, 72, 74, 78, 81, 81, 83, 84, 92, 96, 99, 104, 108, 108, 114, 114, 115, 116, 117, 119, 122, 132, 132, 151, 218, 303	312	25 \pm 39	59, 61, 67, 68, 68, 69, 69, 69, 72, 73, 74, 75, 78, 81, 83, 83, 84, 92, 111, 114, 117, 130, 141, 142, 146, 149, 305, 315, 348	0.95	1	0.3362
Grouped	97	28 \pm 30	91, 108, 123, 132, 135, 175	69	25 \pm 54	55, 63, 112, 441	0.84	1	0.3679
Social	45	23 \pm 35	58, 59, 69, 75, 76, 114, 183	36	21 \pm 38	55, 234	0.48	1	0.5101

Table 6.12.4. Tina

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	170	29 \pm 36	74, 82, 95, 96, 113, 118, 119, 119, 136, 140, 157, 172, 200, 219	128	28 \pm 51	63, 66, 71, 73, 78, 81, 83, 89, 96, 97, 112, 151, 204, 215, 454	0.12	1	0.7374
Grouped	64	30 \pm 25		99	26 \pm 51	62, 74, 77, 78, 82, 86, 88, 196, 456	0.35	1	0.5581
Social	22	43 \pm 57	144, 164, 183	50	43 \pm 64	162, 208, 218, 334	0.13	1	0.7194

Table 6.12.5. Sinead

Major Behaviour	Former enclosure			New enclosure			F Value	d.f	ANOVA p-value
	n	Average \pm SD (sec)	*Additional data points (sec)	n	Average \pm SD (sec)	*Additional data points (sec)			
Solitary	142	26 \pm 36	64, 66, 74, 74, 75, 77, 83, 98, 111, 132, 142, 169, 174, 264	177	23 \pm 49	53, 65, 66, 70, 73, 74, 91, 99, 100, 116, 167, 304, 520	0.01	1	0.9189
Grouped	111	28 \pm 32	65, 67, 67, 71, 85, 99, 114, 137, 141, 171, 173	87	18 \pm 25	60, 62, 144, 166	3.33	1	0.0790
Social	111	36 \pm 63	90, 112, 121, 181, 214, 231, 247, 274, 454	61	45 \pm 75	137, 406, 409	0.01	1	0.9254

* Additional data points relate to outlying values on the corresponding modified box-and-whisker plots.

6.3 APPENDIX C

6.3.1 Full interpretation of Abu's response to relocation

6.3.1.1 Absent or infrequently occurring behaviours that reinforce the preceding individual description and summary discussion of Abu's responses to relocation.

Male homosexual activity (i.e. *simulated mating*) occurs in the wild and serves an appeasement function when co-ordinated behaviour is required (Kummer 1995). As was the case with the absence of overt notification by Abu (in the form of *visual presentation* towards another male), the absence of *simulated mating* by Abu provided some indication that his co-ordination role was passive. The single instance of *visual presentation* observed during focal sampling of Abu was annotated to indicate that the gesture was used to attract a grooming response from a young, unattached female, rather than directed at another male as a co-ordinating gesture.

Herded by tail was also absent from focal samples for Abu. This behaviour was interpreted earlier as an example of aggressive herding behaviour, such as that employed by harem leaders to enforce the coherence of their units. By contrast, Abu was seen to herd his females (*tail holding*). Similar observations of the colony's other one-male unit leader and focal male (i.e. Randy) reinforce that this particular herding response was the domain of harem leadership.

Abu did not undertake *licking*, *scraping* and *relocating object* behaviours, as did other focal animals upon their relocation, accentuating Abu's protective function as a harem leader. These "minor" behaviours were described earlier as 'new' forms of exploration, occurring as a consequence of the provision of unique surfaces in the new enclosure. More clearly defined roles (including 'peripheral' female and 'central female'), within both harems became evident upon the colony's relocation. A function of the 'peripheral' female is "habitat orientated behaviours" (Sigg 1980:265). It is this female, rather than the harem leader, which undertakes ecological exploration (Sigg 1980). Due to this protective function (and his consequent "look out" behaviour), the male leader has less time to explore the resource state in search of food (Sigg 1980:285). Instead, he pays attention to the activity of the 'peripheral' female (Kummer 1995) and, if the food resources she discovers during exploration are large enough, the entire one-male unit will 'exploit' her effort (Sigg 1980).

Instances of *manipulating environment*, a "play" behaviour, by Abu occurred exclusively and infrequently in focal samples from the former enclosure. Similarly, Abu was not observed increasing the complexity of his environment by *reaching out* of either enclosure, as did the combined focal animals. The infrequency of interaction with his surroundings, including the external environment (i.e. that beyond the enclosure) also signalled his lack of interest in exploration and in increasing environmental variability. This was also a likely consequence of his protective function.

Play fighting was also absent from focal samples for Abu from both the former and the new enclosures. A study of a similar sized captive hamadryas baboon colony at Zurich Zoo found that adult males spent only one percent of their activity budget on play fighting behaviour (Kummer and Kurt 1965). A similarly low overall occurrence in focal samples of Abu was expected for reasons pertaining to his age and position as harem leader. Firstly,

play fighting in free-ranging hamadryas baboons reaches its peak when the animals are three years old. From then on, it begins to decline (Kummer 1995). Whilst incidences of play fighting behaviour in captive hamadryas baboons have been found to occur for an extended period into sub-adulthood (Kummer and Kurt 1965), as a 10 year old adult male, Abu was likely to have outgrown this “minor” behaviour, despite his captive state. Secondly, play fighting is an example of a friendly social interaction between male hamadryas baboons that ceases upon mate acquisition (Kummer 1995), whereupon harem leaders endeavour to keep their units apart.

In addition to those absent or infrequently occurring behaviours, Abu was the only animal to undertake *intervention*. The occurrence of this “minor” behaviour further reinforces Abu’s description as a protective harem leader. A characteristic of harem leadership is that unit leaders typically aid females with which they have “persistent high-frequency bonds”, more often than they aid others (Seyfarth 1978:232). They defend these females regardless of their current sexual condition (Kummer 1968). Abu was the only focal animal seen to aid (in the form of *intervention*) conspecifics of any description (albeit infrequently in both enclosures) during agonistic interactions. One of the three such occasions on which Abu intervened involved both of his harem females. On another occasion, Abu aided an unattached female distressed by non-routine keeper disturbance.

6.3.1.2 Abu’s individual response to relocation

Focal samples indicated that 65.63 percent of “minor” behaviours undertaken by Abu occurred in both the former and new enclosures. Those behaviours seen to occur exclusively in a single enclosure are interpreted below and begin to reflect Abu’s developing co-ordination role upon the colony’s relocation.

In contrast to the combined focal animals, no statistically significant difference was discernible in the odds of each of the “major” behavioural categories occurring per focal sample for Abu between the former and new enclosures. This indicated that the number of “major” behavioural categories occurring per fifteen-minute focal sample for Abu did not change significantly upon his relocation. In addition, and as was the case with the combined focal animals, no statistically significant difference was discernible between the enclosures in the odds of each of the “minor” behavioural categories occurring per sample. Together, these results indicated that the size of each sample repertoire did not significantly change upon Abu’s relocation. As for the combined animals, the composition of “major” and “minor” behaviours recorded in each enclosure, and the relative occurrence of each of these behaviours, were more revealing in terms of response to relocation than the number of behavioural categories that occurred per sample. This was also the case for each of the remaining focal animals.

- “Major” and “minor” behaviours seen exclusively in a single enclosure in contrast to the combined focal animals

There was a decline in relative repetition of *visual aggression* by the combined focal animals upon relocation. This same “minor” behaviour was exclusive to the former enclosure in focal samples for Abu for different reasons. Dependent on their temperaments, one cause of this type of aggressive response by high-ranking primates, such as Abu, is the behaviour of subordinates, including restlessness (Dolhinow 1972). 15 of the 20 instances of *visual aggression* involving Abu in the former enclosure involved juvenile animals. One way animals cope with the restrictions of a captive environment is to perform acts that create situations to which they

can react (Morris 1964). “Once created, these situations can be reacted to in a normal way” (Morris 1964:101). In the former, smaller and relatively less stimulating enclosure it seems likely that these younger animals were coping with the restrictions of their confinement by enticing an aggressive response from Abu. Abu responded to such provocation in a manner similar to that described by Kummer and Kurt (1965) for captive males at Zurich Zoo. Serious attacks by adult males towards juvenile males are infrequent in the wild (Kummer 1995). When such attacks do occur they continue until either the pursued animal has eluded the aggressor or has been caught (Kummer and Kurt 1965). Within the Wellington Zoo hamadryas baboon colony, and as observed at Zurich Zoo, aggression by adult males towards younger conspecifics took the form of “mock attacks” in which the adults “rushed at the juveniles, stopped abruptly, and quietly returned to their places” (Kummer and Kurt 1965:76). In the current study, this behaviour was categorised under *visual aggression* (i.e. aggression without physical contact) and described as “feinting”. Just as for the combined focal animals, involvement in *physical aggression* (i.e. aggression with physical contact - fighting, contesting, attempting contact by prolonged chasing) by Abu was infrequent in both the former and new enclosures, possibly to minimise opportunities for his females to be sequestered by opportunistic males.

Of the remaining five instances of *visual aggression* recorded for Abu in the former enclosure, on only one occasion was Abu not interacting specifically with a conspecific. As such, unlike the combined focal animals, Abu did not appear to be endeavouring to increase environmental variability beyond the restrictions of the former enclosure by interacting in this way with members of the public. This supports the interpretation that Abu’s protective function within the colony, accentuated upon his relocation, caused him to be less interested in generating external variation (Sigg 1980).

Instances of *resting* by the combined focal animals were recorded in both the former and new enclosures. Upon relocation, there was a decline in the overall occurrence and relative repetition of this “minor” behaviour. A contributing factor to this decline was its occurrence exclusively in the former enclosure in focal samples for Abu. Unlike the combined focal animals, for which a decline in *resting* upon relocation was attributed to an increase in time spent *foraging* and on associated “locomotion”, the overall occurrence of *foraging* in focal samples for Abu remained unchanged between the former and new enclosures. Rather, the absence of *resting* in focal samples for Abu upon relocation would appear to be consistent with his increasing “locomotion” as he became more actively involved in cohesive group movement. A reduction in *resting* and an increase “locomotion” by Abu was thought to have increased his visibility to the colony in the new enclosure. A “passive co-ordination-function”, through increased visibility, observed in free-ranging hamadryas baboons, has been referred to as the “flag function” (Sigg 1980:274). Due to their striking appearance, it is the adult male baboon that is most suited to this role (Sigg 1980).

The low overall occurrence of *tactile appeasement* (i.e. one instance in the new enclosure) and the absence of *vocal appeasement* by Abu can be interpreted in the same way as for the combined focal animals and, in particular, corresponded with low levels of high-intensity conflict [i.e. chases, grappling, biting... (Castles and Whiten 1998:135)]. A significantly higher incidence of “appeasement” by Abu in the former enclosure despite a considerable number of incidences of *visual aggression* was not expected for the following reasons. Firstly, such “feinting” by Abu could only be considered as low-intensity conflict [i.e. threats and lunges (Castles and

Whiten 1998:135)] and probably insufficient to warrant “appeasement” gestures. Secondly, “appeasement” in the form of reconciliation, [i.e. “affiliative interaction occurring between former opponents soon after aggression” (Castles and Whiten 1998:127) by other another *Papio* baboon species (i.e. *Papio anubis*)] has been found to most likely to occur between (Castles and Whiten 1998:140):

(i) Closely related animals. Because of his young age, Abu had not sired a single offspring at the outset of this investigation. Furthermore, Wellington zoological records (i.e. taxon report) indicate that only two of the immature males within the colony, i.e. those animals seen to provoke aggression from Abu, were his full brothers; and,

(ii) Those of similar rank. *Visual aggression* by Abu in the former enclosure typically involved provocation by immature, subordinate animals.

- Results for changes in “major” and “minor” behaviours between the former and new enclosures that deviate from the combined focal animals

Whereas the combined focal animals were found to experience an increase in both overall occurrence and relative repetition of *foraging* upon the colony’s relocation, both of which were related to increased foraging opportunities in the new enclosure, no differences in *foraging* behaviour between the enclosures were found for Abu. Two reasons for this pertain to Abu’s dominance and position of responsibility as protector of his harem:

(i) It is probable that places of highest food density will be monopolised by male baboons due to their authority (Sigg 1980). As a result of such monopolisation of the best locations, Abu, a high-ranking male and harem leader, may have received sufficient food during the colony’s daily feeding by keepers that he did not need to forage. (Note: As the colony’s “major” daily feeding was interrupted by keepers duties and, therefore, not included in focal sampling, this interpretation cannot be substantiated statistically).

(ii) The second reason why *foraging* behaviour by Abu did not alter, despite the provision of increased foraging opportunities, may relate to the more overt roles adopted within Abu’s harem upon its relocation to the new enclosure. As mentioned above, the ‘peripheral’ female takes an exploratory role, while the unit leader, concentrating on a protective role within the colony, has less time to search for food and, instead, utilises resources discovered by ‘peripheral’ females (Sigg 1980).

Unlike the combined focal animals, for which the overall occurrence and relative repetition of “grooming” was found to decline upon the colony’s relocation, no such differences between the enclosures were found for this “major” behaviour in focal samples for Abu. In particular:

(i) Unlike the combined focal animals, no statistically significant difference was evident between the enclosures in the overall occurrence of *grooming self* by Abu. The infrequency of this “minor” behaviour in his focal samples meant that no change in its mean bout length (or relative repetition) could be ascertained from the results. The decline in the overall occurrence and relative repetition of *grooming self* exhibited by the combined focal animals was attributed to the provision of increased enrichment, resulting in a decline in such self-directed

behaviour. By contrast, and a probable result of his lack of interest in ecological matters, Abu was not seen to undertake significantly more self-directed behaviour in the relative simplicity of the former enclosure.

(ii) In contrast to the combined focal animals, no difference in the overall occurrence and relative repetition of *receiving grooming* by Abu was detected. This occurred despite the significant reduction in the overall occurrence of *grooming other* by the harem female belonging to Abu and sampled in this investigation (i.e. Sinead) as she adopted an increasingly 'peripheral' position. The most plausible explanation for the absence of a decline in *receiving grooming* by Abu pertains to his high-ranking position. As Abu maintained this position within the colony in both the former and new enclosures, subordinate conspecifics may have been equally likely to engage in grooming behaviour with him both before and after relocation. Due to the ritualisation of grooming behaviour, and its consequent function as an appeasement behaviour noted above (Kummer 1995), "high ranking (sic hamadryas baboon) group members can be expected to be groomed most often, especially when the one doing the grooming needs their support in a dispute or has reason to feel threatened by them" (Kummer 1995:32).

Another explanation for the absence of a decline in the rate at which Abu was recorded *receiving grooming* may be that a decline in *grooming other* by Sinead was over-shadowed by an increased amount of time spent by Abu's other harem female (i.e. Makele) on social grooming behaviour. This may have been the case if Makele (for whom independent focal sampling was not undertaken) adopted an increasingly 'central' and, subsequently, social role.

(iii) In contrast to the combined focal animals, for which no difference was found between the former and new enclosures, Abu experienced an increase in the overall occurrence and relative repetition of *grooming other* upon relocation. The most plausible explanation for this was that Abu groomed his harem female (specifically the central female) more upon relocation as a consequence of her developing role within the unit and the changing bonds she shared with her leader associated with this role. Male hamadryas baboons have several techniques for bonding a female to themselves. One such technique is "to groom a female of whom they are not yet or no longer certain" of their bonds (Kummer 1995:247).

An increase in the mean bout length of "locomotion" by Abu, which was in contrast to the combined focal animals, can be partially attributed to his participation in the "new" cohesive group behaviours and, specifically, *troop movement* and *troop patrol*, which were recorded exclusively in the new enclosure. In particular, out of all of the five focal animals, Abu participated in the highest overall occurrence per sample of *troop movement* and the second highest incidence per sample of *troop patrol*. On average, these two "minor" behaviours were longer in duration (i.e. mean bout length) than any other "locomotion" behaviour undertaken by Abu during the course of this investigation.

In addition, unlike the combined focal animals, Abu's "locomotion" across the broader space of the new enclosure was not interrupted by increasingly more frequent bouts of *foraging*. As such, and in contrast to the combined focal animals, the mean bout length of *walking*, in particular, by Abu increased. This contributed to an increase in the overall occurrence of this "minor" behaviour, and "locomotion" in general, by Abu upon his relocation.

The combined focal animals spent significantly more time overall “out of sight” with greater relative repetition upon relocation. No such differences between the former and new enclosures were discernible for Abu. Three factors can be used to interpret this deviation in “out of sight” behaviour between Abu and the combined focal animals:

(i) As a dominant male, with competition for his mates inhibited by the ‘early bird principle’, Abu did not need to seek refuge as much as subordinate members of the colony;

(ii) Instead, Abu appeared to choose locations within each enclosure where he could view the colony and surrounding environment, just as adult male baboons studied in Uganda seek vantage points for observation in the wild (Rowell 1972). This interpretation is supported by observations of captive *Papio* baboons in which it was found that high-ranking baboons, typically males, monopolised ladders (Kessel and Brent 1996). It was from these points that the animals were thought to be able to get the best view of both their harems, as well as neighbouring units (Kessel and Brent 1996). This particular result relates to the protective role dominant males have within the troop (Kessel and Brent 1996) and, in particular, the “observer function” with consequent “look-out” behaviour [i.e. “...sitting at an elevated position (tree or rock) with unobstructed sight onto the area around...” (Sigg 1980:284)] which is undertaken mostly by group leaders within the troop during their daily march (Sigg 1980).

(iii) Whereas the combined focal animals took advantage of an increase in shady resting areas in the new enclosure (resulting in an increase in the overall occurrence of “out of sight”), as an adult male with a developing role as a co-ordinator within the colony, Abu was thought to have remained visible as a reference point (specifically “flag function”) for the co-ordination of group behaviour (Kummer and Kurt 1965:274), including *troop movement* and *troop patrol*.

- Similar results in “major” and “minor” behaviours between the former and new enclosures as the combined focal animals but with different interpretations in accordance with Abu’s individual response to relocation

Both the combined focal animals and Abu experienced a reduction in the overall occurrence, mean bout length, and also, possibly, the relative repetition of *climbing*. Unlike the combined focal animals, similar results for Abu could not be attributed to an increase in *foraging* enrichment as no change in *foraging* behaviour was discernible for Abu between the former and new enclosures. Rather, this result corresponds with the second interpretation given for the combined focal animals i.e. that structural enrichment in the restricted former enclosure provided the best observation points. This interpretation corresponds with Abu’s ‘look out’ behaviour as a harem leader and adult male within the colony. This caused him to seek vantage points on structural enrichment in the former enclosure that he could achieve in the new enclosure, because of its sloping nature, without *climbing*.

As was the case with the combined focal animals, Abu experienced a decline in the relative repetition of *receiving vocal presentation* upon relocation, resulting in a decrease in the overall occurrence of this “minor” behaviour. In samples of individual focal animals, it was apparent that *receiving vocal presentation* was most commonly associated with adult males and/or harem leaders i.e. 97.4 percent of instances of this behaviour (from

data sets of overall occurrence) were received by Abu or Randy. Likewise, neither of these adult males were recorded *giving vocal presentation*. Consequently, it would appear that this behaviour within the Wellington Zoo hamadryas baboon colony was largely used to generate the attention of the adult males and/or harem leaders. As both females and immature males were seen attempting to attract the adult males' attention in this way, there was evidence to suggest that this "minor" behaviour served not only a solicitation function (i.e. an invitation to copulate) but, also, a conciliatory function within this colony.

One reason why *receiving vocal presentation* declined in overall occurrence and relative repetition in focal samples for Abu was explained by comments made on spreadsheets during data entry. Specifically, instances in which two animals simultaneously presented to Abu vocally (or vocally and visually) declined upon relocation. Eight out of 18 instances involved two animals in the former enclosure compared with two out of 12 corresponding instances in the new enclosure. On a further two occasions in the former enclosure, the animal presenting to Abu directed vocalisation towards a third party in a manner directly comparable to descriptions of the 'protected threatening' response observed within the Zurich Zoo hamadryas baboon colony. 'Protected threatening' behaviour involves a female preventing a female opponent from fleeing to the dominant male figure whilst simultaneously presenting submissively towards her leader (Kummer 1995). In so doing, the female can entice the male to attack her opponent whilst also securing their own safety (Kummer 1995). Such behaviour has been found to exist in only "elementary components" in free-ranging hamadryas baboon societies, whereupon females have been observed screaming at their opponents but without presenting their hindquarters (Kummer 1995:134). The most noticeable decline in *vocal presentation* towards Abu by any one animal upon the colony's relocation was by one of his harem females (i.e. Makele). Specifically, in the former enclosure, six of the 18 instances in focal samples for Abu in which he *received vocal presentation* involved Makele (five of these also occurred simultaneously with presentation by another animal and one corresponded directly to 'protected threatening' behaviour). In the new enclosure, only one of 12 such instances involved Makele. In as much as Sinead, Abu's other harem female and focal animal, was seen to exhibit more clearly definable 'peripheral' tendencies upon relocation (with a corresponding increase in "solitary" behaviour and reduction in "social" behaviour), Makele's need to compete for access to Abu may have declined upon relocation. This effect was likely to have been heightened if, at the same time, Makele had adopted a 'central' role within their harem, as such positions afford females closer proximity to their mates (Kummer 1995).

- Deviations from the combined focal animals in response to relocation for which no interpretation can be given in accordance with the observer's understanding of the particular behaviour and the individual focal animal

The advent of *relocating food* by Abu in the new enclosure corresponded with an increase in this "minor" behaviour by the combined focal animals upon the colony's relocation. Unlike the combined focal animals, however, this cannot be directly attributed to an increase in *foraging* behaviour by Abu as no such change occurred in his behaviour upon relocation. From the description of Abu above, no alternative explanation could be found. The observer can only speculate that an increase in *foraging* behaviour by other colony members (as was evident in results from the combined focal animals), and the resultant increase in feeding competition within

the new enclosure (which was thought to have promoted an increase in *relocating food* by the combined focal animals) may have caused a similar competitive response from Abu.

- Results from statistical analysis and deduction of changes in the social states between the former and new enclosures that deviate from the combined focal animals

In contrast to the combined focal animals, no differences in the overall occurrence or relative repetition of the “social” state upon relocation to the new enclosure were discernible in focal samples of Abu. Abu did not experience a change in the non-social activity upon relocation to the new enclosures (i.e. an increase in *foraging* and the advent of new exploratory behaviours) which were interpreted to have suppressed the “social” behaviour of the combined focal animals upon their relocation. For this reason, the overall occurrence and relative repetition of the “social” state by Abu was deemed to have remained constant between the former and new enclosures.

- Similar results in the social states between the former and new enclosures as the combined focal animals with different interpretations in accordance with Abu’s individual response to relocation

Results for the combined focal animals, in particular an increase in the overall occurrence and relative repetition of the “solitary” state and a decrease in overall occurrence and relative repetition of the “grouped” state, were partially attributed to an increase in *foraging* behaviour. Similar results for Abu could not be directly interpreted in the same way due to an absence of changes in his *foraging* behaviour between the former and new enclosures.

However, additional interpretations of these similar responses by the combined focal animals were also applicable for Abu. In particular:

- (i) As for the combined focal animals, increasingly “solitary” behaviour by Abu may have been attributable to his increasing “locomotion” given that locomotion (and feeding) in free-ranging hamadryas baboons has been found to cause an increase in inter-individual distances (in particular, between harem leaders and females) relative to when the animals are resting (Kummer and Kurt 1965),
- (ii) Results for Abu support the contention that a reduction in the “grouped” state, and subsequent increase in “solitary” behaviour by the combined focal animals, upon the colony’s relocation was partially attributable to the behaviour of the colony’s adult males. In the smaller, former enclosure, the activity of harem leaders served to ensure the spatial coherence of their units in the close and continuous presence of rivals. This behaviour diminished upon the colony’s relocation to the new enclosure, whereupon rivals could be kept at greater distance and harem females were able to gain greater spatial independence from their leaders.

6.3.2 Full interpretations of Randy's response to relocation

6.3.2.1 Absent or infrequently occurring behaviours that reinforce the preceding individual description and summary discussion of Randy's responses to relocation.

In relation to Randy's position as a one-male unit leader, similar explanations as those given for Abu can be used to interpret the absence of *herded by tail*. Similarly, Randy's adulthood and position as a harem leader can also be used to interpret the absence of *play fighting*. [However, as Randy begins to relinquish his harem, and become increasingly less physically imposing, he may re-establish play bonds with younger animals. Such behaviour was observed in relation to the sole dominant adult male within the Zurich Zoo colony upon the gradual loss of his harem (Kummer 1995)].

Reaching out and *manipulating environment*, thought to increase environmental variability, were absent from focal samples for Randy, as were episodes of *visual aggression* towards the public. (All episodes of *visual aggression* by Randy involved interaction with pen-mates). The observer speculates that the absence of these "minor" behaviours in focal samples for Randy exemplified his different use of enrichment and lower activity levels of some "major" behaviours in comparison to younger focal animals. This may also explain the absence of *licking*, *scraping* and *relocating object* in focal samples of Randy upon his relocation, in contrast to the combined focal animals. This occurred despite evidence to suggest that Randy, unlike Abu, responded to increased feeding and, in particular, foraging enrichment upon relocation as a result of his decreasing harem leadership role.

Another indication of Randy's decreasing activity as a male unit leader was the absence of *intervention*, a function undertaken naturally by harem leaders (Seyfarth 1978). This was in contrast to Abu, who was seen to intervene in agonistic interactions, including situations involving his unit females.

At no stage in focal samples for Randy, or his harem female and fellow focal animal, Tina, was either animal observed participating in *troop patrol* behaviour. This indicated that Randy's harem was excluded from this activity. The observer speculates that *troop patrol* behaviour by other focal animals resembled the initiation, upon relocation, of two-male team type behaviour, from which Randy and his harem females were exempt.

6.3.2.2 Randy's individual response to relocation

Focal sample analysis for Randy revealed that only one of the eight "minor" behaviours recorded exclusively in a single enclosure (i.e. *troop movement*) occurred upon relocation to the new enclosure. This indicated that Randy's behavioural repertoire did not greatly increase upon introduction to the new and enriched enclosure. This may also be attributable to Randy's age and consequent lower activity levels of some behaviours.

The occurrence of seven "minor" behaviours exclusively in the former enclosure suggests that Randy experienced some decline in the extent of his repertoire of "minor" behaviours upon relocation. However, due to the infrequent occurrence of many of these behaviours (specifically *vocal aggression*, *drinking*, *grooming self* and *running*) little could be implied from these particular observations about the extent of change in Randy's behavioural repertoire between the former and new enclosures. Results for Randy did, however, indicate that, out of the five focal animals, he had the greatest percentage of "minor" behaviours common to both enclosures (i.e. 69.23 percent).

Whereas many behaviours absent or infrequent in focal samples for Randy could be interpreted in the same way as they were for Abu due to their common positions as adult males and harem leaders, their behavioural response to relocation differed significantly. Results indicated that the deviations in the response of Randy compared to Abu to relocation can be attributed, at least in part, to differences in their relative age and activity in harem leadership, as well as dominance.

- “Major” and “minor” behaviours seen exclusively in a single enclosure in contrast to the combined focal animals

Of the five “minor” behaviours exclusive to a single enclosure in focal samples for Randy, in contrast to the combined focal animals, only one (i.e. *alert*) was recorded on more than a single occasion.

Two of the three instances of *alert* by Randy, which occurred exclusively in the former enclosure, were in response to episodes of aggression involving Abu. This provided some indication that the decline in *alert* by Randy upon relocation was consistent with the reduction in the frequency of some “minor” aggressive behaviours by the combined focal animals upon relocation and, in particular, “feinting” (i.e. *visual aggression*) by Abu towards conspecifics.

The absence of *alert* and, also, *vocal presentation* by Randy upon his relocation, in contrast to the combined focal animals, also corresponded with an increase in overall occurrence, through greater repetition, of “out of sight” by Randy. This may have afforded him additional refuge from social pressure and, subsequently, a reduction in involvement in aggressive interactions.

- Results for changes in “major” and “minor” behaviours between the former and new enclosures that deviate from the combined focal animals

Unlike the combined focal animals, Randy experienced an increase in the overall occurrence, through greater relative repetition, of “solicitation” behaviour upon relocation. This result correlates directly with increases in two “minor” behaviours:

(i) Firstly, an increase in the overall occurrence of *receiving vocal presentation*. Too few instances of this “minor” behaviour were recorded in focal samples for Randy in the former enclosure to deduce differences in mean bout length and relative rate of repetition between the enclosures. The occurrence of six instances of this “minor” behaviour in the new enclosure, in contrast to only a single occurrence prior to relocation, in focal samples for Randy provided some indication that the increase in the overall occurrence of *receiving vocal presentation* was a consequence of its increased frequency. Together with an increase in *vocal presentation* by Randy’s mate and focal female, Tina, there was some evidence to suggest that Randy may have received an increase in this “minor” behaviour as a consequence of intensified intra-sexual competition between his unit females upon relocation. This was in contrast to competition amongst Abu’s unit females. In a previous investigation of hamadryas baboons, it was observed that each one-male unit investigated was “qualitatively” different (Sigg 1980:272). For example, the units experienced different degrees of competition among females for access to the leaders (Sigg 1980;

(ii) Secondly, Randy also experienced an increase in the overall occurrence and relative repetition of *pursuit* upon relocation. This correlates with increased *foraging* effort by Randy in the new enclosure, interpreted as promoting discontinuous *walking*. This, in turn, was likely to have been mimicked by at least one harem female at any one time. It is interesting to note that similar behaviour (i.e. following processions) has not been observed in units belonging to old, free-ranging male hamadryas baboons (Kummer 1968).

A decline in overall occurrence, attributable to a reduction in relative repetition, was observed for “agonistic” behaviour in focal samples for Randy upon relocation. This was in contrast to the combined focal animals. No significant difference in overall occurrence of any “minor” “agonistic” behaviour occurring in both enclosures was discernible in focal samples for Randy upon relocation. There were too few occurrences of each of these “minor” behaviours to determine differences in mean bout length or relative repetition. The decline in the repetition of “agonistic” behaviour was likely to have been coincident with:

(i) The absence of *alert* and *vocal aggression* by Randy upon relocation to the new enclosure; and/or,

(ii) A reduction in the number of instances of *avoidance* by Randy, as indicated by insufficient instances in the new enclosure to determine a difference in mean bout length or relative repetition between the enclosures. This reduction in instances of *avoidance* behaviour by Randy further reflected the increased amount of time that he sought refuge and privacy “out of sight” upon relocation. This is supported by Barton (1993, cited in Kessel and Brent 1996:41) who proposed a similar idea, suggesting that subordinate animals “may avoid conflict and thereby aggression, by occupying locales away from more dominant animals”.

In contrast to the combined focal animals, Randy experienced an increase in the bout length and overall occurrence of “feeding activity” upon relocation to the new enclosure. These results correspond best with the increase in overall occurrence and mean bout length of *foraging* by Randy. This increase in *foraging* effort by Randy in the new enclosure occurred despite evidence of more obvious roles being adopted by focal females within their harems and speculation that this promoted consistent foraging effort by the other focal male and harem leader (i.e. Abu) between the former and new enclosures. This deviation in the response of Randy to relocation compared with that of Abu was consistent with the conjecture that Randy’s leadership of his harem was decreasing i.e. he was spending less time on protective duties and more time searching for food.

A further indication that Randy was experiencing decreasing activity as a unit leader was the reduction in overall occurrence, through decreasing relative repetition, of *grooming other* in his focal samples upon relocation. This was in contrast to the combined focal animals, for which there was no discernible difference. A reduction in the relative repetition and overall occurrence of *grooming other* by Randy indicated that he groomed his females more in the close proximity of the former enclosure, potentially to his assert his possession of them and inhibit advances by rivals. However, and in contrast to Abu, it would appear that Randy did not seek to reassert his bonds with his females despite evidence to suggest some change in their respective roles within their harem upon relocation to the new enclosure. This observation may be attributable to the understanding that ageing unit leaders become increasingly tolerant towards their females, such tolerance extending to straying behaviour (Kummer 1968). It has been suggested that this is associated with the gradual and non-aggressive release of females from the ageing leader’s control (Kummer 1968).

In comparison to the combined focal animals, Randy did not experience a great enough decrease in the relative repetition of any “minor” “inactivity” behaviour (i.e. *sitting*, *resting* and *standing still*) to constitute a significant difference in overall occurrence. However, when data for these three “minor” behaviours are cumulated into the “major” category “inactivity”, a decrease in overall occurrence, through a reduction in relative repetition, becomes apparent upon Randy’s relocation. A reduction in this “major” behaviour corresponds with the interpretation given for the reduction in *sitting* and *resting* by the combined focal animals and can be attributed to a significant increase by Randy in enrichment directed *foraging* behaviour.

Unlike the combined focal animals, which undertook significantly reduced bout lengths and, subsequently, a decline in overall occurrence of *climbing*, no such difference between the former and new enclosures was discernible for Randy. Rather, and possibly as a consequence of his advancing age, Randy undertook limited *climbing* in both the former and new enclosures. Furthermore, in contrast to Abu, who sought ‘look out’ observation points on climbing structures in the confinement of the former enclosure in accordance with his protective function, the infrequent occurrence of *climbing* by Randy supports the contention that he did not seek out similar vantage points from which to observe his harem. This further emphasises decreasing activity by Randy as a unit leader.

- Similar results in “major” and “minor” behaviours between the former and new enclosures as the combined focal animals but with different interpretations in accordance with Randy’s individual response to relocation

The results derived from analysis of focal samples of Randy that were similar to those of the combined focal animals also share similar interpretations.

- Deviations from the combined focal animals in response to relocation for which no interpretation can be given in accordance with the observer’s understanding of the particular behaviour and the individual focal animal

Unlike the combined focal animals, for which no changes in *feeding* were discernible between the former and new enclosures, Randy experienced a decrease in the relative repetition and subsequently overall occurrence of this “minor” behaviour upon relocation to the new enclosure. No interpretation for this deviation is offered given the understanding of Randy as described above and the interpretation given for the consistency with which the combined focal animals undertook this “minor” behaviour in the former and new enclosures.

Furthermore, despite an increase in *foraging* effort by Randy and the combined focal animals upon relocation, deemed to increase feeding competition amongst the Wellington Zoo hamadryas baboons, Randy was not observed in either enclosure attempting to minimise feeding competition by distancing himself with major food items (i.e. *relocating food*). By contrast, the combined focal animals experienced an increase in the relative repetition and overall occurrence of this “minor” behaviour upon being presented with increased foraging opportunities in the new enclosure. Given that the more dominant adult male, Abu, began *relocating food* upon relocation to the new enclosure, Randy’s relative hierarchical position amongst the colony cannot explain why he was not seen undertaking this response.

- Results from statistical analysis and deduction of changes in the social states between the former and new enclosures that deviate from the combined focal animals

The increase in the “solitary” state and decrease in “grouped” state by the combined focal was deemed to occur as a consequence of increased inter-individual distances due to increased foraging effort and “locomotion” in the new enclosure. Randy also experienced an increase in *foraging* and “locomotion” upon relocation. However, unlike the combined focal animals, he experienced an increase in the relative repetition and overall occurrence of both the “solitary” and “grouped” states. This would appear to contradict the interpretation given previously. Despite a decrease in “social” behaviour by Randy upon his relocation, of all the five focal animals he still had the greatest percentage of time per sample in social interactions in both the former and new enclosures. However, and in contrast to the combined focal animals, a decline in the “social” state by Randy upon his relocation would appear to have caused the amount of time that he spent in both the “solitary” and “grouped” states to increase to a statistically significant degree.

An increase in the overall occurrence and relative repetition of the “solitary” state, and a corresponding decline in the “social” state, by Randy illustrates a positive effect of the new enclosure in encouraging increasingly naturalistic behaviour. In particular, social time has been found to diminish with age in free-ranging hamadryas baboons, while tending to increase within captive populations (Kummer and Kurt 1965).

- Similar results in the social states between the former and new enclosures as the combined focal animals with different interpretations in accordance with Abu’s individual response to relocation

The results derived from focal analysis of social states for Randy that were the same as those for the combined focal animals also share similar interpretations.

6.3.3 Full interpretation of Toka’s response to relocation

6.3.3.1 Absent or infrequently occurring behaviours that reinforce the preceding individual description and summary discussion of Toka’s responses to relocation.

Toka did not *receive vocal presentation* in either enclosure. This reiterated his position within the colony as a single, subordinate and sub-adult male. Unlike the colony’s mature males, Abu and Randy, Toka did not have harem females to compete for his attention. Furthermore, as a subordinate sub-adult, Toka lacked the authority within the colony that attracted *vocal presentation* from other animals towards Abu and Randy when seeking their support. The absence of *intervention* in Toka’s focal samples can also be attributed to his absence of a harem and his limited command within the colony.

The absence of *tactile appeasement*, and the infrequent occurrence of *vocal appeasement*, (both of which corresponded with extremely low levels aggression) by Toka can be interpreted in the same way as for combined focal animals. Unlike the sexually mature sub-adults at Zurich Zoo, Toka was not recorded embracing others or receiving embraces during situations evoking fear (Kummer 1995).

Tail holding/herded by tail were also absent from focal samples for Toka. *Tail holding*, directed by the colony's harem leaders towards their mates, was interpreted to exemplify an aggressive herding behaviour. The absence of these two "minor" "solicitation" behaviours in focal samples for Toka can be attributed to his position as an unpaired male.

The absence of *physical* and *visual aggression* suggests that Toka, like other subordinate primates, had learnt to "inhibit his behaviour and to keep out of the way of the dominant on many occasions" (Dolhinow 1972:382). Unlike the colony's juvenile males, who tried to provoke an aggressive response from Abu to which they could react, as a sub-adult male Toka was unlikely to receive a restrained response like that afforded to juveniles (Kummer 1995).

In contrast to Randy and Abu, Toka was the *receiver* of only a single instance of *visual presentation* (a "minor" behaviour which can be either sexual or pseudo-sexual i.e. notification). This result supports the following two contentions:

(i) As a single sub-adult male, Toka had less opportunity for sexual interaction than his older male counterparts [sub-adult males are less likely than adult males to receive presents from swollen females (Seyfarth 1978)]. Supporting this, Toka experienced only a single instance of heterosexual *mating* during the course of this investigation. This further emphasised his position as a single sub-adult 'follower' affiliated with Randy's harem as discussed above. At the onset of sub-adulthood, 'follower' males virtually cease to mate until they have their own females (Kummer and Kurt 1965). If they are caught copulating with a 'follower' male, both captive and free-ranging hamadryas baboon females will be severely chastised by their harem leaders (Kummer and Kurt 1965);

(ii) At this age, free-ranging sub-adult male hamadryas baboons do not yet co-operate in the leadership of their units or participate in the co-ordination of activity involving the broader group, both of which involves presentation (i.e. notification) between adult males (Kummer 1995). This was supported by the infrequency of *simulated mating* involving Toka such as that also undertaken by male hamadryas baboons during situations that require co-ordinated behaviour (Kummer 1995). At sub-adulthood, free-ranging males may begin to show traces of notification behaviour that will eventually enable them to take part in unit leadership (Kummer 1968). These initial notification gestures are slightly different in form than those undertaken by mature males (Kummer 1968).

Unlike the combined focal animals that were seen *grooming other* in both enclosures, only a single instance of this "minor" behaviour was observed for Toka. This as recorded in the new enclosure. The extremely low frequency of occurrence of this "minor" behaviour may be attributable to the colony's demographics, specifically the absence of other sub-adult and unpaired adult males. While sub-adult males have a relatively solitary existence (Kummer and Kurt 1965), they maintain an attraction to other males that diminishes upon establishing harems (Kummer 1968). The absence of other sub-adult and adult bachelors was likely to have limited Toka's friendly social interaction, including mutual grooming. Such grooming is synonymous with sub-adult and adult males of all ages before harem leadership and later upon losing their mates (Kummer 1968).

6.3.3.2 Toka's individual response to relocation

Of the five focal animals, Toka had the largest behavioural repertoire consisting of 36 “minor” behaviours. In addition, results for Toka indicated that he experienced the least percentage (i.e. 58.33 percent) of “minor” behaviours common to both enclosures and therefore the greatest repertoire change. However, little can be inferred about Toka's response to relocation from the extent of his repertoire in each enclosure as many (i.e. 9 of the 15) “minor” behaviours exclusive to a single enclosure (i.e. the new enclosure) in focal samples for Toka occurred on only a single occasion. It is possible, of course, that some of these rarely occurring “minor” behaviours were also undertaken by Toka prior to relocation but their infrequency meant they were not recorded during sampling. Some of these infrequently occurring “minor” behaviours, including *receiving visual presentation*, *simulated mating* and *groom other*, were described above as illustrative of Toka's age and sex classification and relative social position rather than his response to relocation.

- “Major” and “minor” behaviours seen exclusively in a single enclosure in contrast to the combined focal animals

Unlike the combined focal animals, for which *drinking* was recorded in both enclosures, this “minor” “feeding activity” behaviour was only apparent in the new enclosure during focal sample analysis for Toka, whereupon five occurrences were recorded. By contrast, prior to relocation, the frequency of *drinking* by Toka was so low that it did not feature during focal sampling. It would appear that, upon relocation to the new enclosure, Toka gained increased access to water. The observer speculates that Toka's comparatively limited access to water in the former enclosure was attributable to his lower ranking position within the colony. The provision of three separate water sources in the new enclosure (as opposed to one in the former enclosure) meant that more dominant animals could not control access to this resource.

The absence of *vocal aggression* in the new enclosure in focal samples for Toka can be interpreted in the same way as the apparent decline in the relative repetition of this “minor” behaviour by the combined focal animals upon the colony's relocation. This related to three factors:

- (i) The enclosure's increased physical complexity provided opportunities for the Toka to minimise confrontation with conspecifics;
- (ii) Provision of increased space allowed a more appropriate ‘flight distance’ between the animals and the viewing public; and,
- (iii) Increased enrichment provided opportunities for greater activity, which was thought to reduce the animals' aggressive interaction with the public - a means to generate environmental variability and complexity.

Similarly, Toka experienced a considerable reduction in instances of *reaching out*. Whereas 20 occurrences from the former enclosure were recorded in his focal samples, only a single instance was recorded upon his relocation. (The absence of a statistically significant difference in the overall occurrence of *reaching out* between the former and new enclosures in focal samples for Toka can be attributed to an anomaly in the results, in particular the considerable length of the single instance of this “minor” behaviour in the new enclosure. This

single instance prevented statistical testing for a difference in the mean bout length between the former and new enclosures). *Reaching out* was also interpreted as exemplifying the animals' attempts to increase environmental complexity by employing external elements. Upon relocation, Toka's attention was on the more spacious, naturalistic and variable enclosure. Consequentially, there were instances in his focal samples in the new enclosure of each of the new exploratory behaviours i.e. *licking*, *scraping* and *relocating object*.

- Results for changes in "major" and "minor" behaviours between the former and new enclosures that deviate from the combined focal animals

Upon relocation, and in contrast to the combined focal animals, Toka experienced an increase in the relative repetition and overall occurrence of "solicitation" behaviour. The only "minor" solicitation behaviour exclusive to the new enclosure in focal samples for Toka was *mating*. This particular "minor" behaviour was recorded on only a single occasion. This increase in "solicitation" behaviour can be attributed largely to the increased repetition with which Toka undertook *pursuit* upon his relocation. Initially, it was thought this coincided with increased "locomotion" behaviour by Randy's harem and subsequent pursuit by Toka. However, examination of the particular instances of this "minor" behaviour in each enclosure using details recorded on spreadsheets showed that, in fact, it was *pursuit* involving Toka and pen-mates not belonging to his "affiliated" harem that increased upon his relocation. In particular, Toka began engaging in *pursuit* with the juvenile male 'Pharaoh'. This probably occurred as a consequence of the increased space of the new enclosure that enabled Toka to exercise greater independence from the harem to which he was affiliated, just as free-ranging followers will separate from their units during the daily march (Kummer 1968).

No reference to *pursuit* behaviour between unpaired males could be found in the literature. The observer can only speculate that *pursuit* interactions between immature males, noted previously as accompanying the aggressive herding of females by adult male harem leaders, exemplified 'role play'. This is supported by the understanding that "sexual and dominance behaviour develop and are practised in play" (Dolhinow 1972:323). In a similar way, the fear induced embracing referred to above (which, in the wild, is typically undertaken by harem leaders towards females when neighbours are fighting, or by mothers towards frightened infants) that was seen to occur between sub-adult males within the Zurich Zoo colony was deemed to be role playing activity (Kummer 1995).

Toka also experienced an increase in the relative repetition and overall occurrence of "agonistic" behaviour between the former and new enclosures. This was in contrast to the combined focal animals for which there was no discernible difference. No new "minor" "agonistic" behaviours occurred in focal samples for Toka upon relocation to the new enclosure to explain such an increase. Rather, increasingly "agonistic" behaviour by Toka can be largely attributed to a greater relative repetition and overall occurrence of *avoidance*.

On all but one of the 25 occasions from both enclosures in which Toka acted to avoid a conspecific, he was supplanted by Abu. This occurred even though greater space enabled broader inter-individual distances in the new enclosure. The increased rate of repetition of *avoidance* by Toka correlated with increased "locomotion" by the more dominant Abu. Toka was recorded glancing towards Abu and moving off when Abu moved in his direction, even from distances estimated to be as great as 15 meters (Figure 6.2). Unlike Randy, who retreated in

an ‘unconcerned’ fashion, Toka’s behaviour during occasions of *avoidance* was often abrupt and exaggerated, especially in the former enclosure i.e. he ran or leapt away from Abu. This may be indicative of Toka’s relative immaturity. Researches have observed adult male primates, including hamadryas baboons, retreating ‘casually’ on such occasions. This has led to some speculation that these adult males may have discovered that they are involved in fewer confrontations when they move off quietly (Kummer 1995).



Figure 6.2. Toka reacting to the approach of a conspecific

Just as for the combined focal animals, Toka experienced no change in overall occurrence, mean bout length or relative repetition of “feeding activity” between the former and new enclosures. However, whereas the combined focal animals were found to have an increased relative repetition and overall occurrence of *foraging* upon relocation, no such change was discernible for Toka. Rather, Toka consistently maintained the highest average percentage of *foraging* per sample in each enclosure of any of the five focal animals. The observer speculates that consistently high *foraging* by Toka, relative to the other focal animals, was related to his position as a single, sub-adult male in two ways:

- (i) Whereas each of the other focal animals had social interaction within established harems to occupy their time in the restricted former enclosure, Toka, as a sub-adult ‘follower’, had comparatively limited social contact. Results indicated that of the five focal animals, on average, Toka spent the lowest percentage of time per sample in both enclosures in the “social” state. Instead, he appeared to occupy himself with non-social activity, such as *grooming self* and *foraging* (despite the absence of a range of foraging opportunities in the former enclosure). Rather than increasing the percentage of time spent *foraging* upon relocation, Toka appeared to respond to the variety of foraging opportunities offered in the new enclosure by undertaking new methods of exploration;
- (ii) Just as he appeared to be largely excluded from the single water source provided prior to relocation, a high incidence of *foraging* by Toka in each enclosure provided some indication that, as a subordinate, he may also have been precluded from the colony’s main daily feed in each enclosure. This was typically distributed by keepers within a similarly small space in each enclosure and may have enabled dominant animals to obtain a disproportionate share of the food. It is probable that this forced Toka to forage more to compensate for a lower share. The expropriation of a disproportionate amount of food by dominant conspecifics is an acknowledged problem associated with feeding group-housed animals (Chamove et al. 1982).

An increase in foraging effort by the combined focal animals was attributed to causing an increase in the relative repetition and, consequently, the overall occurrence of “locomotion” and, specifically, to promoting an increase

in discontinuous *walking*. As a consequence of consistent relative repetition, mean bout length and overall occurrence of *foraging* by Toka between the former and new enclosures, no similar change in “locomotion” (and, in particular, *walking*) was discernible in his focal samples.

Toka experienced a decrease in overall occurrence of *climbing* upon relocation. This was the result of a reduction in relative repetition, in contrast to the combined focal animals. This reduction in the repetition of *climbing* by Toka can be attributed to the increased space and physical diversity of the new enclosure. This provided areas of refuge from social pressure, such as approach-avoidance conflict, that Toka often sought by *climbing* prior to relocation.

Unlike the combined focal animals, Toka experienced an increase in the mean bout length and a decrease in relative repetition of *running* upon relocation. This was attributable to two factors:

(i) In the former enclosure, instances of *running* by Toka were often (i.e. in four out of seven instances) associated with *avoidance* behaviour which tended to be particularly abrupt. Increased space in the new enclosure meant that Toka did not have to react as quickly when approached by dominant animals because of greater inter-individual distances;

(ii) Additional comments made on spreadsheets indicated that, upon relocation, instances of *running* by Toka increased in mean bout length as they became increasingly associated with his hurrying across the enclosure to rejoin the unit to which he was affiliated as it advanced in *troop movement*. Instead of pursuing his harem on such processions, Toka, exercising increased independence as a ‘follower’ male, allowed them to gain some considerable distance before hastily running to catch up with them. Late arrival at such processions provided a further indication that Toka did not yet co-operate in the co-ordination of such new cohesive group behaviour which, in the wild, is typically lead by ‘I-males’ and other young adult males (Kummer 1968).

Unlike the combined focal animals, and for the reasons noted above, Toka did not experience an increase in *foraging* (and associated “locomotion”). This has been attributed to causing a decline in “inactivity” by the combined focal animals upon relocation. Instead, Toka undertook new exploratory behaviours in response to the provision of increased foraging opportunities in the new enclosure. Instances of these ‘new’ “minor” behaviours were too short or infrequent to cause a decrease in the mean percentage of time per sample that Toka remained inactive.

The increase in relative repetition and, consequently, overall occurrence of *sitting* by Toka upon relocation, in contrast to the combined focal animals, corresponded with his reduction in the relative repetition and overall occurrence of *resting*. In the new enclosure, with its increased physical diversity, Toka spent less time basking in the sunshine (i.e. *resting*) and more time *sitting* in the increased variety of sheltered areas. This was indicative of Toka’s preference for shade cover and/or taking refuge in areas of privacy as he experienced social pressure associated with Abu’s increased “locomotion”. The latter is supported by an increase in the relative repetition and overall occurrence of “out of sight” by Toka in the new enclosure. Many areas inaccessible to public view (such as the fully covered den area) provided the animals with not only shade and shelter, but also visible barriers to one another.

- Similar results in “major” and “minor” behaviours between the former and new enclosures as the combined focal animals but with different interpretations in accordance with Toka’s individual response to relocation

Just as did the combined focal animals, Toka experienced a decrease in the overall occurrence of *receiving grooming* as a consequence of a reduction in relative repetition. However, unlike the combined focal animals, this result cannot be attributed the ‘early bird principle’, as Toka did not maintain his own harem over which to assert possession. [A similar difference in grooming effort was discovered in a comparison of captive and free-ranging hamadryas baboons. In that study, it was observed that sub-adult males in the confines of a fourteen by twenty-five-meter enclosure were groomed by conspecifics 15 percent of the time during which they were observed. By comparison their free-ranging counterparts were seen being groomed only 8.2 percent of observation time (Kummer and Kurt 1965:73)]. The observer speculates that a decline in the relative repetition and overall occurrence of this “minor” “grooming” behaviour by Toka was attributable to a reduction in the amount of time he spent in close proximity and interacting socially with his affiliated harem, bearing in mind:

- (i) Indications of his increased spatial independence from his ‘affiliated’ unit; and,
- (ii) It was primarily females from this unit that were seen to groom Toka in each enclosure.

In a similar way to the combined focal animals, Toka experienced a decrease in the relative repetition and, consequently, overall occurrence of “play” and *manipulating environment*, upon relocation. Whilst this did not correlate directly to greater foraging effort by Toka (as was the case for the combined focal animals), a reduction in the amount of time that Toka handled non-edible objects in the new enclosure can be similarly attributed to an increase in environmental complexity. By contrast, in the former enclosure, Toka may have been compensating for a relatively simplistic environment by using the limited number of objects at his disposal in a variety of ways.

The majority of instances (i.e. 92 percent) of *play fighting* recorded during sampling of the five focal animals involved Toka. Unlike the two adult focal males, Abu and Randy, Toka’s position as a captive sub-adult and unpaired male afforded him the opportunity to play fight, typically with other immature males. Unlike the sub-adult males within the Zurich Zoo hamadryas baboon colony who were recorded play fighting during nearly 20 percent of observation minutes (Kummer and Kurt 1965:75), Toka spent, on average, less than one percent of time per sample on comparable behaviour. This declined further upon the colony’s relocation. The low and declining occurrence of this “minor” behaviour indicated that Toka had almost outgrown his playgroup. Such behaviour by the Zurich Zoo sub-adults was deemed to illustrate the “retarding influence of captivity on the development of some behaviour patterns” (Kummer and Kurt 1965:75).

- Deviations from the combined focal animals in response to relocation for which no interpretation can be given in accordance with the observer’s understanding of the particular behaviour and the individual focal animal

An explanation was given for each deviation in Toka’s response to relocation compared with that of the combined focal animals.

- Results from statistical analysis and deduction of changes in the social states between the former and new enclosures that deviate from those of the combined focal animals

Unlike the combined focal animals for which there was a decline in the relative repetition and overall occurrence of socialisation upon relocation, no change in the “social” state between the former and new enclosures was discovered in focal samples for Toka. As the only single, sub-adult male, Toka consistently experienced the lowest mean percentage “social” and “grouped” behaviour per sample of any of the five focal animals in both enclosures. Single captive and free-ranging sub-adult males alike go through a relatively solitary phase (Kummer and Kurt 1965). By this time they have outgrown playgroups, but are not yet leading a harem of their own (Kummer and Kurt 1965). Older sub-adults have been found to spend less than half the time socially than any other class (Kummer 1968). The demographics of Toka’s colony and, in particular, the absence of other single sub-adult and adult males, was likely to have exacerbated this by limiting Toka’s naturally occurring social interaction, such as mutual grooming as discussed above (Kummer 1968). In addition, unlike the other focal animals, Toka experienced inhibited social interaction within the unit he followed. ‘Follower’ males seldom engage in open social interaction with their group, with the exception of occasional grooming bouts with adult females (Kummer and Kurt 1965). This is because interaction may provoke a threat response from the male leader (Kummer and Kurt 1965).

Other focal animals undertook heightened socialisation in the restricted former enclosure. This declined with the provision of increased non-social activity opportunities upon their relocation to the new enclosure. By contrast, Toka acted relatively independently in each enclosure in order to occupy himself and became increasingly independent upon his relocation. The increase in exploratory behaviours experienced by Toka upon release into the new exhibit proved to be insufficient in both duration and frequency to cause a reduction in the already limited amount of time he spent interacting socially.

- Similar results to the combined focal animals in the social states between the former and new enclosures but with different interpretations in accordance with Toka’s individual response to relocation

Just as did the combined focal animals, Toka experienced an increase in the relative repetition and overall occurrence of the “solitary” state and consequent decline in the “grouped” state. However, unlike the combined focal animals, this cannot be directly attributed to increased *foraging* and associated “locomotion” by Toka as these behaviours did not vary significantly in his focal samples between the enclosures. However, an increase in *foraging* by the combined focal animals upon relocation was interpreted to cause increased feeding competition within the colony resulting in increased time spent by the animals at greater inter-individual distances. This was likely to have impacted upon Toka as “individuals of low rank should be more dispersed to avoid contest competition and aggression from dominant animals” (Busse 1984; van Noordwijk and van Schaik 1987; Janson 1990, cited in Cowlshaw 1999:68).

Furthermore, because of the space restrictions in the former enclosure, Toka spent more time in close proximity to his affiliated harem. In the new and comparatively spacious enclosure, this unit became increasingly mobile. Results for Toka show that, instead of remaining with his unit as they moved and *foraged*, Toka, who was not seen to *forage* significantly more upon relocation, would often allow this unit to travel some considerable

distance before rejoining them. This increased independence from his affiliated harem was also likely to have contributed to a reduction in the relative repetition and overall occurrence of the “grouped” state by Toka upon relocation.

6.3.4 Full interpretation of Tina’s response to relocation

6.3.4.1 Absent or infrequently occurring behaviours that reinforce the preceding individual description and summary discussion of Tina’s responses to relocation.

At no time during focal sampling was Tina seen *receiving vocal presentation*. This reinforces the observer’s earlier contention that *vocal presentation* was primarily the domain of adult males within the Wellington Zoo colony as females and immature males sought to attract their attention or aid.

Likewise, Tina was not recorded *receiving visual presentation* during focal sampling. Rather, instances of this “minor” “solicitation” behaviour within focal samples typically involved females presenting to males as an invitation to copulate. *Visual presentation*, including that undertaken by females, may also serve as a submissive gesture towards superior partners or potential aggressors (Kummer 1968). Tina was not recorded receiving this gesture from other females during sampling. This may have been because such clear dominance interaction amongst females seldom occurs (Sigg 1980).

On occasion, hamadryas baboons may ‘present’ to entice a grooming response (Kummer 1968). Given Tina’s social function and grooming effort as a ‘central’ female, she could have been expected to be seen *receiving visual presentation* on such occasions. In addition, as sub-adult male baboons initiate grooming bouts with females (Seyfarth 1978), and as it was Tina who primarily was seen to groom Toka, it could have been anticipated that Tina would be seen *receiving visual presentation* by Toka at the onset of these occasions. This lends support to the observer’s earlier contention that the baboons within the Wellington Zoo colony undertook a limited presentation.

No instances of *simulated mating* (i.e. homosexual mating activity) were recorded in focal samples for Tina. Unlike male hamadryas baboons, homosexual behaviour among females is not typical of free-ranging hamadryas baboons (Kummer 1995). Instances of female homosexual activity amongst hamadryas baboons have been recorded in captivity, specifically at Zurich Zoo. In this particular population, seven sexually mature females had access to only a single adult male. During oestrus, these females were seen to engage in mating type activity with one another (Kummer 1968). The absence of female homosexual behaviour during focal sampling at Wellington Zoo may reflect, therefore, the appropriateness of the colony’s demographics during this investigation, whereby each mature female was assimilated into a harem. The size of each of these harems was consistent with reports of free-ranging one-male hamadryas baboon units which, in Ethiopia, were, on average, found to consist of barely two females per male (Kummer 1995).

As a female, Tina did not partake of *tail holding*. This was seen to be a herding behaviour performed exclusively by the colony’s one-male unit leaders to enforce the coherence of their harems. In addition, at no stage was Tina seen to be led by her tail (i.e. *herded by tail*), despite her harem leader’s use of this herding technique prior to the colony’s relocation. The absence of this “minor” solicitation behaviour provided some

indication that Tina had a predisposition towards a 'central' role prior to relocation in as much as 'central' females tend to remain closer to, and be more obedient towards, their unit leader than 'peripheral' females (Kummer 1995).

At no stage during sampling was Tina recorded undertaking *physical* or *vocal aggression*. As a female, Tina was defended by her harem leader (Sigg 1980). In addition, Tina's additional social interaction with the unit leader [including a greater amount of mutual grooming relative to the 'peripheral' female (Kummer 1995)] may also have afforded her increased protection from agonistic encounters as a result of the 'early bird principle' discussed previously. Furthermore, the proximity and compliance demonstrated by Tina, that meant she was not forcefully herded by her harem leader, was likely to also have reduced her involvement in aggressive interaction. This is because an agonistic response by unit leaders towards their females can be generated by anything that compromises the behavioural or spatial dynamics of the unit (Kummer 1968). The absence of such confrontations with her unit leader during her focal samples provided a further indication that Tina maintained a degree of obedience, typical of 'central' females (Kummer 1995), prior to relocation.

Kummer (1968) did not observe aggression between female hamadryas baboons of different units in wild populations. However, he did record aggressive interactions amongst females from different units at Zurich Zoo (Kummer 1968). In such situations, opposing females were herded back to their units by their respective mates (Kummer 1968). No *physical aggression* between females of opposing units was recorded in focal samples for Tina. Nor were episodes of *physical aggression* recorded between Tina and the other (by inference) lower ranking female within her harem. Artificial feeding trials have provided some insight into why agonistic interactions between females are rare. These trials generated speculation that (Sigg 1980:289):

- (i) Females share stable dominance relationships that are "strictly respected by the subordinate"; and,
- (ii) Aggression is minimised as a consequence of the dominant female's tolerance.

The absence of *vocal appeasement* and the low overall occurrence of *tactile appeasement* (i.e. one instance in the new enclosure) by Tina can be interpreted in the same way as for combined focal animals and corresponded to low levels of participation by Tina in aggressive interaction.

As an established member of Randy's harem, which appeared to be excluded from the two-male team type processional behaviour undertaken by some of their pen-mates upon relocation, Tina did not participate in *troop patrol* locomotion.

At no stage in the former enclosure was Tina seen to *manipulate environment* or undertake overt exploratory behaviour. In addition, vestigial *digging* was recorded in focal samples for Tina on only a single occasion prior to relocation. The tendency to forgo such reconnoitring continued into the new enclosure. Most noticeably missing from Tina's focal samples upon relocation were the 'new' exploration type behaviours (i.e. *licking*, *scraping* and *relocating object*) undertaken by other focal animals in response to the more spacious and naturalistic enclosure. This observation was consistent with Tina's role as a 'central' female. Unlike 'peripheral' females, 'central' females are less interested in ecological matters (Kummer 1995), such as the

discovery of new food resources (Sigg 1980) and, instead, concentrate their efforts on the social sphere (Kummer 1995).

The absence of *play fighting* by Tina was consistent with her age. Juvenile females join in playgroups centred around sub-adult or adult males (Kummer 1968) that can intervene in altercations (Kummer 1995). Even during this time, females play more delicately than their male counterparts. For example, biting games are much more frequent amongst males (Kummer 1995). Play by females is most common amongst three to five year old animals, although they begin to withdraw from more boisterous games at two and a half years (Kummer 1995).

6.3.4.2 Tina's individual response to relocation

Focal sample analysis revealed that Tina experienced 61.54 percent of "minor" behaviours in her behavioural repertoire common to both enclosures. Only two behaviours undertaken by Tina upon relocation had not already been demonstrated by the combined focal animals prior to relocation. These were:

- (i) *Hunting*, which occurred so infrequently that it may not have been captured during sampling of the focal animals in the former enclosure; and
- (ii) *Troop movement*, a new and cohesive group behaviour.

Tina's response as an adult female occupying a more clearly discernible 'central' position was unique amongst the focal animals. It was primarily changes in the relative repetition and, consequently, overall occurrence of behaviours in her existing repertoire prior to relocation that characterised her individual response to the new enclosure more so than the absence of formally occurring activities or development of new behaviours.

- "Major" and "minor" behaviours seen exclusively in a single enclosure in contrast to the combined focal animals

Unlike the combined focal animals, Tina only undertook *vocal presentation* in the new enclosure, where five instances were recorded. This result coincides with data for her harem leader, Randy, who was found to have a significant increase in the overall occurrence of *receiving vocal presentation* upon relocation. As Tina came to occupy a more clearly recognisable 'central' role within her unit, her position may have afforded her an increasingly high-frequency social bond with Randy, relative to Jackie (Randy's other harem female) (Appendix A, Figure 6.1). This is likely to have been reinforced by a higher incidence of mutual grooming between Tina and Randy upon their relocation, as grooming is considered to be a bonding behaviour (Sigg 1980). Female baboons, sharing high-frequency social bonds with their leaders, have been found to terminate 'presentation' and grooming bouts by females sharing lower-frequency social bonds with their unit leaders (Seyfarth 1978). This occurs equally often throughout their reproductive cycle (Seyfarth 1978). Furthermore, Kummer (1968) observed that high ranking female hamadryas baboons prevented low ranking females from interacting with their unit's leader with the same frequency. In this particular instance, an increase in *vocal presentation* by Tina may have coincided with such competition with other females (and, in particular, the other female in Randy's harem) as they established more discernible social bonds with their leader as a result of their developing positions within their unit.

Only a single instance of *visual aggression* occurred in focal samples of Tina. This occurred in the former enclosure. However, other observations of Tina, that were not recorded on video, indicated that she frequently reacted in a visually aggressive manner (i.e. brow-raising, teeth bearing, ground beating...) when provoked. Such provocation included overt eye contact and excessive noise by passers by. Anecdotal observations suggest that this behaviour was intensified in the confines of the former enclosure. Such a reaction by Tina towards the public in the former enclosure was indicative of her less clearly defined 'central' role prior to relocation. It is typically unit leaders or 'peripheral' females that react to such potentially hostile situations (Kummer 1995). The infrequency of *visual aggression* by Tina during focal sampling was probably attributable to the public's response to the presence of a video camera. This caused them to moderate their behaviour towards the animals.

The absence of *resting* by Tina upon relocation cannot be attributed in the same way to a reduction in the overall occurrence of the same "minor" behaviour by the combined focal animals, as the latter was directly the result of an increase in foraging effort. Focal samples for Tina revealed a decrease in *foraging* upon relocation. Rather, the absence of *resting*, together with the significant decline in the occurrence of *sitting*, in the new enclosure in focal samples for Tina corresponded with the reduction in "inactivity" experienced by Tina. Greater activity by Tina upon relocation was associated with her increased "locomotion". This was coincident with her unit's participation in *troop movement*, as well as Tina's growing socially active role as a 'central' female.

The occurrence of *reaching out* by Tina exclusively in the former enclosure can be interpreted in the same way as the decrease in the relative repetition of this "minor" behaviour by the combined focal animals. More specifically, the absence of *reaching out* (i.e. to grasp at surrounding vegetation) by Tina upon relocation to the new enclosure reflected the increased complexity of the new enclosure. This meant that the animals no longer needed to employ external elements to increase environmental variability. In addition, the absence of this "minor" "feeding activity" behaviour by Tina upon her relocation corresponded with her increasing lack of interest in ecological matters and greater interest in social interaction consistent with her developing 'central' position.

- Results for changes in "major" and "minor" behaviours between the former and new enclosures that deviate from the combined focal animals

Unlike the combined focal animals, no change in the overall occurrence or relative repetition of "solicitation" was recorded between the enclosures in focal samples for Tina. The five instances of the only 'new' "minor" "solicitation" behaviour (i.e. *vocal presentation*) were insufficient to cause a significant difference in the overall occurrence of this "major" behaviour. Contributing to this deviation from the combined focal animals were results for two of the three "minor" "solicitation" behaviours recorded in both enclosures in focal samples for Tina. Specifically, no differences in overall occurrence, mean bout length or relative repetition were apparent between the enclosures for *mating* and *pursuit*. The similarity in the amount and, in particular, relative repetition of *pursuit* exhibited by Tina in each enclosure provided further indication that, prior to relocation, Tina maintained some obedience typical of 'central' females, a role that became more clearly defined upon her relocation.

In contrast to the combined focal animals, too few instances of *visual presentation* occurred in focal samples for Tina in the former enclosure to enable a statistical comparison between the enclosures of the mean bout length and, therefore, deduction of the relative repetition of this “minor” behaviour. By contrast, four instances of this “minor” behaviour were recorded in focal samples for Tina upon the colony’s relocation. A greater number of instances of *visual presentation* by Tina in the new enclosure coincided with the advent of *vocal presentation* by her upon relocation. In particular, competition by Tina towards Jackie (as she interacted with their mutual harem leader) may have taken a form similar to ‘protected threatening’ behaviour, which may encompass both *visual* and *vocal presentation* (Kummer 1995).

Unlike the combined focal animals, Tina experienced a decrease in the relative repetition and, consequently, overall occurrence of “feeding activity” between the former and new enclosures. This decline was most directly attributable to a reduction in the relative repetition and overall occurrence of *foraging* by Tina upon relocation. This result was in keeping with Tina’s increasingly obvious role as a ‘central’ female, which afforded her closer proximity to her leader in the new enclosure. Such proximity to dominant males is thought to give ‘central’ females access to positions of higher food concentration (in this instance, during the colony’s major daily feeds) relative to the ‘peripheral’ female (Sigg 1980). This, in turn, is thought to reduce the ‘central’ female’s need to search for food (Sigg 1980).

In contrast to the combined focal animals, Tina experienced an increase in the relative repetition and overall occurrence of “grooming” upon relocation. This corresponded with results for *grooming other*. An increase in the relative repetition of *grooming other* by Tina was consistent with her increasingly ‘central’ position upon relocation and, in particular, her increasingly social function. Grooming within one males units is subject to both competition amongst females as well as partiality on the leader’s behalf (Kummer 1968). However, ‘central’ females have been found to groom their mate more often than ‘peripheral’ females (Kummer 1995). This is thought to indicate a strong bond with their unit leaders (Kummer 1995). Furthermore, ‘central’ females are thought to be the “social centre” of the group, extending grooming effort, a bonding behaviour, to younger members of their units (Sigg 1980:273) and to individuals belonging to surrounding groups (Kummer 1995). In the former enclosure, 28.57 percent of instances of *grooming other* by Tina were directed towards conspecifics beyond her immediate unit i.e. animals other than Randy, Jackie and the unit’s ‘follower’ male, Toka. Upon relocation, this increased to 71.43 percent. These figures support the observer’s earlier contention that, in the new, naturalistic enclosure, some individuals began grooming outside of their respective harems more frequently.

An increase in relative repetition of *grooming other* by Tina upon relocation was also consistent with her increasing involvement in intraspecific competition over access to her unit leader. Female hamadryas baboons have been found to engage in short grooming bouts with their mates after interacting aggressively with other females (Kummer 1968). This may be indicative of the additional “appeasement” function attained by the ritualisation of grooming behaviour.

Tina was seen *receiving grooming* relatively infrequently in each enclosure, with no statistically significant differences in the overall occurrence, mean bout length or, by deduction, relative repetition between the former and new enclosures. Tina received less grooming than she gave for two reasons:

(i) Grooming by unit females is primarily concentrated on their leader and on their own infants with very little being done amongst themselves (Kummer 1968); and,

(ii) Female hamadryas baboons groom their males more than their males groom them (Sigg 1980).

The most prominent difference in “minor” “locomotion” behaviour between Tina and the combined focal animals was that no change in the overall occurrence of *climbing* was discernible in focal samples for Tina. There were insufficient instances of *climbing* behaviour by Tina in the new enclosure to enable a statistical comparison of the mean bout length or, by inference, its relative repetition between the former and new enclosures. In the former enclosure, five instances of *climbing* were recorded in samples for Tina, in contrast to only a single instance upon relocation. This provided some indication that Tina *climbed* less frequently in the new enclosure and suggests that the similarity in overall occurrence of *climbing* by Tina in each enclosure may be a statistical anomaly associated with log linear modelling. A decrease in the frequency of *climbing* by Tina would be in keeping with the observation that, in order to avoid male displays, female hamadryas baboons in captivity often seek refuge in areas (such as wire fencing and struts) which are difficult for males to access due to their larger size (Kessel and Brent 1996). In the former enclosure, such displays were intensified as the colony’s immature males provoked aggressive responses from dominant males.

- Similar results in “major” and “minor” behaviours between the former and new enclosures as the combined focal animals but with different interpretations in accordance with Tina’s individual response to relocation

The results derived from analysis of focal samples of Tina that were similar to those of the combined focal animals also share similar interpretations.

- Deviations from the combined focal animals in response to relocation for which no interpretation can be given in accordance with the observer’s understanding of the particular behaviour and the individual focal animal

Just as was the case with the combined focal animals, no change in “agonistic” behaviour between the former and new enclosures was discernible in focal samples for Tina. However, in contrast to the combined focal animals, Tina experienced a decrease in the mean bout length and an increase in the relative repetition of *avoidance* upon her relocation. These findings also differed from those of her harem leader, Randy. The observer can only speculate that an increase in the relative repetition of *avoidance* behaviour by Tina was related to her developing social role as a ‘central’ female. Tina’s resultant social effort was shown to extend beyond her immediate harem, whereupon she was no longer ‘within’ the security and reassurance of her own unit.

Upon relocation to the new enclosure, and in contrast to the combined focal animals, Tina experienced an increase in the relative repetition and, consequently, overall occurrence of *standing still*. The observer speculates that this related to the obedience associated with her developing ‘central’ position and the increased repetition of *walking* by her unit leader in the new and spacious enclosure. In particular, the increase in the overall occurrence of *standing still* by Tina may have been indicative of her increased interest in Randy’s whereabouts and changes of direction.

Whereas no statistical increase in the overall occurrence of “locomotion” was found for Tina between the former and new enclosures as it was for the combined focal animals, the increase in overall occurrence of this “major” behaviour by Tina approached significance.

Contributing to this result was an increase in the overall occurrence and relative repetition of *walking*. A similar response to relocation was found for the combined focal animals and was attributed to an increase in *foraging* and opportunities for exploration. Unlike the combined focal animals, and as a result of her more clearly defined role as a ‘central’ female, Tina experienced a decrease in *foraging* and did not demonstrate new exploratory behaviours. Therefore, an increase in *walking* cannot be interpreted in the same way. Given the data available, one plausible alternative explanation was that an increase in *walking* by Tina corresponded with greater *foraging* and associated locomotion by her harem leader, Randy (whose movements were followed by Tina). However, this explanation was unsubstantiated by statistical analysis that showed no evidence of an increase in *pursuit* behaviour by Tina upon relocation. The observer can only speculate that an increase in the repetition and, consequently, overall occurrence of *walking* by Tina was consistent with her role as a ‘central’ female as she actively moved to extend her social effort both within and between units.

- Results from statistical analysis and deduction of changes in the social states between the former and new enclosures that deviate from the combined focal animals

Changes between the former and new enclosures in the overall occurrence and relative repetition of each of the three social states by Tina deviated from the response of the combined focal animals. These deviations further illustrated Tina’s developing position as a ‘central’ female.

The decrease in relative repetition and, consequently overall occurrence of the “solitary” state by Tina corresponded with an increase in relative repetition and overall occurrence of the “grouped” and “social” states.

Whereas all harem females experience some crowding by their unit leader (Kummer 1968), there are differences between the distances of harem females to their unit leader (Sigg 1980). The spatial position occupied by females within one-male units provides some index upon which to differentiate their specific roles (Sigg 1980). As Tina’s role as a ‘central’ female became more clearly defined upon relocation, she gained closer proximity to her leader (Kummer 1995). This can be attributed to causing a reduction in the amount of time Tina spent “solitary” and the increase the amount of time she spent “grouped”.

Results for the combined focal animals indicated a reduction in the relative repetition and, consequently, overall occurrence of the “social” state upon relocation. This was attributed to greater available distances between units and potential rivals in the spacious new enclosure relative to the confines of the former exhibit and an increase in non-social activity opportunities, including possibilities for *foraging* and exploration. In contrast to the combined focal animals, Tina experienced an increase in the “social” state. This was probably a consequence of her developing position as a ‘central’ female, her subsequent lack of interest in ecological matters and the gregarious nature of this role. This was particularly evident in her grooming behaviour, which increased significantly towards others upon relocation.

- Similar results in the social states between the former and new enclosures as the combined focal animals with different interpretations in accordance with Tina's individual response to relocation

There were no similarities in the response of Tina and the combined focal animals with regard to changes in social states between the former and new enclosures.

6.3.5 Full interpretation of Sinead's response to relocation

- 6.3.5.1 Absent or infrequently occurring behaviours that reinforce the preceding individual description and summary discussion of Sinead's responses to relocation.

Receiving visual presentation and *receiving vocal presentation* occurred infrequently in focal samples for Sinead, although they were more prominent prior to her relocation. The particular infrequency of these "minor" behaviours in Sinead's focal samples in the new enclosure corresponded with the observer's earlier conjecture that competition, in the form of *vocal* and *visual presentation*, by Makele (Abu's other established female) for access to their leader declined upon relocation.

Intra-sexual competition amongst females is one factor affecting the frequency of social interaction between males and females (Seyfarth 1978). Focal samples for Abu revealed a tendency by Makele (i.e. Abu's other harem female) to terminate social interactions involving Abu and other animals, such as invitations to copulate. This provided some indication why *mating* occurred so infrequently in focal samples for Sinead (i.e. on only a single occasion). Male preference for particular females also plays a part in the frequency of social interaction between males and females (Seyfarth 1978). It was also a plausible reason for the infrequency of *mating* between Sinead and her harem leader during focal analysis. Sinead was unlikely to have attempted *mating* with males other than her harem leader, as such behaviour may have severe repercussions (Kummer and Kurt 1965).

For the same reasons given for Tina relating to the infrequency of this behaviour by free-ranging female hamadryas baboons and the appropriateness of her social setting, no instances of *simulated mating* were observed for Sinead. In addition, and as with Tina, Sinead was not recorded *tail holding* during focal sampling.

Just as for the combined focal animals, *physical aggression* was infrequent in focal samples for Sinead in both the former and new enclosures. However, due to her disposition towards and developing role as a 'peripheral' female, Sinead was more susceptible to involvement in *physically aggressive* interactions than Tina, a 'central' female, for the following reasons:

- (i) 'Peripheral' females are less obedient than 'central' females (Kummer 1995). Disobedient behaviour, such as straying, is typically met by an aggressive response, such as a neck bite, from harem leaders as they seek to ensure the integrity of their units (Kummer 1968). Sinead's disobedience, relative to Tina, was reinforced by samples from the former enclosure that showed Abu herding Sinead forcefully by her tail (i.e. *herded by tail*), a behaviour deemed to be undertaken by harem leaders within this colony as they reinforced the spatial coherence of their units. No such behaviour involving Tina was seen during data analysis;

(ii) Increased distance from their mate, relative to the 'central' female, makes 'peripheral' females comparatively more vulnerable (Sigg 1980). This was seen during analysis of focal samples for Sinead, whereupon she was involved in at least one physically aggressive encounter with an immature and unrelated, non-focal male (i.e. Inubis).

Analysis of Tina's focal samples revealed the frequency with which *avoidance* occurred coincided with the occurrence of this same "minor" behaviour by her harem leader, Randy. This provided some insight into the infrequency of *avoidance* by Sinead, which, in contrast to Tina, was most likely attributable to her harem leader's (i.e. Abu's) dominance and, consequently, the infrequency with which he was supplanted (i.e. acted in avoidance) relative to Randy.

On three of the four occasions on which *avoidance* occurred during focal samples of Sinead she was supplanted by Abu. The most plausible explanation for such *avoidance* of her own harem leader is that, in so doing, she was limiting agonistic contact resulting from her disobedient 'peripheral' behaviour.

On one particular occasion, in the former enclosure, Sinead hastily avoided Abu as he aggressively pursued juvenile males who had provoked him. A high overall occurrence of *climbing* by Sinead in the former enclosure, which declined significantly upon her relocation, was indicative of attempts by Sinead to elude such aggressive displays characteristic of her harem leader prior to relocation. This was in keeping with a similar response by Tina.

As was the case with Tina, the absence of *supplanting* by Sinead during focal sampling may partially be attributable to the infrequency of such clear dominance interactions between females. In addition, evidence presented during focal sample analysis of Abu suggested that Sinead, a subordinate 'peripheral' female with a low-frequency social bond with Abu, was the receiver, rather than the giver, of competition, from Makele. The purpose of this competition was the termination of social interaction between Sinead and their mutual harem leader, Abu. Such contests manifest in 'protected threatening' type behaviour as opposed to approach-avoidance conflict.

The absence of *vocal appeasement*, and low overall occurrence of *tactile appeasement*, in both enclosures by Sinead corresponded with low levels of participation in aggressive interaction and, consequently, the interpretation of infrequent "appeasement" behaviour by the combined focal animals.

Troop patrol behaviour occurred infrequently in focal samples for Sinead despite active involvement in such processions by her harem leader, Abu. The infrequency with which Sinead was observed to follow in formation during such processions relates to the following factors associated with her developing position as a 'peripheral' female:

(i) Rather than following directly in formation, Sinead may have been acting as a 'scout' (Kummer 1995:130), investigating beyond the immediate procession. This corresponds with the contention that 'peripheral' females also "assume the role of reconnoitring potential dangers" (Sigg 1980:285). During an investigation of hamadryas baboons by Sigg (1980), it was found that when "families approached a bend in the bed of a wadi or the ridge of a hill, the one that went ahead of the rest was most often the peripheral female" (Kummer 1995:130).

“This high frequency of “walking ahead” by the peripheral female when at visibility borders in particular is the rule rather than the exception” (Sigg 1980:285). ‘Peripheral’ females have been interpreted to be suited to this particular role as a ‘scout’ due to their experience and willingness to take risks (Kummer 1995). Their small, brown physiques also make females less conspicuous ‘scouts’ than adult males (Kummer 1995). In addition, given that juveniles and infants within harems are found mainly near the ‘central’ female, the risk of losing unit members may be minimised if the ‘central’ female remains close to the unit leader while the ‘peripheral’ female investigates potential dangers (Sigg 1980).

(ii) Sinead’s infrequent involvement in *troop patrol* behaviour may also relate to her increasingly ‘peripheral’ role within her harem, and corresponding disobedience, as well as an apparent reduction in her unit leader’s level of concern with enforcing the spatial integrity of his harem (as emphasised by the absence of aggressive herding behaviour in the new enclosure). This is reinforced by the observation that *pursuit* behaviour by Sinead, such as that undertaken by females upon aggressive herding by their mates, declined in overall occurrence upon relocation, in contrast to the combined focal animals.

The occurrence of only a single instance of *play fighting* during focal sampling of Sinead is consistent with the interpretation given for the absence of this “minor” behaviour in focal samples for Tina i.e. the maturity of these two focal females.

6.3.5.2 Sinead’s individual response to relocation

Results for Sinead indicated that 61.76 percent of “minor” behaviours in her behavioural repertoire were common to both enclosures. Focal samples also revealed that Sinead had the second most extensive behavioural repertoire of the five focal animals. Changes in the relative repetition and overall occurrence of some of those behaviours undertaken by Sinead in both enclosures reflected her developing ‘peripheral’ position.

- “Major” and “minor” behaviours seen exclusively in a single enclosure in contrast to the combined focal animals

Visual aggression, *vocal aggression* and *shaking* occurred exclusively in the former enclosure in focal samples for Sinead. Just as with Tina, instances of such aggression by Sinead were largely in response to intimidating interaction by members of the viewing public. Such responses were heightened in the confines of the former enclosure, where the animals had less room to distance themselves from the public. Sinead’s frequent reaction to threatening behaviour by the public was consistent with her disposition towards ‘peripheral’ behaviour and consequent predator-detecting function (Sigg 1980). In one-male units, the male leader takes a defensive role when danger is imminent. However, when danger is merely suspected, it is the ‘peripheral’ female that reacts (Kummer 1995). In addition, ‘peripheral’ females have also been found to walk more often on the side exposed to danger than the ‘central’ female (Kummer 1995). As was the case with Tina, anecdotal observations indicated that the actual frequency of such reactions was likely to have been higher than recorded during focal sampling as the viewing public moderated its behaviour in the presence of the video camera.

- Results for changes in “major” and “minor” behaviours between the former and new enclosures that deviate from the combined focal animals

Sinead experienced a reduction in the overall occurrence and relative repetition of “agonistic” behaviour upon relocation. This was in contrast to the combined focal animals for which there was no difference in “agonistic” behaviour between the former and new enclosures. This reduction in “agonistic” behaviour by Sinead can be attributed to the occurrence of three “minor” “agonistic” behaviours exclusively in the former enclosure (i.e. *visual aggression*, *vocal aggression* and *shaking*). These were interpreted above as reflecting Sinead’s response to intensified human provocation.

A further deviation in results from the combined focal animals occurred in the “minor” behaviour *feeding*, for which Sinead experienced an increase in relative repetition and, consequently, overall occurrence. This can be partially attributed to the advent of *reaching out* by Sinead upon her relocation. This may have eventuated as a result of her being increasingly displaced from areas of the highest food concentration due to her increasingly ‘peripheral’ position (Sigg 1980). During focal sampling, Sinead was observed reaching though the new enclosure’s wire mesh fence to surrounding foliage, which she subsequently brought back into the enclosure and consumed.

In addition, an increase in the relative repetition and overall occurrence of *feeding* by Sinead upon relocation is consistent with speculation that she often marched as a ‘scout’ in front of her unit during processions, such as *troop patrol* in the new enclosure. In an earlier investigation of hamadryas baboons, it was found that “about half of all feeding places utilised by one-male units were first utilised by peripheral females” (Sigg 1980:279). It has been speculated that part of the initial feeding undertaken by ‘peripheral’ females may be attributable to the fact that these females more often march in front of the unit (Sigg 1980).

Despite an increase in foraging enrichment and her increasingly ‘peripheral’ role within her harem, with consequent reconnaissance behaviour, Sinead showed a decrease in the relative repetition and overall occurrence of *foraging*, in contrast to the combined focal animals. Instead, Sinead’s primary change in habitat-orientated behaviour upon relocation was the advent of exploratory and discovery type behaviours including *licking* and *reaching out*, previously unseen in her focal samples prior to relocation. Whereas it could have been expected that Sinead would forage more in the new enclosure (to compensate for becoming increasingly displaced from feeding areas) results indicated that this was not the case. This may be because, as a ‘peripheral’ female, Sinead was more efficient at foraging than her conspecifics. There is some speculation that “peripheral females learn better foraging techniques, because they perform more discovery-work than all other group members” (Sigg 1980:278).

Unlike the combined focal animals, there was no evidence of an increase in either relative repetition or overall occurrence of *relocating food* upon Sinead’s relocation. The observer attributes this deviation to the increasingly separate spatial position occupied by Sinead upon her relocation due to her developing role as a ‘peripheral’ female. As a consequence of this increased inter-individual distance, Sinead was thought to have reduced feeding competition (associated with increased *foraging* by other members of the colony). Increased foraging competition was thought to cause other focal animals to relocate food items with greater relative repetition in the new enclosure.

In contrast to the combined focal animals, Sinead experienced a reduction in the relative repetition and overall occurrence of *grooming other* upon relocation to the new enclosure. A reduction in this “minor” behaviour may also have been consistent with her increasingly ‘peripheral’ behaviour and subsequent decrease in interest in socialisation. This may have been accentuated by the fact that female grooming effort is largely concentrated on male unit leaders and offspring (Kummer 1968). As a result, a reduction in grooming effort by Sinead may have been attributable to the fact that ‘peripheral’ females groom their harem leaders less often than ‘central’ females (Sigg 1980).

Just as was the case with the combined focal animals, focal samples for Sinead revealed a reduction in the relative repetition and, consequently, overall occurrence of “inactivity” upon relocation. However, unlike the combined focal animals, results for Sinead indicated that the similarity in overall occurrence of *standing still* between the former and new enclosures was the result of an increase in the rate of repetition of this “minor” behaviour by Sinead. An increase in the repetition of *standing still* is in keeping with earlier speculation that Sinead, as she developed an increasingly ‘peripheral’ position within her harem, assumed a reconnoitring role as a ‘scout’. In another investigation of hamadryas baboons, ‘peripheral’ females, in sharing the job of observing the environment with the male, were recorded glancing around the non-social environment significantly more often than ‘central’ females (Sigg 1980).

In contrast to the combined focal animals, no change was discernible in the relative repetition or overall occurrence of “locomotion” in focal samples for Sinead. This deviation from the combined focal animals can be largely attributed to the absence of a statistical difference in the overall occurrence of, or apparent change in the relative repetition of, *walking* in focal samples for Sinead between the former and new enclosures. Unlike other focal animals, Sinead did not experience an increase in *foraging* in the new enclosure thought to contribute to an increase in the relative repetition and, consequently, overall occurrence of *walking* (i.e. discontinuous walking) by the combined focal animals.

Unlike the combined focal animals, for which a decline was recorded, instances of “play” behaviour and, in particular, *manipulating environment*, by Sinead occurred at a similar overall occurrence and relative repetition in both the former and new enclosures. The continuation of this particular “minor” behaviour by Sinead upon relocation was indicative of the exploratory tendency associated with her developing ‘peripheral’ position and consequent interest in ecological matters, and especially the discovery of food resources (Sigg 1980).

- Similar results in “major” and “minor” behaviours between the former and new enclosures as the combined focal animals but with different interpretations in accordance with Sinead’s individual response to relocation

Just as for the combined focal animals, the primary contributor to the greater relative repetition and overall occurrence of *receiving grooming* by Sinead prior to her relocation was likely to have been the ‘early bird principle’. There was no evidence to suggest that her harem leader, Abu, sought to reassure his bond with Sinead upon relocation through increased grooming. Such behaviour by Abu was thought to be concentrated on his other harem female. In addition, the increased spatial distance and declining interest in socialisation,

characteristic of Sinead's increasingly 'peripheral' position, may also have contributed to a reduction in the amount of grooming she received by other members of the colony upon relocation.

As was the case for the combined focal animals, the relative repetition and, consequently, the overall occurrence of "inactivity" (in particular, *sitting* and *resting*) by Sinead was found to decline. However, unlike the combined focal animals, a decline in such behaviour cannot be attributed to an increase in *foraging* and associated "locomotion" by Sinead. Rather, it is more likely that Sinead experienced decreased "inactivity", as she became increasingly 'peripheral', and had reduced access to areas of high food concentration (Sigg 1980). This position probably afforded Sinead less time to sit idly, requiring increased effort towards exploration and reconnaissance. This was illustrated by the advent of *reaching out* and a significant increase in associated *feeding* upon her relocation.

- Deviations from the combined focal animals in response to relocation for which no interpretation can be given in accordance with the observer's understanding of the particular behaviour and the individual focal animal

The absence of *digging* in focal samples for Sinead was an unexpected outcome. This "minor" behaviour was interpreted earlier to have been undertaken by other focal animals as a result of the comparatively limited foraging opportunities available in the confines of the former enclosure. Given this interpretation, *digging* by Sinead could have been anticipated because of her predisposition towards 'peripheral' behaviour and consequent interest in ecological matters prior to relocation. The absence of *digging* by Sinead may be at least partially attributable to the provision of visible and accessible water in each enclosure. Experimentation reported in another study determined that 'peripheral' females dig to uncover water sources, frequently utilised by the rest of the unit, more accurately and frequently than 'central' females (Sigg 1980).

Given the observer's understanding of this particular focal animal and the "minor" behaviour involved, no interpretation can be given for the infrequent instances Sinead was recorded *grooming self*. This "minor" behaviour was recorded on only a single occasion i.e. in the new enclosure. Unlike the combined focal animals, for which a reduction in this particular self-directed behaviour was attributed to the provision of increased enrichment in the new enclosure, no change in *grooming self* was seen for Sinead. This was in spite of her use of increased enrichment upon relocation and, especially, exploration type behaviours such as *reaching out*, *manipulating environment* and *licking*.

- Results from statistical analysis and deduction of changes in the social states between the former and new enclosures that deviate from the combined focal animals

The results derived from focal analysis of social states for Sinead were the same as those of the combined focal animals.

- Similar results in the social states between the former and new enclosures as the combined focal animals with different interpretations in accordance with Sinead's individual response to relocation

Whereas Sinead experienced similar changes in each of the social states upon relocation as the combined focal animals, these changes cannot be interpreted in exactly the same way. In particular, a reduction in the relative repetition and overall occurrence of the “social” and “grouped” states, and an increase in “solitary” behaviour, does not reflect an increase in *foraging* and associated “locomotion” as was interpreted for the combined focal animals. Rather, these results reflect Sinead’s increasing lack of interest in the social sphere (Kummer 1995), and increased spatial distance from her unit (Sigg 1980), each afforded by her increasingly ‘peripheral’ position. In a study of free-ranging hamadryas baboons, it was found that the animal most often the furthest away from the centre of the one-male unit was the ‘peripheral’ female, with dominance thought to influence spacing by females as well as access to male unit leaders (Sigg 1980).

An additional reason why Sinead experienced a reduction in “social” behaviour is that ‘peripheral’ females are able to dedicate less time to social activities relative to ‘central’ females. This is because of the reduced access to areas of high food concentration and the resultant insecurity of their social and consequent spatial position relative to ‘central’ females (Sigg 1980).



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