The social behaviour and captive management of Bennett's wallabies, *Macropus rufogriseus rufogriseus*.

by

E.
Michelle Chapman BSc (Hons.)

Submitted in fulfilment of the requirements for the Degree of Master of Science

University of Tasmania (June, 2003)

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.

M. Chapman.

M. Chapman.

Abstract

The Bennett's wallaby, *Macropus rufogriseus rufogriseus,* is frequently exhibited in wildlife parks and zoos in Australia and overseas. The social behaviour of the Bennett's wallaby was investigated and its role in developing captive management strategies was considered. A questionnaire was mailed to 31 wildlife parks and zoos within Australia and New Zealand to collect information on current husbandry practices and to provide a basis for experimental manipulations of a captive group. A comprehensive behavioural inventory was compiled using observations of captive Bennett's wallabies at Bonorong Wildlife Park and the University of Tasmania, as well as wild wallabies at Coal Mines Nature Reserve on the Tasman Peninsula and Mt Field National Park in south-eastern Tasmania. Wallabies at the university enclosure devoted the greatest portion of both the day and night time browsing or attending feeding stations, although more time was devoted to browsing during the day and feeding at night.. Alert postures were sustained for longer periods during the day than at night. These activities were alternated with long and frequent periods of resting. Social interactions of any kind were rarely observed, particularly during the daytime.

The collection of Bennett's wallabies established at the University of Tasmania were utilised in experimental manipulations examining the effects of varying the number and position of feeding stations available, stocking rates and the age and gender of group members on the frequencies of performing elements of behaviour and occupying sectors of the enclosure. When four feeders were spaced throughout the 1000 m^2 of the enclosure wallabies occupied more sectors, were more active and interacted significantly more often than when feeders were positioned near to each other or their numbers reduced. When stocked at rates of three, six or nine animals per 1000 m^2, wallabies were more visible and active and interacted amicably more frequently at the medium stocking rate than at other times. When more adults were included in the captive group than members of other age classes, the proportion of time that wallabies were hidden from view in refuges within enclosure vegetation slightly increased but was offset by increased activity at other times, when wallabies alternated browsing and feeding with the adoption of alert postures, increased locomotory activity, more grooming and a greater number of social interactions.

These findings were used as a basis from which were developed principles of best practice in the captive management of Bennett's wallabies and other macropodoids.

Acknowledgements

This project was undertaken with assistance from the M. A. Ingram Trust, for which I gratefully acknowledge them.

Thanks to my supervisors for their support, good advice and well wishes throughout. Thanks particularly to Dr Sue Jones for all the support over the long haul and for helping to keep me on track. I've really appreciated it.

Thanks to all the people who assisted with trapping and handling wallabies, particularly Aisha Williams, whose help was a godsend, Brett Gartrell and Dr Colin McCoull. Thanks also to Brett for invaluable veterinary assistance and advice.

Finally, thanks go to Jamie Chapman for all the astounding support and patience over these years, particularly recently, for the proofreading and all the other jobs I've roped you into.

Table of Contents

Chapter 1 General Introduction

1.1 Introduction

The captive management of animals in zoos and wildlife parks is often based only upon empirical evidence gathered from observations of the animals in their captive setting (Crockett, 1996). Observations of the species' behaviour in the wild can form a solid foundation for understanding how the animals may respond to captivity (Morris, 1964; Veasey *et al.*, 1996). However, experimental studies of how the animals respond to variations in specific environmental parameters, such as stocking rates, composition of the group and the provision of feeding stations, provide a sounder basis from which to develop guidelines for captive husbandry (Eisenberg and Kleiman, 1977).

This thesis examines the behavioural responses of Bennett's wallabies to manipulations of the captive environment, with the ultimate aim of recommending strategies for best practice in the captive management of this subspecies that can be generalised to other macropods.

1.2 Study Species

1.2.1 General description

The Superfamily Macropodoidea is a diverse taxonomic group comprising the kangaroos, wallabies, tree-kangaroos and rat kangaroos (Ride, 1970). This assemblage contains about 50 extant species, in a number of genera (Peacock *et al.*, 1981; Sharman, 1989). Members of the Macropodoidea are found naturally only in Australia and Papua New Guinea (Jarman, 1991) and are the dominant large terrestrial and arboreal herbivores of this region (Dawson, 1989; Flannery, 1989). As a group, macropodoids are typified by their bipedal locomotion (Calaby, 1983; Baudinette, 1994). This specialised form of locomotion is assisted by related adaptations of the cardiovascular, respiratory and musculoskeletal systems (Baudinette, 1994).

As marsupials, macropodoids are pouched mammals: the pouches of these species are forward-opening. Although there are four teats, only one offspring is generally present at a time (Calaby, 1983). Females typically have a post-partum oestrus and experience periods of embryonic diapause of varying lengths. Macropodoids may undergo lactational quiescence, during which the development of the new blastocyst is inhibited during lactation; some species also exhibit seasonal quiescence (Tyndale-Biscoe *et al.*, 1974). A young at foot and a pouch young are frequently suckled concurrently from two teats supplying milk of different composition, an unusual occurrence among mammals (Calaby, 1983).

Macropodoids have a significance other than their locomotory and reproductive specialisations. Members of this superfamily are held in a special regard by the Australian people, both as a national symbol and as protected species (Select Committee, 1988). This special status can be seen by their appearance on the coat-of-arms, coins, postage stamps, corporate symbols and advertisements (Calaby, 1989).

The Bennett's wallaby *Macropus rufogriseus rufogriseus* (Plate 1) is a large, forest-dwelling wallaby common in Tasmania and its islands (Cronin, 1991). The dorsal fur of these animals is grey-brown (Johnston and Sharman, 1979), while the belly and chest are light grey. The neck fur is characteristically reddish brown and a white strip runs along the face from the upper lip. The nose, paws and longest toe are black. The first digit on the hind feet is absent and the second and third digits are fused. The fourth digit is substantially longer than the others (Calaby, 1983).

Plate 1.1: Male and female Bennett's wallabies. The female is in the foreground and has a small, non-emergent pouch young.

1.2.2 Taxonomy

Macropus rufogriseus was first described from King Island in the Bass Strait (Johnston and Sharman, 1979). The Tasmanian populations have previously been referred to as *Protemnodon ruficollis bennetti, Halmaturus ruficollis* and *Protemnodon rufogriseus frutica* (Walker, 1977). In 1934 Iredale and Troughton classified 3 subspecies: *M. r. rufogriseus* on King Island (Desmarest 1817); *M. r. fruticus* in Tasmania and Flinders Island (Ogilby, 1937) and *M. r. banksianus* (Quoy and Gaimard, 1825), from southern Queensland, New South Wales, Victoria and South Australia (Johnston and Sharman, 1979).

Johnston and Sharman (1979) used electrophoretic, chromosomal and morphometric evidence to reclassify these subspecies. The new nomenclature recognised *M. rufogriseus banksianus* on mainland Australia and *M. r. rufogriseus* in Tasmania and the Bass Strait islands. Little genetic variation between populations of the two subspecies was revealed and there were no karyotypic differences between individuals from Tasmania and the Bass Strait islands. Morphometric studies indicated the various populations were "strikingly similar". Two characters that do vary between the subspecies are breeding patterns and coat colour. *M. r. banksianus* is a continuous breeder whose light grey coat has reddish areas around the head, neck, shoulders, arms and hindquarters towards the tail. *M. r. rufogriseus* is a seasonal breeder on which the longer coat is generally grey-brown.

1.2.3 Distribution and ecology

The Bennett's wallaby is widespread and abundant in Tasmania. Members of this subspecies may occupy most vegetation types found in Tasmania, including sclerophyll forests, woodlands with dense understories and heathlands (Johnstone and Sharman, 1979; Merchant and Calaby, 1981); suitable habitat can be found on over 80% of the state. However, they exhibit a preference for sclerophyll forest with an open understorey, providing suitable refuge (Johnson, 1971; Walker, 1977, Tasmanian National Parks and Wildlife Service, 1984).

Female *M. rufogriseus* individuals maintain home ranges that are smaller than those of males. This disparity in the sizes of the home ranges of members of each sex can be related to reproductive behaviour, discussed below (Johnson, 1987). Bennett's wallabies radio-tracked at Kempton, approximately 50km north of Hobart, occupied individual but overlapping home ranges of approximately 100 ha. These were roughly elliptical, extending from forest to pasture, such that the longer axis was perpendicular to the forest edge (Johnson, 1977). Bennett's wallabies occupy cryptic positions within dense shrub during the day (Walker, 1977; Calaby, 1983), emerging to browse on native grasses and other monocotyledons in the late afternoon (Tighe *et al.*, 1981; Calaby, 1983; Cronin, 1991). Wallabies radio-tracked at Kempton travelled up to 1 km and moved up to 440 m from the forest edge to browse on pasture (Johnson, 1977). The length of time individuals spend browsing has been related to pasture type, sward length and lactational state (Clarke and Loudon, 1985).

Bennett's wallabies have also been reported to browse on swamp gum, *Eucalyptus regnans,* and pine seedlings (Tighe *et al.*, 1981) and are considered to be a pest species causing economic loss through browsing activities on pastures, crops and forestry plantations (Coulson, 1980; Tighe *et al.*, 1981; Statham, 1994; McArthur, 2000; le Mar and McArthur 2000; le Mar and McArthur 2001).

1.2.4 Reproduction, growth and population biology

Age at sexual maturity differs between the sexes. Female Bennett's wallabies are sexually mature at around 14 months of age, males at 19 months (Merchant and Calaby, 1981).

Spermatogenesis in Bennett's wallabies occurs throughout the year (Curlewis, 1991). Although the weights of testes and epididymides do not vary seasonally, the sizes of the prostate and Cowper's glands do. Maximum weight gain synchronises with the mating season, but plasma testosterone levels in males also vary seasonally and are low or non-detectable outside of the breeding season, while plasma prolactin concentrations do not differ markedly seasonally.

Female Bennett's wallabies are polyoestrus and monovular (Tyndale-Biscoe *et al.,* 1974). This subspecies is a seasonal breeder, a characteristic that distinguishes this subspecies from the continuous breeder *M. r. banksianus* (Merchant and Calaby, 1981). The breeding season for captive Bennett's wallabies in the southern hemisphere has been reported to last from January to August (Merchant and Calaby, 1981). In the northern hemisphere it covers the period July to January (Fleming *et al.,* 1983). Wild Bennett's wallabies in Tasmania have a breeding season that begins 1-2 months after the summer solstice (Curlewis and Loudon, 1989) and ends 2-6 weeks after the winter solstice

(Brinklow and Loudon, 1993). Gestation lasts between 29 and 30 days. Females give birth to a single infant (Tighe *et al.*, 1981) and have a post-partum oestrus. The average length of the oestrus cycle is 32.9 ± 2.3 days, with a range of 28 to 40 days, which differs from the period between mating and post-partum oestrus (30.8 ± 1.7 days, range 29-41). Females exhibit both lactational and seasonal diapause (Merchant and Calaby, 1981).

The pouch life of Bennett's wallabies extends for approximately nine months (Catt, 1978; Merchant and Calaby, 1981). Offspring first emerge from the pouch at around 230 days and the period spent outside the pouch increases until weaning (Fleming *et al.*, 1983). Offspring may continue to suckle until 12-17 months of age (Calaby, 1983). The size of the teat from which the offspring suckles decreases as it ages and the type of milk produced changes (Merchant and Calaby, 1981).

Fleming *et al.* (1983) trapped and examined 76 female and 50 male Bennett's wallabies free-ranging at Whipsnade Park Zoo. The maximum weight and length from nose to tail tip for females was 15.5 kg and 144 cm; for males this was 27.5 kg and 176.5 cm. Merchant and Calaby (1981) reported measurements of these characteristics for females to be 15.5 kg and 145 cm and 27.0 kg and 175 cm for males.

Cronin (1991) suggested that Bennett's wallabies may live to be 18 years of age. Fleming *et al.* (1983) also x-rayed 20 skulls of Bennett's wallabies from Whipsnade Park and used the molar index to determine the age of individuals. The oldest two animals were both male. One had an estimated age of 13-14 years and the other 14-15 years. Of 990 animals that died of natural causes over a 12 year period, 58% were males. However, the authors also noted that 64 of the 104 offspring born in Whipsnade Park and sexed for their study were male, differing slightly but significantly from a 1:1 ratio. The sex ratio of offspring of Bennett's wallabies in another captive colony did not significantly differ from a 1:1 ratio; 21 of the 39 animals able to be sexed were male.

Catt (1979) examined Bennett's wallabies shot in South Canterbury, New Zealand, and reported an uneven number of male to female offspring (1 male : 0.75 female), although this was not significantly different to parity. The proportion of females in the samples was highest in August-September and lowest in October-November, when females had large young at foot. The low period may have been due to females with offspring staying closer to cover and being under-represented in samples.

1.2.5 Behaviour

Very little detailed examination of the behaviour of Bennett's wallabies has been undertaken. Bennett's wallabies exhibit few social behaviours. Murböck (1977) noted that social groups did not form within captive colonies of Bennett's wallabies. Groups in large enclosures spread out across all available space so that densities were low and the number of interactions approximated zero, with the exception of occasional agonistic interactions during the breeding season. Field studies of *M. r. rufogriseus* conducted by Murböck (1977) yielded similar results; the median size of groups was 1.5 animals.

The majority of interactions between Bennett's wallabies fall into the areas of mother-offspring interactions and behaviours associated with reproduction. Merchant and Calaby (1981) described behaviour at the time of parturition. The birth position Bennett's wallabies were seen to adopt was comparable to that seen in *M. rufus,* the red kangaroo. The hind limbs of females Bennett's wallabies were less extended than the red kangaroos and pouch cleaning and cloacal licking were less intense and prolonged.

The sexual behaviour of free-ranging Bennett's wallabies was briefly described by Fleming *et al.* (1983). The authors noted that males opportunistically inspected the pouches and anogenital areas of females throughout the year. Groups of several males were sighted proximal to females during the breeding season. One male was seen to attempt to copulate with a female. His efforts were unsuccessful due to overt agonistic interactions with other males. Males kicked and boxed strenuously, generally for around 1 min; they also growled and salivated and their forelimbs twitched. In between bouts they groomed, browsed and dug up grass and leaves, grasping these to their chests. Females maintained crouching positions during interactions of this kind and accepted attempts by males to mount them. If the female moved away, males followed in a line with larger males closer to the female. Copulations observed between Bennett's wallabies have been reported to last around 5 minutes, although semen exuded from the cloaca within seconds of intromission (Merchant and Calaby, 1981).

A typical form of mother-offspring interaction within *M. r. rufogriseus* is play fighting. Play fighting between mothers and their male young at foot within a group of captive Bennett's wallabies was described by Murböck (1977). Around the time of weaning, young males participated in play fighting between themselves and later join in ritualised agonistic interactions.

LaFollette (1971) observed captive Bennett's wallabies and noted that the majority of agonistic interactions occurred between males. Some male-female and female-female agonistic interactions were also observed and these grew from other behaviours, such as grooming and sexual behaviours. Dominance relationships between particular pairs of animals were seen to affect other dominance relationships within the captive group and dominance reversals were achieved by removing and reintroducing males; on some occasions, reversals were permanent. Murböck (1977), examining agonistic interactions between males in a captive group, noted that dominance relationships remained stable, except in the presence of females in oestrus. Captive males engaged in overt agonistic interactions during matings that were considered to be more intense, probably because of the lack of opportunity to escape.

1.3 Keeping *M. r. rufogriseus*, the Bennett's wallaby, in captivity.

Bennett's wallabies have been bred and maintained in zoos and wildlife parks for more than 160 years (Fleming *et al.*, 1983). They reproduce with great success in captivity and are reputedly the most frequently exhibited marsupial in zoos and private and public wildlife parks in Australia, Britain and Europe. Of the two subspecies, *M. r. rufogriseus* is the more commonly displayed (Merchant and Calaby, 1981).

Around 150 zoos and aquaria operate as private businesses in Australia, as well as several large zoos that are at least partially funded from the public purse. These institutions range from poorly maintained zoos with pens and wire cages to larger and more modern examples containing well-maintained, naturalistic exhibits (Weigel, 1992). As well as variability in the type of housing provided to captive macropodoids, the sizes and composition of groups, times of feeding and the presence of visitors or members of other species may all differ from one institution to the next (Hosey, 1997). However, no systematic study has yet explained the implications of such differences for optimal husbandry of the subspecies in captivity.

1.4 Aim and scope of this project

This study examined the hypothesis that varying specific components of the captive environment will result in significant differences in the frequencies and durations of various elements of behaviour performed by members of captive groups and in the spatial utilisation of enclosures. The ultimate aim of the project was to propose principles of best practice for the captive management of Bennett's wallabies in zoos and wildlife parks.

In order to achieve this, an initial descriptive phase of the project was devised. A questionnaire was designed for delivery to zoos and wildlife parks throughout Australia, where, as previously mentioned, *M. r. rufogriseus* individuals are commonly exhibited (Merchant and Calaby, 1981; Fleming *et al.*, 1983). These institutions formed a resource from which information regarding the management of captive macropodoids could be solicited from industry experts. This information served two purposes. Firstly, it provided an understanding of what comprised the captivity environment for macropodoids, particularly the Bennett's wallaby, in currently operating zoos and wildlife parks. The type and range of these components could then be considered for inclusion in the experimental section of this study. Secondly, it provided a subjective assessment of the importance of the various components of the captivity environment, both in terms of the welfare of the captive animals and their successful management. This information was used to help determine which of these variables would be included in experimental investigations.

In order to achieve the central aim of this study, an understanding of the general and, in particular, social behaviour of the Bennett's wallaby was essential. Through the quantification of the frequencies and durations of individual behavioural elements, the effects of varying specific captivity conditions could be examined. Therefore, a preliminary step before undertaking experimental manipulations was the compilation of a comprehensive inventory of behavioural elements. In order to maximise the number of behavioural elements observed, observations of wild and captive individuals were utilised.

Following this, the effects of varying specific components of the enclosure environment were investigated through experimental manipulations of captive groups. Firstly, the effect of altering the number and position of feeding stations available to a captive group of Bennett's wallabies was quantified through the measurements of the frequencies with which particular behavioural units and categories of behaviour were observed, as well as the frequencies with which the various sectors of the enclosure were occupied.

The effect of varying stocking rates were also examined by measuring the frequencies and durations of the performance of key individual elements of behaviour, the frequencies with which behaviours belonging to various categories were observed and the frequencies with which individuals occupy the sectors of the enclosure.

Finally, the effects of varying the composition of groups of captive Bennett's wallabies was quantified to measure the effects of varying, firstly, the number of individuals from each age group and, secondly, the number of individuals of each sex included in the captive group.

By varying the conditions of captivity and measuring the responses of individuals to these changes, it may be demonstrated that management decisions can be based on behavioural measurements. In this study, these measurements were utilised in the formulation of specific management recommendations for keeping Bennett's wallabies in captivity in zoos and wildlife parks. Finally, management strategies that can be used to keep captive macropodoids for specified purposes, with particular regard to welfare considerations, have been proposed.

Chapter 2 General Materials and Methods

2.1 Study site

2.1.1 Location

All subjects used for observational or experimental studies were housed in enclosures at the University of Tasmania in Hobart. These were situated on Mt Nelson in Hobart's south. The enclosures were below a private road frequently used by pedestrians but separated from this by a 17 m wide band of vegetation, including adult eucalypts and thick shrub, as well as an 8.5 m wide firebreak.

2.1.2 Physical description - size, shape, vegetation

Two enclosures were utilised to house captive subjects. All experimental and observational investigations were conducted in one of these; this is referred to as the experimental enclosure. Animals not currently required for experimental or observational study were housed in the holding enclosure.

The experimental enclosure was roughly rectangular, 50 m long and approximately 20 m wide. One of the longer fence lines was not straight, as can be seen in Figure 2.1; this design arose from the necessity of fitting the fence around existing adult trees. The holding enclosure was rectangular in shape, 50 m long and 12 m wide.

Both enclosures contained natural vegetation. The northeastern areas had a mixture of saplings and adult eucalypts, as well as an understorey of fireweed and grass. In the southwestern localities, fewer adult trees and no understorey were present. However, grass was more abundant in this area.

Over the term of the project, the enclosure vegetation was heavily browsed by captive subjects. A sprinkler was employed irregularly to encourage regrowth.

2.1.3 Provision of food and water

Pasture replacement pellets and lucerne chaff were mixed together using a 5 L bucket in a ratio of five buckets of pellets to three of chaff and placed in feeding stations. These two ingredients were combined in this way to prevent wallabies preferentially consuming the pellets. The provision of food was arranged so that feed was always available and at least two feeding stations were always used. In

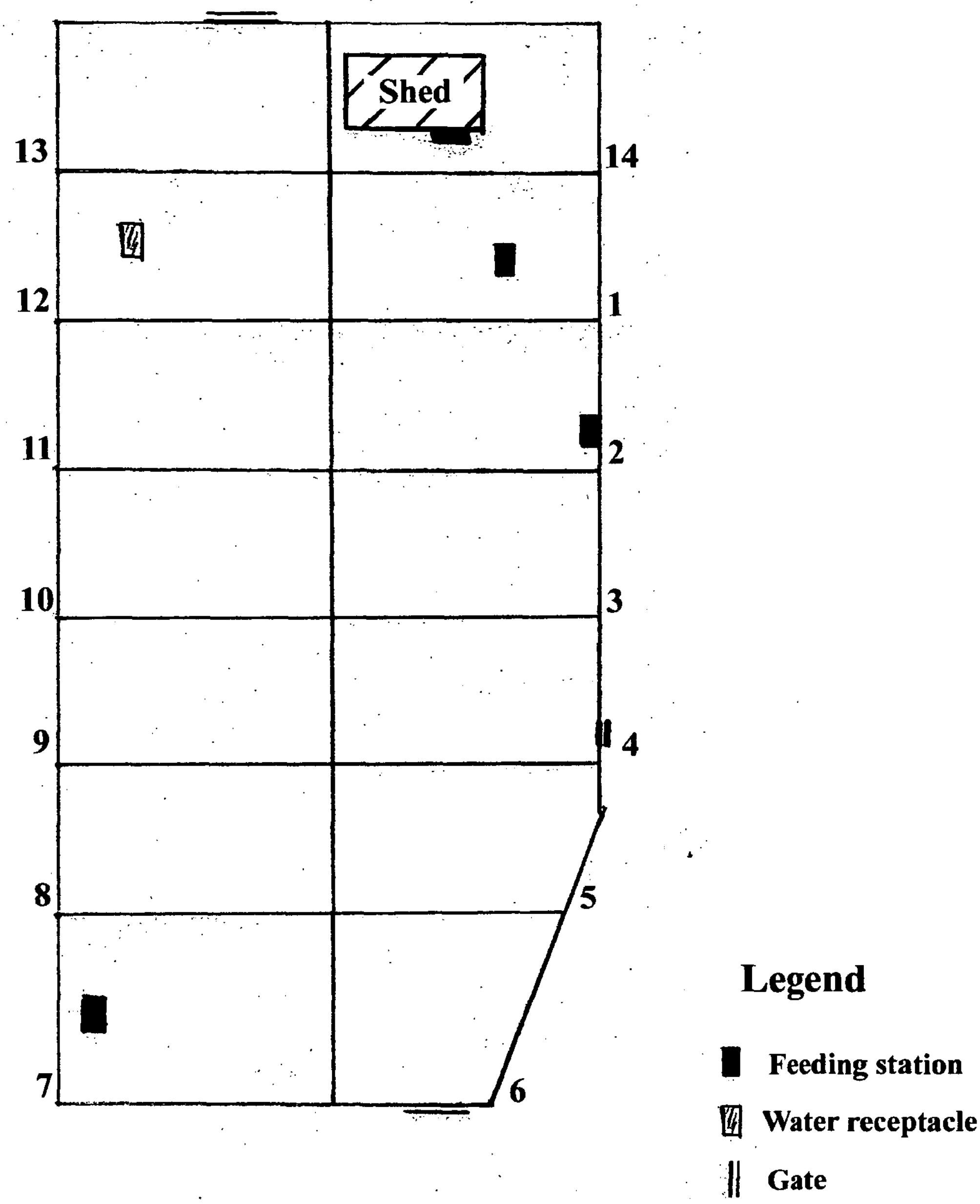


Figure 2.1: The experimental enclosure, showing the numbered sectors used for recording the location of individuals. Three gates were located in sectors 13, four and six. Feeding stations generally in use were located in sectors 14, two, four and seven. A water receptacle was located in sector 12.

addition, subjects were irregularly given apples, carrots, lettuce, cabbage or celery. Native browse was provided daily; initially subjects browsed on enclosure vegetation but once this was reduced, additional browse was collected and spread evenly through the enclosure.

Water was always available in a water receptacle, a bath tub sunk to ground level, in each enclosure. Water was checked daily and replenished as required.

2.1.4 Division into sections, observation site

The enclosure was divided into 14 roughly equal areas, the corners of which were denoted by wooden stakes. Reflective tape was tied around the top of each stake to make them more readily visible, especially after dark. These divisions are displayed in Figure 2.1.

All observations were made from within a shed in the southwest corner of the enclosure. A view of the rest of the enclosure was available from one window, with the exception of the area behind the shed, which was a patch of bare ground running to the fence line, angled from the shed, between 0.3 m and 1.3 m wide.

Spotlights were positioned in both windows of the shed, around a tree halfway down the slope of the enclosure and along the southeastern fence line. These were turned on before the end of daylight, so that this event was less detectable to the wallabies.

2.2 Subjects

Bennett's wallabies were acquired from three sources: trapping wild wallabies, donations of hand-reared animals from wildlife parks or carers and captive breeding.

2.2.1 Acquisition of *M. r. rufogriseus* individuals from external sources

Bonorong Wildlife Park provided three animals at the start of the project in 1996. All had been hand-reared by carers. Two of these were subadult males, approximately 7 months old, while the third was an adult female. The two males were transported inside hessian sacks by car and released into the enclosure. The adult female was transported inside the sleeping bag in which she had been brought to Bonorong Wildlife Park. An additional subadult female was acquired from another source in 2000; this animal had also been hand-reared. In each instance, wallabies were monitored after release into the enclosure shown in Figure 2.1 for signs of capture myopathy for a period of 2 h.

During two visits to Mr Herman Meyer's property at Kettering in southeastern Tasmania, additional animals were trapped from the wild, using a method similar to that described in Section 2.3. During the initial visit, five adult females were trapped and transported by car to the university in hessian sacks. On a subsequent visit in 1998, one adult male and one adult, one sub-adult and one juvenile female were trapped and transported. On each occasion, subjects were not sedated and were monitored for a period of 2 h after release into the enclosure at the university. No sign of capture myopathy was evident on any occasion. Handling was kept to a minimum; animals were sexed visually at a later date.

Whenever a new female subject was released into the existing captive population, males immediately approached her and attempted to inspect her pouch and anogenital region, presumably to assess her reproductive state. All males present in the group would engage in this activity concurrently. Young females or those who were relatively naïve in terms of female-male interactions, particularly hand-reared females, attempted to move rapidly away from approaching males and chases would ensue for periods of up to 20 min. During this period, females showed signs of distress, hopping rapidly in seemingly random directions so that, on occasion, they would collide with the fence, panting and licking their forelimbs and crouching in vegetation. When necessary, the observer approached the pursuing males until inside their flight zone; they then generally moved away before the observer reached the female's flight zone, so that she could rest for a few moments. Males resumed the chase within a minute of the observer leaving. Once males completed an inspection, they rapidly lost interest and moved away.

2.2.2 Captive breeding

Additional subjects were acquired through the breeding of experimental animals during the term of the project. All but one adult female of breeding age produced pouch young; the female that did not breed died suddenly at two years of age. As no post-mortem was conducted, it cannot be determined if her comparatively poor fertility was related to her early death. One wild-captured female had a chronic facial infection at the time of capture. Although it was successfully treated with antibiotics and surgery, she lost condition over the months of her illness and was eventually euthanased, her pouch young being placed with a wildlife carer. At the time of capture this individual had a non-emergent pouch young which subsequently disappeared. The following year her male offspring drowned in the water receptacle on an early excursion from the pouch;

the receptacle was subsequently filled with large rocks and a wooden frame with mesh attached up to a depth of 80mm below the surface of the water. Another adult female had a pouch young that disappeared from the enclosure; this offspring probably escaped through a depression at the base of the fence line.

Eight offspring survived to enlarge the captive group. During the first year that wallabies were stocked in the enclosure, one male and one female offspring emerged from the pouch and joined the captive group. The following year another male and female offspring emerged and were retained in the captive group. During the final year one male and three female offspring emerged and all except one of the captive females had new pouch young.

2.2.3 Disposal of experimental animals

At the end of all experimental investigations, all subjects were released onto the property of Mr Simon Talbot, with the following exceptions. One hand-reared female was placed in a soft-release program due to her lack of acquisition of predator-avoidance skills. The remaining subjects were transported over several nights by car, inside hessian sacks, to the release site. They were released near the border between the forest and paddock and rapidly made their way into the cover of the forest. Although no monitoring of animals that had been released was undertaken by the experimenter, most were reported by the land owner to feed in the paddock over subsequent weeks. They were distinguishable from wild animals by both the remainder of their ear tags, which were trimmed prior to release, and by their early emergence, in comparison to other resident Bennett's wallabies.

2.3 Trapping and handling subjects

A purpose-designed trap was developed and constructed to allow subjects to be captured and handled with speed and efficiency, reducing the incidence of handling stress that may lead to serious problems such as injuries or capture myopathy. This section has been written on the form of a note with the intention of submitting it to Australian Mammalogy.

The collection of biological data from captive animals usually requires that the animal be caught and handled. A variety of methods have been used to trap and immobilise free-ranging captive macropods; hand nets, trap yards, baited traps, cannon nets, drugged baits and syringe darts. The various methods differed with regard to the number of handlers required, the ability to selectively trap particular individuals and the frequency of injury resulting from trapping or handling (Coulson, 1996; Lentle *et al.*, 1997).

A successful method of live-trapping large wallabies is one that minimises injuries and the possibility of subsequent infection. Walker (1977) trialed several methods of trapping Bennett's wallabies in the wild, including the use of snares, funnel nets, corner traps and false-fence traps. During 610 nights of trapping covering six field sites, only 22 female and 36 male Bennett's wallabies were captured. The most successful traps were cages positioned at holes in the fence lines of several properties, with a chicken wire funnel leading to the fence hole. At least five animals caught using this method had to be euthanased due to injuries sustained in the traps (Walker, 1977). Bennett's wallabies have been noted to be especially susceptible to secondary infections from traumatic injuries, leading at times to severe pneumonia with multiple abscessation (Presidente, 1978).

In mammals, physiological stress associated with trapping can result in capture myopathy, a condition which can damage the skeletal and cardiac muscles and kidneys. Even when great care has been taken to prevent injuries during trapping, handling stress can still result in a sudden and rapid death (Shepherd, in Hand, 1995). Bennett's wallabies are particularly vulnerable to capture myopathy (Statham, pers. comm.); trapping must therefore be undertaken with speed and efficiency, with minimal handling.

When designing a trap for large wallabies, consideration must be given to maximising the probability that animals will initially enter the trap and will re-enter on subsequent occasions. Individual Bennett's wallabies have been shown to exhibit trap avoidance related to several factors, including the novel aspects of the trap, such as its shape and smell. Therefore: (1) any trap design must minimise the probability of wallabies injuring themselves whilst inside the trap and (2) wallabies must be permitted to familiarise themselves with the trap before trapping sessions so that they do not avoid it (Walker, 1977).

As part of this study, Bennett's wallabies were repeatedly trapped over a period of several years to permit physiological data to be collected. It was necessary to collect samples quickly for three reasons; to increase the validity of the data, to decrease the possibility of an animal developing capture myopathy and to prevent traumatic injuries. Using the method described below, wallabies were trapped and processed rapidly and with little disturbance, permitting blood and faecal samples to be collected and body weight to be measured.

The trap designed for this project, shown in Figure 2.2, was constructed from steel mesh 1500 mm long, 700 mm wide, 800 mm high and weighs 24 kg. It is portable and could be positioned on any relatively flat piece of ground. A detachable rectangular frame hooks on to the rear of the trap and supported a sack 1.8 m in length, made from 8 ounce canvas. A rope is threaded through belt loops, sewn in four equidistant positions around the end of the sack furthest from the trap, 150 mm from the edge, allowing the sack to be closed firmly. Four more belt loops were sewn around the opposite end of the sack 600 mm from the frame. A second piece of rope, 2.4 m in length, was threaded through here and tied off with a slip knot so that the sack could be quickly closed once the animal has entered from the trap.

The trap door was held open by a pin tied to a 15 m rope held by the observer. When the pin is pulled free, the door falls shut. It was prevented from reopening by a sliding bar which lays across the top of the door when open and falls to the ground when closed. Once trapped, the wallaby was encouraged into the sack by handlers standing alongside and, once it has entered, the slip knot is pulled tight to prevent it re-entering the trap. The frame could then be lifted off the trap. The wallaby may be examined and then released or transported while remaining in the sack. Alternatively, the rope around the back end of the sack could be untied to provide hand access, allowing transfer of the wallaby to a hessian sack to be transported.

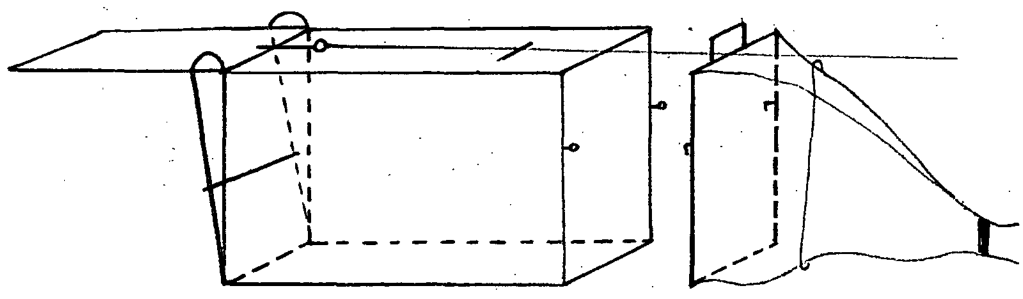


Figure 2.2: A diagrammatic representation of the trap designed for this study.

Using this method all wallabies from the captive group, male and female juveniles, subadults and adults, were trapped every three to four weeks over a three year period. These wallabies were free-ranging in the enclosure at the University of Tasmania, comprising of a 1000 m^2 of natural bush, included a thickly wooded section. In this enclosure, conventional trapping methods such as hand netting and fence line trapping were not effective.

Before commencing a trapping program, the trap was set each evening for several days with the detachable frame removed; this allowed the animals to become familiar with it. The trap was introduced into the enclosure during late afternoon. Individual wallabies approached and entered as soon as 10 min after it was first positioned within the enclosure. Food was placed in the trap to encourage wallabies to enter confidently. Although carrots, apples and native browse were all tried, pasture replacement pellets proved extremely attractive as bait and were less likely to be nudged against the walls of the trap, from where wallabies could eat them from the outside.

Trapping sessions were conducted over several consecutive nights every three to four weeks. Sessions began around dusk and continued until two or three animals were successfully trapped. Pellets were placed in the trap as bait; wallabies entered the trap and moved to the back end to feed. On some occasions, up to three animals occupied the trap at once, but usually more dominant individuals actively excluded subordinate animals until they had finished feeding. Once an animal entered the trap, the door was dropped and the handler moved immediately to encourage the animal into the detachable sack. Animals were then either transferred to a nearby, well-lit position while still in this sack or the far end was untied to allow the animal to be grasped by the tail and transferred to a hessian sack for further examination. Once transferred, wallabies were weighed and sexed. If blood or faecal samples were required, the end of the sack furthest from the trap was untied and the animal's tail was drawn through the opening; the handler knelt over the sack to immobilise the animal while grasping the tail. A section of skin near the base of the tail was shaved with a very sharp razor blade, swabbed with alcohol and blood drawn from the lateral tail vein using a 5 ml syringe with a 19 gauge needle. Faecal samples were collected by stimulating the wallaby's anus by hand. Once familiar with the techniques involved, all samples required could be collected within 3-4 minutes.

The Bennett's wallabies involved in this trapping program readily entered the baited trap and at times waited in the open trap for feed to be placed inside. On one trapping night, the dominant male in the captive group, was trapped three times within 2 h, each time re-entering the trap to feed. On the first trapping occasion, this individual was sexed and ear tagged, but this was not a sufficient deterrent to discourage re-entry. No injuries were caused by any trapping event during this study.

The trapping method described here has proved to be very successful for handling *M. r. rufogriseus* individuals. Bennett's wallabies have been noted previously to thrash about inside traps, injuring themselves seriously and, at times, fatally (Walker, 1977). The main section of the trap described here is large enough to ensure that wallabies demonstrated no signs of panic from being enclosed, as can be seen from Plate 2.1 below. Wallabies entering the trap to feed seemed unconcerned when the trap door closed and continued to feed until approached by handlers.

The transfer of an animal into the canvas sack generally happened swiftly, within 2-3 min, as did the further transfer to a hessian sack when required. Handling stress, which can lead to capture myopathy and death, was therefore held to a minimum.

Plate 2.1: The trap used in the current study, shown readied for use. The trap door is propped open and can be closed by pulling the rope, which has been braced around the tree behind the trap. The detachable frame at the rear of the trap has been tied off furthest from the main body of the trap and left open nearest the trap so that a wallaby can enter from the main section.

These short handling times also increased the validity of a study of the stress physiology of these animals, using blood samples including concentrations of cortisol and glucose in the blood.

Trap avoidance did not occur at levels that interfered with the trapping program until stocking rates had decreased to three animals per 1000 m^2. Trap avoidance appeared to be related to a general increase in nervousness rather than a fear of entering the trap itself. At this time these wallabies not only avoided the trap, but also open areas, emerging from cover an hour or more later than usual in the evenings. They were also more likely to assume alert postures or suddenly and rapidly return to cover more frequently than at higher stocking rates. When higher numbers were present, individual animals readily entered one or more times a night. Typically, between one and five animals could be trapped and processed during the same session.

Thus, the key to the successful live capture of large wallabies appeared to be careful planning to prevent injuries and stress, with direct handling held to a minimum. The trap described above permits the live-capture and re-capture of large wallabies, and the subsequent collection of biological samples, safely and reliably.

Chapter 3 Questionnaires

3.1 Introduction

3.1.1 The zoo environment

The zoo environment can differ greatly from the natural habitat of a species. As a result, the behavioural repertoire expressed by captive individuals may also differ greatly from that of wild conspecifics. The degree to which this occurs is affected by a number of factors, including the circumstances of development, genetics and the physical structure of the enclosure (Carlstead, 1996). Over recent years, concerns about the welfare of captive individuals have become both a focus of scientific investigation and the subject of public interest that effect the formulation of management policies for enclosure design and the husbandry of captive individuals (Fraser *et al.*, 1997; de Courcy, 1999).

Approximately 10,000 zoos exist worldwide (de Courcy, 1999). Over the past two and a half centuries, the modern zoo has evolved to serve four main purposes: conservation; education; research and recreation (Jakob-Hoff, 1992; de Courcy, 1999). Contributions to conservation are made by the modern zoo through researching and sharing information about the general biology, husbandry and veterinary care of their captive species and by creating a resource of skilled workers in these fields (Mumaw, 1992). As well as funding and undertaking research projects, valuable knowledge is gained and recorded simply through the daily activity of zookeepers (Denney, 1996).

Today's zoo visitors are better informed about the general biology of captive species from sources such as wildlife documentaries on television (Croke, 1997) and their schooling (Hopkins, 1992) and more sophisticated in their expectations of exhibits (Wallberg, 1999). As visitors become more informed, sentiment about the conditions of captivity to which animals are subjected strengthens; this has become a force of change over the past half a century (de Courcy, 1999). Subsequently, naturalistic and enriched zoo environments are more frequently seen, although this does not yet describe all exhibits (Croke, 1997). As a result of such changes, there has been an increase in the number of institutions that maintain a smaller number of species in more complex enclosures, and other trends, such as an increasing prevalence of non-breeding groups are evident (Hosey, 1997). By considering the effects of the physical environment of captive individuals and husbandry methods employed, such as the timing of feeding, boredom and abnormal behaviours can be minimised (Murray, *et al.*, 1998).

However, concerns expressed by zoo visitors and the desire to fulfill educational imperatives can have conflicting effects on the modifications of zoo enclosures for welfare purposes. For example, captive predators may be provided with live prey as an enrichment tool, but this practice would almost certainly result in negative feedback from visitors (Robinson, 1998). The practice of providing chimpanzees with destructible items for enrichment purposes provoked complaints about the cleanliness of the enclosure at Edinburgh Zoo (Murray *et al.*, 1998). Such negative impressions engendered in zoo visitors detract from the impact of conservation and other educational messages. Visitors are attracted to naturalistic exhibits where individuals have room to explore and exhibit a wide range of behaviours from their repertoires. However, functional substitutes are not always acceptable to the visiting public who may harbour misconceptions about what comprises normal or abnormal behaviour and what stimuli will satisfy the various motivational drives of captive individuals. In order to maximise welfare considerations, it is increasingly necessary to combat public misconceptions (Robinson, 1998).

3.1.2 Animal welfare in zoos

Over recent decades, zoos have placed a greater importance on the welfare of animals exhibited (Wallberg, 1999). Animals that do not thrive in a zoo environment can demonstrate a variety of obvious symptoms, including hyperphagia, autophagia, over-sleeping, compulsive over grooming, increased levels of aggressive behaviour, anorexia, failure to reproduce, poor parenting skills and self-mutilation. Other, not so obvious, symptoms of poor welfare are increases in pathological problems and elevated levels of stress hormones (Hurst *et al.*, 1999).

Both the physical structure of enclosures and the range of activities animals are provided with the option of participating in are two critical factors in providing an adequate environment for captive animals (Croke, 1997). Environments that are unchanging, characterised by routine, (for example, the consistently timed provision of feed) and socially isolating can result in stereotyped behaviours (Glickman and Sroges, 1965). Captivity environments should permit animals to exhibit behaviours that are normal for members of the species existing in their natural habitat; these include maternal behaviour, communication and anti-predator behaviour (Croke, 1997).

Injuries and death can result from inappropriate social structures in captive populations. A population of yellow-footed rock-wallabies, *Petrogale xanthopus,* bred in captivity in Canberra over 13 years produced at least 68 offspring. However, during this period mortality was high, with one of the major reasons for this being fighting between captive individuals (George, 1990). Calaby and Poole (1971) noted that among the various macropod species maintained in captivity, the success of captive breeding was high when groups included only a single male. When multiple males were present within a breeding group, fighting and at times fatal injuries occurred and reproductive success was lowered.

3.1.3 Considerations for enclosure designs for captive macropods

When designing macropod enclosures, a number of important factors must be considered. These include the provision of feed, water, rest areas, shelter from the weather and space (Finnie, 1982; Williams, in Hand, 1995; Poole, 1982). The probability of macropods suffering from disease can be increased by stress and unhygienic conditions within an enclosure environment. Stressors may include an insufficient number of resting sites and shelter or the inability of macropods to access feeding stations (Finnie, 1982). Further, enclosure design should permit macropods to move away from a source of disturbance; this can be facilitated both through the enclosure size and by planting quick-growing shrubs as a barrier. However, several species, including *M. rufogriseus,* are efficient browsers, so that shrubs will usually need to be protected from browsing activity (Poole, 1982).

Another design feature to be considered if injuries are to be minimised is fence construction. Circular enclosures, lacking corners, may assist in this regard, although this must be balanced against the constraints of the location of the enclosure within the zoo. Ensuring straining wires are adequately spaced reduces the probability that macropods will become entangled and also minimises injuries. Fence material should continue underground to prevent animals digging underneath and escaping or pests entering (Williams, in Hand, 1995). Historically, enclosures have been constructed from surfaces that are hard, uniform and easy to clean. These surfaces can give rise to behavioural problems, physiological stress and disease (Croke, 1997). Correct substrate choice can also reduce injuries, while hard surfaces can result in tail and hind limb injuries (Williams, in Hand, 1995).

Other welfare concerns that should be covered by management strategies are the reduction of injuries and illness. Injuries can result from the necessity of trapping and handling animals. For example, agile wallabies, *M. agilis,* have been noted to run with an upright posture in close proximity to fence lines during trapping exercises with the result that the lips and nostrils can be caught and injured on the fence (Calaby and Poole, 1971). Many of the large macropod species can be difficult to maintain in captivity if they were originally wild-caught. Normal handling activities can lead to frequently fatal injuries from collisions with fences (Calaby and Poole, 1971; Keep, 1976).

It can be seen that for a wildlife park or zoo to consider their management strategies for captive macropods to be successful, a number of factors must be taken into consideration and balanced against one another, in order that welfare considerations are adequately addressed and the educational purposes of the institutions are met. As a result, a number of conditions of captivity must be incorporated in a management plan, including various physical aspects of the enclosure, the construction of captive groups and husbandry methodologies.

Prior to designing the experimental manipulations that would form part of the present study, a questionnaire was mailed to zoos and wildlife parks across Australia and in New Zealand. The purpose of this was threefold. Firstly, it provided a tool to gather information about the species of macropods and the numbers of each of these, particularly the Bennett's wallaby, held in captivity. Secondly, information on the composition of captive groups could be collected regarding the sexes, ages and species of individuals present and various other conditions of captivity in which they are maintained. Finally, current macropod managers could be requested to nominate any issues related to maintaining Bennett's wallabies in captivity that they considered to be of key importance. This information was synthesised to provide:

1) A general review of current practices in husbandry of captive macropods in Australasian zoos and

2) The basis of the design of experiments in which the behavioural responses of Bennett's wallabies to manipulation of the captive environment were investigated (refer Chapters 5, 6 and 7).

3.2 Materials and Methods

3.2.1 Selection of zoos and wildlife parks to be surveyed

Questionnaires were sent to 100 wildlife parks and zoos in all states and territories of Australia in order to maximise the number of responses received and to cover as large a variety of institutions as possible. Parks and zoos were selected from several sources: Yellow Pages advertisements; RACV Accommodation Australia; Accommodation Guide, the "Rough Guide to Australia"; the Tasmania Book and tourist brochures.

The questionnaire was mailed out with a cover letter. The name of the recipient park or zoo was printed at the top of each survey so that they could be identified upon return. A reply-paid, self-addressed envelope was also included, to encourage recipients to respond. Zoos and parks that did not return their questionnaires were not mailed again, but staff were occasionally contacted directly, either in person, by telephone or via email, and requested to provide verbal responses.

3.2.2 Design of the Questionnaire

The questionnaire was designed to collect information on particular issues. These were -

1) Which macropod species are held in captivity,
2) the sexes and ages of the animals in the captive groups
3) the captive conditions of these animals and
4) the key issues in managing captive macropods, in the opinion of current managers.

The questionnaire was made as brief (2 ½ pages) and easy to complete as possible in order to encourage responses. For example, the first question asked for a list of species held in the park or zoo. Provision was made to list these alongside a pre-completed list of reference numbers that could be used to answer further questions about the group composition of each of these species.

The complete questionnaire is presented in Appendix 1.

3.3 Results

3.3.1 Respondents to the Questionnaire

A total of 32 wildlife parks and zoos (Appendix 2) responded to the questionnaire. Responses were received from institutions in all states and the Northern Territory. As well, two zoos from the north island of New Zealand were included.

3.3.2 Responses to the Questionnaire

Responses to each question are listed separately.

3.3.2.1 Question 1 What kangaroo and wallaby species do you have?

The information in Tables 3.1 and 3.2 summarises the information contained in Appendix 3, which contains the complete list of macropodoid species held by each wildlife park or zoo. The number of species from the Macropodoidae held by individual institutions varied from 1 (Mogo Zoo) to 16 (Melbourne Zoo). The mean number of species held was 6.3. A total of 34 macropodoid species were maintained in collections by the responding zoos and wildlife parks. Of these, the most commonly held were red kangaroos, *Macropus rufus,* (22 parks), Bennett's and red-necked wallabies (20 parks) and eastern grey kangaroos, *M. giganteus,* (20 parks). Swamp wallabies, *Wallabia bicolor,* were also commonly reported to be exhibited (15 parks), while species such as the black wallaroo, spectacled hare-wallaby, bridled nailtail wallaby, black-footed rock-wallaby, short-eared rock-wallaby and narbalek were present in the lowest numbers (one park per species).

Of the 20 institutions that reported holding stock of *M. rufogriseus*, nine kept the subspecies *Macropus r. rufogriseus*, the Bennett's wallaby, while the remaining 11 had individuals from the subspecies *M. r. banksianus*, the red-necked wallaby.

Table 3.1: The numbers of wildlife parks and zoos that held species from the Superfamily Macropodoidea, in decreasing order of frequency.

Species Name	Common Name	No. of Zoos and Parks
Macropus rufus	Red kangaroo	22
M. rufogriseus	Bennett's/red-necked wallaby	20
M. giganteus	Eastern grey Kangaroo	20
Wallabia bicolor	Swamp wallaby	15
M. fuliginosus	Western grey kangaroo	13
M. robustus	Common wallaroo/euro	12
M. parma	Parma wallaby	9
M. eugenii	Tammar wallaby	7
Petrogale xanthopus	Yellow-footed rock-wallaby	7
Thylogale billardierii	Tasmanian pademelon	7
M. parryi	Whiptail wallaby	6
M. dorsalis	Black-striped wallaby	5
M. agilis	Agile wallaby	5
Potorous tridactylus	Long-nosed Potoroo	5
T. thetis	Red-necked pademelon	5
Setonix brachyurus	Quokka	5
T. stigmatica	Red-legged pademelon	4
Dorcopsis luctuosa	Grey dorcopsis	4
M. antilopinus	Antilopine wallaroo	3
Bettongia penicillata	Brush-tailed Bettong	3
Aepyprymnus rufescens	Rufous bettong	3
Dendrolagus goodfellowi	Goodfellow's Tree-kangaroo	3
B. gaimardi	Tasmanian bettong	2
B. lesueur	Burrowing bettong	2
Lagorchestes. hirsutus	Rufus Hare-wallaby	2
Onychogalea unguifera	Northern Nailtail wallaby	2
D. matschiei	Matschie's Tree-kangaroo	2
M. bernardus	Black wallaroo	1
L. conspicillatus	Spectacled Hare-wallaby	1
O. fraenata	Bridled Nailtail wallaby	1
Petrogale lateralis	Black-footed rock-wallaby	1
P. penicillata	Brush-tailed rock-wallaby	1
P. brachyotis	Short-eared rock-wallaby	1
Peradorcas concinna	Nabarlek	1

Table 3.2: The total number of macropodoid species held by each zoo or wildlife park.

State/Territory	Wildlife Park or Zoo	No. of Species Held
Tasmania	Bonorong Wildlife Park	5
Tasmania	Talune Wildlife Park	4
Tasmania	Trowunna Wildlife Park	4
Tasmania	Zoo Doo	2
Victoria	Ballarat Wildlife and Reptile Parl	3
Victoria	Currawong Bush Park	3
Victoria	Gumbuya Leisure Park	7
Victoria	Healesville Sanctuary	9
Victoria	Melbourne Zoo	16
Victoria	Werribee Zoo	3
New South Wales	Birdland Animal Park	4
New South Wales	Coffs Harbour Zoo	8
New South Wales	Mogo Zoo	1
New South Wales	Taronga Zoo	10
New South Wales	Western Plains Zoo	9
Queensland	Currumbin Sanctuary	12
Queensland	Fleays Wildlife Park	10
Queensland	Lone Pine Koala Sanctuary	4
Queensland	Qld Reptile and Fauna Park	5
Queensland	South Bank Parklands	8
Northern Territory	Territory Wildlife Park	9
Western Australia	Bannamah Wildlife Park	7
Western Australia	Caversham Wildlife Park and Zoo	11
Western Australia	Greenough Wildlife & Bird Park	3
Western Australia	Perth Zoological Gardens	10
South Australia	Adelaide Zoo	10
South Australia	Cleland Wildlife Park	7
South Australia	Dundee's Wildlife Park	3
South Australia	Monarto Zoological Park	2
South Australia	Urimbirra Wildlife Park	9
New Zealand	Auckland Zoological Park	2
New Zealand	Wellington Zoological Gardens	2

3.3.2.2 Question 2 Do you hold each species in separate enclosures?

Responses to this question are detailed in Appendix 4. The majority of enclosures (21 out of 30) in responding zoos and wildlife parks housed several species together. Only four institutions maintained both enclosures containing a single species and those with multiple species co-habiting. These were Melbourne Zoo (16 species, 95 individuals), Adelaide Zoo (10 species, 58 individuals), South Banks Parklands (eight species, 46 individuals) and Bannamah Wildlife Park (seven species, 31 individuals).

3.3.2.3 Question 3 If not, which species do you keep together?

The various species that are housed within multi-species enclosures were sought with this question. The groups of species held together are listed below in Table 3.3. The number of species held within a single enclosure varied from 2 to 6, with the mean being 3. The species most commonly sharing enclosures with other species were *M. rufogriseus* (13 enclosures), *M. giganteus* (11 enclosures) and *M. rufus* (8 enclosures). Nine of the thirteen collections of *M. rufogriseus* in multi-species enclosures contained the subspecies *M. r. rufogriseus.*

Table 3.3: Species housed together within a single enclosure.

Respondents	Species
Bonorong Wildlife Park (Tas)	*M. r. rufogriseus, M. giganteus* and *T. billardierii.*
Talune Wildlife Park (Tas)	*M. giganteus* and *M. r. rufogriseus.*
	M. r. rufogriseus and T. billardierii.
Trowunna Wildlife Park (Tas)	*M. giganteus, T. billardierii* and *M. r. rufogriseus.*
Currawong Bush Park (Vic)	*W. bicolor, M. giganteus* and *M. eugenii.*
Gumbuya Leisure Park (Vic)	*M. giganteus* and *M. fuliginosus.*
Healesville Sanctuary (Vic)	*M. rufus, M. giganteus* and *M. robustus.*
	M. parma, M. r. rufogriseus, P. penicillata, T. billardierii and *W. bicolor.*
Melbourne Zoo (Vic)	*M. dorsalis* and *M. r. rufogriseus.*
	D. goodfellowi, D. luctuosa and *T. stigmatica.*
Werribee Zoo (Vic)	*M. rufus, M. giganteus* and *M. r. rufogriseus.*
Coffs Harbour Zoo (NSW)	*M. r. rufogriseus, M. parma, M. eugenii* and *W. bicolor.*
Fleays Wildlife Park (Qld)	*M. dorsalis* and *M. giganteus.*
	M. r. banksianus, M. agilis, M. rufus and *W. bicolor.*
Queensland Reptile and Fauna Park (Qld)	*M. rufus, M. giganteus, M. parryi, M. r. rufogriseus* and *M. dorsalis.*
Southbanks Parklands (Qld)	*M. r. banksianus, M. dorsalis, W. bicolor, M. parma, M. giganteus* and *M. parryi.*
Territory Wildlife Park (NT)	*M. agilis, M. robustus* and *M. bernadus.*
	M. rufus and *M. antilopinus.*
Bannamah Wildlife Park (WA)	*M. rufus, M. fuliginosus* and *M. robustus.*
Greenough Wildlife and Bird Park (WA)	*M. rufus, M. fuliginosus* and *M. robustus.*
Perth Zoo (WA)	*M. rufus* and *M. fuliginosus.*
	P. xanthopus and *M. robustus.*
Cleland Wildlife Park (SA)	*M. fuliginosus* and *M. eugenii*
	M. robustus and *P. xanthopus*
Dundee's Wildlife Park (SA)	*M. rufus, M. parma and W. bicolor.*
Urimbirra Wildlife Park (SA)	*M. giganteus, M. eugenii* and *T. billardierii.*
	M. fuliginosus, M. eugenii and *T. billardierii.*
	M. rufus, M. parma, M. eugenii, W. bicolor and *M. r. banksianus.*
Auckland Zoo	*M. r. banksianus* and *M. parma*

3.3.2.4 Question 4 How many of each species do you have?

The numbers of individuals belonging to each species held by each wildlife park or zoo are displayed in Appendix 5. The mean number of macropodoid individuals held in a zoo or wildlife park was 62 and the range was from 3 (Mogo Zoo) to 223 (Currumbin Sanctuary) animals. The total numbers of individuals of each species across the 32 responding institutions are displayed in Table 3.4.

The numbers of individuals of the various species held by each of the responding wildlife parks and zoos ranged from 332 eastern grey kangaroos to one spectacled hare-wallaby and one narbalek. The average number of individuals from the one species held in captivity was 58. After the eastern grey kangaroo, the next most populous species held *in toto* were *M. rufus* (267 individuals) and *M. rufogriseus* (225 individuals). Of the latter, 150 were members of the subspecies *M. r. rufogriseus.*

Table 3.4: The combined total numbers of individuals of each species held by respondents, in decreasing order of frequency.

Common Name	Species name	No. of individuals.
Eastern grey kangaroo	*M. giganteus*	332
Red kangaroo	*M. rufus*	267
Western grey kangaroo	*M. fuliginosus*	253
Red-necked and Bennett's wallabies	*M. rufogriseus*	225
Euro	*M. robustus*	153
Swamp wallaby	*W. bicolor*	121
Yellow-footed rock-wallaby	*P. xanthopus*	105
Tasmanian pademelon	*T. billardierii*	80
Tammar wallaby	*M. eugenii*	68
Parma wallaby	*M. parma*	54
Quokka	*S. brachyurus*	51
Whiptail wallaby	*M. parryi*	34
Antilopine wallaby	*M. antilopinus*	33
Red-necked wallaby	*T. thetis*	27
Red-legged pademelon	*T. stigmatica*	21
Agile wallaby	*M. agilis*	19
Black-striped wallaby	*M. dorsalis*	17
Rufus hare-wallaby	*L. hirsutus*	16
Brush-tailed bettong	*B. penicillata*	15
Grey dorcopsis	*D. luctuosa*	15
Burrowing bettong	*B. gaimardi*	14
Matschie's tree-kangaroo	*D. matschiei*	12
Long-nosed potoroo	*P. tridactylus*	11
Goodfellow's tree-kangaroo	*D. goodfellowi*	9
Rufous bettong	*A. rufescens*	6
Northern nailtail wallaby	*O. unguifera*	6
Black wallaroo	*M. bernardus*	4
Black-footed rock-wallaby	*P. lateralis*	4
Brush-tailed rock-wallaby	*P. penicillata*	4
Bridled nailtail wallaby	*O. fraenata*	3
Short-eared rock-wallaby	*P. brachyotis*	2
Burrowing bettong	*B. lesueur*	2
Spectacled hare-wallaby	*L. conspicillatus*	1
Narbalek	*P. concinna*	1
Total macropodoid individuals		**1984**

3.3.2.5 Question 5 How many of the adult animals are male and how many female?

Of the 168 collections of the various species described in the responses to this questionnaire, 36% were composed of either an even number of males and females or a difference of no more than one. A further 35% comprised mixed-sex collections in which more females than males were present. Only 8% of mixed-sex collections contained a greater number of males than females. Single sex collections of females accounted for 13% of the total, while male-only collections accounted for 8%. Of the nine collections of Bennett's wallabies, two had an approximately even number of males and females, two had only females and the remaining five contained more females than males. In addition, seven collections of red-necked wallabies were reported. Four of these contained an even number of males and females, while three had more females than males. The total numbers of males and females of each species held in captivity at each institution are listed in Appendix 6.

3.3.2.6 Question 6 Are your animals breeding?

Of a total of 192 collections of all species and subspecies compiled from responses from all zoo and wildlife parks, 120 (63%) contained animals that were breeding, 66 (34%) contained no animals that were reproducing and the breeding status of seven (3%) could not be ascertained. The three species nominated earlier as the most populous in captivity, *M giganteus, M. rufogriseus* and *M. rufus* had varying numbers of breeding collections in existence. Nine out of 19 collections of eastern grey kangaroos contained breeding individuals, while nine did not and the breeding status of one group could not be determined. Similarly, nine collections of red kangaroos contained animals that were reproducing, seven did not and one could not be determined. All but one of the populations of *M. r. rufogriseus* contained animals that were reproducing, while the breeding status of the last collection not determined. Seven of the ten collections of *M. r. banksianus* contained breeding animals. Another three were not breeding groups and the status of the final collection could not be determined. The responses for all institutions are displayed in Appendix 7.

3.3.2.7 Question 7 Approximately how many of your animals are adults, how many weaned juveniles, how many young-at-foot and how many are pouch young?

No clear trend in the age composition of captive groups was evident; indeed, a great many different types of groups were reported. Detailed responses are provided in Appendix 8.

3.3.2.8a Question 8a From where do you acquire your animals?

In total, 32 responses to this question were received; these are detailed in Appendix 9 and summarised here. The greatest source of new stock was through the purchase or trading of animals between institutions, a practice in which 20 respondents participated. Captive breeding provided additional stock for 16 of the respondents. Donations of orphaned or injured wildlife increased the existing collections at an additional 13 parks and zoos.

3.3.2.8b Question 8b How do you deal with excess stock?

Information about methods employed for removing excess stock was received from 27 wildlife parks and zoos. Trading and selling excess wildlife was a common solution for the wildlife parks and zoos responding to this question; 20 participated in the practice. Ten institutions participated in culling excess stock, while controlled breeding through methods such as vasectomising males was employed by three parks or zoos. Animals were released into the wild, at times as part of repopulation plans, or with the assistance of carers, from six parks and zoos. This information is summarised in Table 3.5. Detailed responses are presented in Appendix 10.

Table 3.5: Summary of methods of controlling excess stock.

Method of control	**No. of parks or zoos utilising this method**
Trading with other institutions	20
Culling	10
Release into the wild or a sanctuary	6
Vasectomies	3
Managing intake of new stock	2
Self-regulation (death resulting from agonistic interactions)	1

3.3.2.9 Question 9 How big are the enclosures and what are their shapes?

Descriptions of enclosures were provided by 25 parks and zoos. The information obtained is provided in Appendix 11. Macropod enclosures occurred in a large variety of shapes and sizes, from square, rectangular, diamond and oval to irregular. Sizes varied from smaller enclosures, especially for smaller species, to large areas where medium to large wallabies and kangaroos free-ranged.

3.3.2.10 Question 10 Are the enclosures of the look-in (where visitors are excluded from the enclosure) or walk-through (where visitors may enter the enclosure) type?

The total number of enclosures that visitors could enter (44) was similar to that to which entry was prohibited (48). The total number of institutions that had both types of enclosures was also similar to the number that had only one type present; 12 compared to 14. However, of the 14 parks and zoos with enclosures that fell into only one of these categories, Mogo Zoo, Fleay's Wildlife Park and Zoo Doo were the only respondents that only maintained enclosures from which visitors were excluded. Mogo Zoo had only 3 hand-reared Eastern Grey kangaroos. Zoo Doo has a policy of minimising interactions with the general public. The other eleven institutions had only enclosures where visitors could interact with individuals on exhibit. This information is detailed in Appendix 12.

3.3.2.11 Question 11 Can visitors feed the animals?

Responses to this question are detailed in Appendix 13. Feeding of macropodoids in parks and zoos by visitors was a common practice, engaged in by 63% (18 out of 29) of the respondents.

3.3.2.12 Question 12 What do the animals eat (plants growing in the enclosure, feed from feeders, other)? and

3.3.2.13 Question 13 If fed by you, what are the animals fed, how frequently are they fed and what time if day are they fed?

Enclosure vegetation was available as a source of food at all but two (Birdland Animal Park and Bannamah Wildlife Park) of the responding parks and zoos. A variety of other types of feed were also given to captive macropods, including macropod pellets, hay, chaff, fruit, vegetables and native browse.

Feeding regimes generally comprised once or twice daily feeds in the early morning or evening. Specific food types were often provided at different times. For example, at Melbourne Zoo, enclosure vegetation and hay were available at all times, while pellets, vegetables and maize were provided in afternoon feedings and, finally, Vitamin E supplements were given weekly. At Currawong Bush Park, animals had constant access to enclosure vegetation and lucerne stick cubes, with additional feeds of maize either early or late in the day. Information about the diets and feeding regimes of captive macropods maintained by the respondents is summarised in Table 3.6 over the page.

Table 3.6: The types of feed provided to captive macropods and feeding regimes employed. Institutions are listed by state.

Wildlife Park/Zoo	Type of feed provided	Feeding regime
Bonorong Wildlife Park	Enclosure vegetation. *M. giganteus* and *M. rufogriseus* fed corn and pellets and vegetables when available. *B. gaimardi* and *P. tridactylus* fed grasses, pellets, corn, carrots, apples, pears, pumpkin and rice crackers.	8:30am feeds daily.
Talune Wildlife Park	Enclosure vegetation, feed.	Approximately 2 buckets of feed per day, one morning, one evening
Trowunna Wildlife	Enclosure vegetation, feed.	-
Zoo Doo	Enclosure vegetation, lucerne chaff, apples, carrots, other green vegetables, fruit, macropod pellets.	Evening feeds each day.
Ballarat Wildlife and Reptile Park	Enclosure vegetation and other feed.	
Currawong Bush Park	50% enclosure vegetation, 50% feed, seasonal supplements.	Daily feeds of maize early morning or late evening. Constant supply of lucerne stick cubes.
Gumbuya Leisure Park	Enclosure vegetation, lucerne chaff, crushed wheat and oats, some prepared pellets.	4pm feeds of lucerne chaff, crushed wheat and oats and pellets.
Healesville Sanctuary	Enclosure vegetation, lucerne hay, macropod pellets, fresh browse, maize and fresh vegetables.	Daily, usually morning feeds.
Melbourne Zoo	Enclosure vegetation, meadow hay, fresh browse occasionally eucalypt branches, lucerne, continual access to mineral lick.	Continued access to meadow hay. Afternoon feeds of macropod pellet mix, apple and carrot mix, dried maize and greens. Vitamin E supplement once per week.

Wildlife Park/Zoo	Type of feed provided	Feeding regime
Werribee Zoo	Enclosure vegetation, 8kg of horse/pony pellets, .5kg lucerne chaff, 8kg 2nd grade lucerne hay.	Morning feeds of pellets, chaff and hay.
Birdland Animal Park	Lucerne hay, pellets, wheat, oats.	Constant access to hay. 4pm feeds of oats, wheat and pellets.
Coffs Harbour Zoo	Enclosure vegetation, feed	Morning feeds of 1 or 2 biscuits of hay, 2 litre pans of pellets and one third of a bucket of chopped apple, carrots, banana, broccoli
Mogo Zoo	Enclosure vegetation, lucerne hay, clover hay, mixture of coprice pellets and 15% stud mix.	Visitors feed through the day. Night feeds of hay and pellets.
Fleays Wildlife Park	Enclosure vegetation, feed.	-
Lone Pine Koala Sanctuary	Enclosure vegetation, feed, other.	-
Qld Reptile and Fauna Park	Enclosure vegetation, small amounts of bread (monitored), parrot mix and lucerne.	Morning and afternoon feeds of parrot mix and lucerne. 11:30am feeds of a small amount of bread.
South Bank Parklands	Enclosure vegetation, feed, lucerne hay, chaff, macropod pellets, root vegetables, leafy vegetables.	-

Wildlife Park/Zoo	Type of feed provided	Feeding regime
Territory Wildlife Park	Native shrubs and grasses in the exhibit, horse nuts (16% protein), lucerne chaff, carrots and apples. Adult *M. rufus* offered a milk supplement of Divetelact once daily as they need a highly digestible protein supplement to survive the wet season.	Daily checks, top-ups as required of horse cubes, lucerne chaff, chopped apple and chopped carrot. 1 piece of bread daily per animal to allow check-ups.
Bannamah Wildlife Park	Modified deer mix containing barley, oats, lupins, pony pellets, goat muesli, chaff. Also, hay and vegetables.	Morning feeds of deer mix. Hay and vegetables ad lib.
Caversham Wildlife Park and Zoo	Enclosure vegetation, lucerne chaff, macropod cubes, maize, oaten hay.	Daily.
Greenough Wildlife & Bird Park	Enclosure vegetation, hay, chaff, cattle nuts, tree cuttings.	Morning and night feeds.
Cleland Wildlife Park	Enclosure vegetation and macropod pellets in hoppers.	Hoppers filled with macropod pellets in bulk.
Dundee's Wildlife Park	Enclosure vegetation, vegetable matter, lucerne chaff.	Generally feed in the late morning.
Urimbirra Wildlife Park	Enclosure vegetation and supplemental feed consisting of low protein pellets, apples, carrots and maize.	Early morning and late afternoon or evening feeds are provided to supplement enclosure vegetation depending on the weather and season.
Auckland Zoo	Enclosure vegetation, hay, vegetables and wallaby pellets.	Morning feeds of raw sweet potato, potato and silverbeet are provided. Wallaby pellets sprinkled with Vitamin E are always available. Carrots and celery are scattered around the enclosure

3.3.2.14 Question 14 Are animals added or removed from the enclosure/s (e.g. separating females with young)?

The composition of captive groups of macropods was manipulated as part of the management strategies at 13 out of the 22 responding parks and zoos, with Monarto Zoological Park indicating that they may also adopt this practice in the future. Only Gumbuya Leisure Park stated that they added animals to existing groups. Other respondents generally removed males to limit aggressive interactions, manage stocking rates and control breeding. Responses to this question are presented in Table 3.7.

Table 3.7: Zoos and wildlife parks that add or remove animals as part of their management strategies.

Wildlife Park/Zoo	Response
Bonorong Wildlife Park (Tas)	Male *B. gaimardi* individuals are held separately to prevent fighting. Juvenile male *M. rufogriseus* are removed occasionally to reduce mortality from fighting.
Talune Wildlife Park (Tas)	No.
Trowunna Wildlife Park (Tas)	Orphaned juveniles held separately to free-ranging adults.
Zoo Doo (Tas)	Younger animals are held in pens with smaller gauge fence material and then moved when they have grown too large to escape alternative enclosures.
Currawong Bush Park (Vic)	No.
Gumbuya Leisure Park (Vic)	Animals are added to species needing to be built up. *M. giganteus* individuals are removed for herd control or controlling the dominant buck for breeding.
Healesville Sanctuary (Vic)	Males are separated into bachelor groups to stagger breeding. New animals added on an as needed basis to increase genetic viability of captive populations.
Melbourne Zoo (Vic)	Animals removed to manage aggressive interactions (usually between males) or for breeding and genetic management.
Werribee Zoo (Vic)	No.
Birdland Animal Park (NSW)	Only *M. giganteus*.
Coffs Harbour Zoo (NSW)	No.
Fleays Wildlife Park (Qld)	Animals removed to manage overstocking, especially when too many males are highly ranked in the dominance hierarchy.
Lone Pine Koala Sanctuary (Qld)	No.
Qld Reptile and Fauna Park (Qld)	No.
South Bank Parklands (Qld)	Yes, on an adds need basis.
Territory Wildlife Park (NT)	All males have been removed or vasectomised from the populations of *M. agilis, M. antilopinus, M. rufus and M. robustus* to prevent surplus breeding.
Bannamah Wildlife Park (WA)	Animals removed to manage aggressive interactions or for treatment. Western greys are added periodically.
Caversham Wildlife Park and Zoo (WA)	Young removed at weaning age.
Greenough Wildlife & Bird Park (WA)	Animals are added or removed due to injuries or to permit veterinary care and to manage interactions within the group.
Cleland Wildlife Park (SA)	Not currently, but under consideration.
Dundee's Wildlife Park (SA)	Some females removed after breeding. Males are separated.
Urimbirra Wildlife Park (SA)	Individuals are removed if they are considered to have "behavioural problems".

3.3.2.15 Question 15 During what times of the day and the year do you get the most visitors?

Weekends, school and public holidays and periods of good weather were generally nominated as times when visitor numbers were greatest. Peaks of visitor numbers occurred during the lunch period. The responses of parks and zoos are listed in Appendix 14.

3.3.2.16 Question 16 What time of the day do you notice that the animals are most active?

Individuals of the various species held in captive collections were generally considered to be most active early and late in the day and during periods of cooler weather. Four of the 20 responding parks and zoos noted that macropodoid individuals were more active when presented with feeding opportunities. The detailed responses of macropod managers are contained in Appendix 15.

3.3.2.17 Question 17 What do you consider to be the most important issues in managing your kangaroos and wallabies (stocking rates, types of feed, etc)?

Several issues were identified by current managers of captive macropods as being key issues for them. These were: limiting the number of males in groups; managing stocking rates; adequate nutrition; managing aspects of reproduction; including genetic variation and reproductive behaviour; managing parasites through worming and removal of faecal matter from living areas; the provision of shelter from other individuals and the weather and familiarisation of animals with contact with both staff and visitors. The detailed responses to this question are listed in Appendix 15.

3.4 Discussion

The questionnaire was designed to answer four questions: what species of macropodoids are kept in captivity; what individuals may be held together in an enclosure; what are some of the other conditions of captivity besides group composition and what are some of the management issues facing current managers of captive macropodoids.

Macropodoids, including Bennett's wallabies, have been reported to be commonly exhibited in wildlife parks and zoos throughout Australia and in other countries, including England, the U.S.A., Germany and New Zealand (Merchant and Calaby, 1981). The 32 parks and zoos responding to this questionnaire together maintained members of 34 different species in captive conditions. These species varied from the small, solitary, nesting brush-tailed bettong to the arboreal Matschiei's and Goodfellow's tree-kangaroos, four species of rock-wallabies to the gregarious Eastern grey kangaroo. These species vary broadly with regard to their natural distribution, habitat, behaviour, reproductive biology, dietary needs and population biology within their natural habitat.

The most popular species held in collections described here, both in terms of the numbers of institutions exhibiting these and the total numbers of individuals maintained, were *M. rufus, M. rufogriseus* and *M. giganteus.* Both the Bennett's and red-necked wallaby were popularly exhibited.

Most of the wildlife parks and zoos surveyed exhibited animals from several different species. Multi-species enclosures were commonly maintained, with between two and six species housed within a single enclosure. *M. rufogriseus* was one of the three species most commonly co-habiting enclosures with members of other species. The majority of collections of macropodoids in captivity contained animals that were breeding and this was particularly true of collections of Bennett's wallabies. These individuals may have home ranges that overlap those of other macropod species. For example, Bennett's wallabies and Tasmanian pademelons may both browse on the same pasture (Tighe *et al.*, 1981). However, housing multiple species of macropods together within the confines of an enclosure where males are unable to disperse and search for females in oestrus may increase the possibility of hybrid offspring arising. *M. rufogriseus* hybrid offspring have been reported to occur within captive colonies, sometimes with physical deformities resulting from genetic incompatibilities (*M. r. rufogriseus* X *M. r. banksianus:* Calaby and Poole, 1971; *M. agilis* X *M. rufogriseus:* Lowry *et al.*, 1995).

Successful breeding colonies also give rise to concerns over increasing stocking rates and the associated problems of stress from overcrowding and agonistic interactions. Subordinate individuals within confined areas, including juvenile males unable to disperse, may not be able to disengage from overt interactions as they would in their natural environment. In captivity, male Matschie's tree-kangaroos must be held in individual enclosures to prevent intense agonistic interactions that can result in injury (Hutchins *et al.*, 1991). Females that are isolated while they have pouch young achieve the greatest success in rearing their offspring, while those housed together have been reported to engage in infanticide, including harassing cage-mates, pulling young out of the pouch of non-related females and aggressively interacting with unrelated juveniles. Behavioural stress has also been suggested as a possible cause of the death of pouch young of females housed in groups.

Captive breeding was an important source of new stock for parks and zoos; more than half the respondents increased their stock this way. However, this may be cause for concern, especially in smaller colonies, as Bennett's wallabies, like many macropods, have a breeding system where males compete for mating rights and the majority of successful matings may go to a single male achieving dominance through agonistic interactions (Murböck, 1977; Fleming, 1983). In a captivity environment, one male may retain dominance over several breeding seasons. Under these circumstances the degree of genetic diversity among captive offspring may be compromised unless carefully managed.

Trading between parks and zoos was another popular means of increasing collections, as was accepting donations of injured and orphaned animals from members of the public. The latter practices have the potential to increase genetic diversity within breeding groups. However, the introduction of new animals to an established group may result in a disturbance of dominance hierarchies that is resolved through agonistic interactions (LaFollette, 1971; Murböck, 1977)

Captive groups, as well as containing as many as six different species, varied in terms of the sexes and ages of the captive individuals. Several zoos and wildlife parks employed strategies to reduce fighting and injuries; stocking rates were managed to prevent overcrowding and groups manipulated to reduce the proportion of males present, especially during the breeding season. The presence of a number of males when a female is in oestrus can result in the distress, injury or even the death of the female brought about by either agonistic interactions to assert dominance or simply over-enthusiasm on the part of a successful mate (Williams, in Hand, 1995). Older males may also be seriously injured by younger members of the group challenging for their position within the hierarchy. Even within all male groups, particular animals can engage in levels of aggressive interactions that require that individual to be removed. Excess animals were managed using similar strategies to those described above; two common methods were trading with other parks and releasing animals back into the wild. Culling and controlling breeding were also employed to manage the numbers of captive macropods.

Information was collated from responses to the questionnaire regarding other aspects of the captivity environment. The diet and provision of food to macropods was another area of captive management considered by the managers to be of great importance. Most feeding regimes included morning and/or evening feeds on a daily basis. The timing of these would probably have been chosen to coincide with peak periods of activity, which were generally reported to be early morning and late evening. Bennett's wallabies in the wild browse from late afternoon through the night in the wild (Tighe *et al.*, 1981; Calaby, 1983; Cronin, 1991). The common exception to these patterns of activity were feeding times and when park visitors bearing food were present; both events precipitated increased activity.

Housing issues were considered to form a significant component of the management of captive macropods. These included providing refuge for subordinate individuals, protection from the weather and habitat enrichment so that a naturalistic environment is provided to encourage natural behaviours. Visitors to wildlife parks and zoos often have an expectation of interacting with the wildlife exhibited there (Croke, 1997). Members of the public could enter half of all enclosures at parks and zoos responding to the questionnaire and were frequently permitted to feed the animals. These experiences can be of great value in terms of economic success and in achieving the aims of individual institutions. Public support for research programs, captive breeding and conservation efforts can be built through these experiences (Croke, 1997).

Bennett's wallabies are solitary in the wild, with a breeding system characterised by intense agonistic bouts between males competing for mating rights (Murböck, 1977; Fleming, 1983). They are reportedly highly susceptible to injuries from trapping and handling, diseases relating to stress and unhygienic captive conditions (Spielman, 2000). However, as evidenced from this sampling of Australian wildlife parks and zoos, this subspecies is commonly exhibited, breeds successfully in captivity and is held in captive conditions in comparatively very high numbers.

From the survey of experienced current managers of captive macropods several issues emerged as being generally considered of key importance to the management of captive macropods. These were: managing stocking rates; the composition of captive groups, especially with regard to the number of males in colonies; managing captive breeding; issues relating to diet and feeding regimes and housing issues, including maintaining a hygienic environment.

Chapters 5, 6 and 7 of this thesis detail experimental manipulations designed utilizing the information provided here to investigate and quantify the influence of such factors on wallaby behaviour. Specifically, managing stocking rates, group structure and the provision of food were investigated. In Chapter 8, a management plan is suggested that will optimize captive conditions for Bennett's wallabies.

Chapter 4 Behavioural Inventory

4.1 Introduction

Coulson (1989) noted that good knowledge of a species' repertoire of behaviour was necessary before comparative studies could be undertaken. This is not only true for comparisons between species; examining and understanding behaviour allows quantitative studies of the responses of individuals to varying specified environmental conditions to be undertaken. Ethological studies can be utilised to predict the responses of captive individuals to different conditions of captivity. Thus, investigations of the behaviour of captive individuals can assist in the sound formulation of ongoing management strategies (Eisenberg and Kleiman, 1977).

Typically, the first step in such investigations is the formulation of a behavioural inventory (Crockett, 1996). It is generally considered that an understanding of the behaviour of an individual in its natural environment and in captivity can be of equal importance when designing enclosures or determining other management strategies (Eisenberg and Kleiman, 1977). Previous studies that have aimed to improve the welfare of animals in captivity have compared the behavioural repertoires of captive individuals to those of their wild conspecifics and, where differences have been identified, it has often been assumed that these point towards problems with management practices for the captive individuals (Veasey *et al.*, 1996).

Although several studies have reported on aspects of the behaviour of the Bennett's wallaby, these have primarily been qualitative, often involving cursory observations obtained while investigating other aspects of the biology of this subspecies (Catt, 1978; Tighe *et al.,* 1981; Merchant and Calaby, 1981; Fleming *et al.,* 1983; Clarke and Loudon, 1985). Research has focused more frequently on aspects of reproduction relating to the two different patterns of breeding exhibited by this subspecies and the red-necked wallaby (Catt, 1978; Walker, 1977; Curlewis *et al.*, 1987; Curlewis, 1989; Curlewis and Loudon, 1989; Russell, 1989; Brinklow and Loudon, 1993; Higginbottom and Johnson, 2000). However, several reviews of macropodoid behaviour, particularly social behaviour, have included descriptions of aspects of the behaviour of *M. r. rufogriseus* (Coulson, 1989; Ganslοßer, 1992). LaFollette (1971) reported on agonistic interactions between dyads of captive male Bennett's wallabies. Murböck (1977) provided descriptions of play fighting between mothers and their male offspring and agonistic interactions between captive males.

A more thorough, three year study of the behaviour of captive Bennett's wallabies undertaken by Murböck (1979) utilised existing groups of captive individuals in five enclosures at two zoos in Germany. Each group was maintained within a different set of conditions, with the number of individuals varying, as well as the size and shape of the enclosures and the number of species present. From observations of these animals, the author drew general conclusions which were intended to form the basis of future behavioural investigations of this subspecies, particularly with regard to their behaviour in the natural habitat.

This section of the present study is therefore intended to elucidate and expand on the existing store of knowledge by providing a comprehensive inventory of behavioural elements and both qualitative and quantitative information about the behaviour of members of this subspecies, in the wild as well as in captivity. This information will then be utilised in examinations of the effects of varying captive conditions, detailed in Chapters 5, 6 and 7. These studies will enable strategies of management to be devised for captive wallabies that address welfare concerns, ensure that the purposes for maintaining collections are met and address economic considerations (refer to Chapter 8).

4.2 Materials and Methods

4.2.1 Observational methods

A. WILD WALLABIES

Wild wallabies were observed over 100 h at Sloping Lagoon in the Coal Mines Nature Reserve, on the Tasman Peninsula in the south east of Tasmania, and Mt Field National Park, also in southern Tasmania. Sloping Lagoon is a large, shallow lagoon surrounded by open, grassy areas extending back from several to approximately 100 m to eucalypt forest, dominated by the black peppermint (*Eucalyptus amygdalina*), the white gum (*E. viminalis*) and the silver wattle, (*Acacia dealbata).* A dense understorey contains species such as the common heath *Epacris impressa,* banksia, (*Banksia marginata*), she-oak (*Casuarina stricta*), bull oak (*Casuarina littoralis*), native cherry (*Exocarpos cupressiformis*) and bracken (*Pteridium esculentum*). This forest extends throughout the Coal Mines Nature Reserve (Storey, 1996). Mt Field National Park comprises a high alpine area, with areas of open hardwood forest up to 15 m at the base of the mountain, dominated by stringbark and black peppermint with an understorey of *Exocarpus* and *Banksia spp.*, a shrub layer of *Epacris impressa, Pultenaea juniperina, Davisea latifolia* and a very sparse ground layer of *Gonocarpus teucroides*. Around the visitor's centre and camping area are large, open grassy areas surrounded by forest and these formed the observation sites.

Wallabies were opportunistically observed employing the focal animal technique described by Altmann (1974) over 30 min sample periods. Where it was possible to determine these, the sexes and age classes of focal individuals were recorded. Three age classes were used: juvenile; subadult and adult. Juveniles were considered to be animals less than one year of age, which includes the period prior to weaning. Subadults were one to two years of age, sexually mature but not yet having achieved their full growth. Adult Bennett's wallabies, at two years of age and greater, were sexually mature and had mostly achieved their adult size. During the sample period, all activities in which the focal animal engaged were recorded. The duration of each event was also noted, unless this was less than three seconds; all events lasting for a period of less than three seconds were assigned a duration of three seconds due to the difficulty of accurately measuring shorter time periods.

These observations were taken between 14:00 and 01:00 h at all times of the year. Although sampling was attempted between 06:00 and 14:00 h, wallabies were rarely observed and generally fled immediately upon sight. During the day, these animals remained in refuges within the dense vegetative understorey where they were difficult to see. When approached, wallabies tended to remain motionless until the observer was in close proximity (several metres), at which point they moved away far too rapidly to be followed. Subsequently, the majority of observations of wild individuals occurred after sunset.

During the afternoon, wallabies were viewed with binoculars when required. After dusk, observations were collected with the aid of a spotlight. Initially, a red light filter was applied to the spotlight in order to make this light source less noticeable to wallabies. However, failure to apply the filter did not result in any noticeable change in activity. The filter did make night observations more difficult, due to the lower resolution available, and so this practice was discontinued. The use of the spotlight for observations meant that wallabies could only be observed if they remained within a distance no more than 20 m from the observer. The observer settled in a concealed position prior to the expected emergence of wallabies and remained seated and still until the termination of all observations. Observations were immediately terminated in the event of any disturbance, for example, the presence of four wheel drive vehicles or bush walkers.

Initially, it was intended that quantitative data would be collected from observations of Bennett's wallabies in the wild. However, animals rarely remained in sight long enough for a sufficient number of observations to be completed for use in quantitative analyses. Wallabies tended to emerge from well-used runways into semi-circular clearings at the edge of the forest. An initial period of approximately 30 min was spent browsing in this area. If no disturbance occurred, the animals moved suddenly and swiftly away from the tree line and out into more open areas to continue browsing. If disturbed, for example by another wallaby emerging from a runway, focal animals often fled quickly from sight. Those individuals that remained at the tree line for extended periods tended to move along its edge, so that their browsing activities took them out of visual range.

B. Captive wallabies

Captive subjects were observed over approximately 1000 h at Bonorong Wildlife Park in Hobart and in an enclosure at the University of Tasmania's Hobart campus. These individuals were observed during 30 min sample periods using the focal animal technique previously described. The sexes and age classes of focal animals were again recorded. Captive individuals at the university enclosure were identified through the use of coloured ear tags, simplifying this process.

Observations at Bonorong Wildlife Park were conducted between 08:00 h and 16:00 h. The observer selected an observation post based on its close proximity to browsing Bennett's wallabies and remained seated while recording focal animals selected opportunistically from free-ranging stock. Generally, an observation post was utilised until a disturbance involving park visitors resulted in individuals moving to another area of the park. Following this, another post would be selected so that wallabies were once again in close proximity.

Observations at the university enclosure were conducted between 09:00 and 01:00 h, although the majority of observations occurred between 15:00 and 00:00 h. Spotlights were permanently mounted throughout the enclosure so that animals could be viewed in all areas, unless they entered limited areas of dense vegetation. Spotlights were turned on at least half an hour prior to sunset, so that this event did not disturb the wallabies. As previously described for observations of wild wallabies, spotlights utilising red bulbs were initially trialed. However, the use of red light made observing individuals after sunset more difficult and had no noticeable benefit; thus this practice was discontinued. All observations were made from inside a shed positioned in one corner of the enclosure. The observer sat at a window from which the entire enclosure could be viewed, with the exception of the small area between the rear wall of the shed and the fence line or the densely-vegetated areas previously mentioned. Although all subjects quickly became accustomed to the observer entering the enclosure, a period of 30 min was allowed to elapse between entering the shed and commencing observations.

4.2.2 Interactions

During the course of recording observations of either wild or captive wallabies, notes were made during any interactions involving the focal animal. The identities of all individuals involved, and the behavioural elements performed by each individual from initiation to termination, were recorded. From these data, qualitative descriptions of types of interactions occurring were developed. These included interactions characterised by sexual, agonistic and maternal behaviours, as well as other, amicable, social interactions.

4.2.3 Spatial Patterns

Two sites were available for examining the spatial patterns of captive individuals. The first of these, the university enclosure, was divided into 14 areas roughly 10 by 12 m in size (refer Figure 2.1). These were numbered sequentially, so that sectors two through to six and sector 14 ran down the hill and comprised an area of scrubby bush that provided good cover. Sectors seven to 13 encompassed the grassy surfaces of the enclosure where less cover was available, but included the water receptacle. Feeding stations were located in areas one, two, three and seven and the water receptacle was located in sector 12.

Bonorong Wildlife Park permits visitors to enter almost all areas of the park, including those sections in which Bennett's wallabies are free-ranging. Visitors may feed the wallabies and frequently interact with them for prolonged periods of time. The approach of visitors often signaled the end of preceding behaviours and interactions, particularly resting and sexual interactions. The presence of visitors and feed, particularly feed left behind on the ground, also stimulated levels of activity and interactions not seen at other times. Bennett's wallabies also shared their enclosure with eastern grey kangaroos and Tasmanian pademelons. Due to these confounding factors, the spatial patterns of captive individuals were not examined in this location.

Quantitative measurements of the spatial distributions of Bennett's wallabies in the wild could not be made for the reasons previously described, although qualitative information was collected.

4.2.4 Data Treatment

Qualitative descriptions of every behavioural element observed were compiled from all observations made, whether these were on wild or captive animals. Descriptions of types of interactions were also formulated from these observations.

A total of 109 hours of the observations recorded were utilised to quantify the frequencies and durations of the performance of particular behavioural elements and the frequency of occurrence of categories of behaviour, including social behaviour. All observations used for quantitative purposes were drawn from those recorded at the university enclosure. Wallabies utilised in these were held at a stocking rate of six animals per 1000 m^2. Records were accumulated over the three year period of this study; therefore subsamples from a number of groups were utilised, comprising male and female individuals of various ages.

Observations were divided into two periods, which are referred to as daytime and nighttime observations. Daytime observations were recorded between 09:00 and 15:00 h. Nighttime observations were drawn from the total set of focal animal samples recorded between 15:00 and 21:00 h. This division was based on the approximate time of day that wallabies in the wild and in the university enclosure were observed emerging in large numbers from positions of refuge into areas where browsing material was utilised. During the nighttime period 73.5 h of observations were recorded from observations of seven focal animals, while 35.5 h of observations of nine focal animals were recorded during the day. All of these observations were used to produce the descriptive statistics.

A total of 71 focal animal samples was utilised from each period. Average scores per animal were calculated and statistically analysed in order to test the hypotheses set out below. In each instance, P values below 0.05 were considered to be significant.

1) Do the mean frequencies with which individuals were recorded in particular areas of the enclosure vary significantly between the day and nighttime periods? A Kruskal-Wallis one-way analysis of variance was employed to examine the rates of occupation of sectors 1-14, when wallabies were in sight.

2) Do the frequencies of behavioural elements performed by *M. r. rufogriseus* individuals differ significantly between the daytime and nighttime periods? A Kruskal-Wallis one-way analysis of variance was employed for this purpose. Do the mean durations of behavioural elements during the day and night time periods differ significantly? A repeated measures ANOVA was utilised to test this hypothesis.

4.3 Results

4.3.1 Inventory

A. Stationary Postures

Lying down

Animals lay on their sides with head and limbs stretched out along the ground, as can be seen in Plate 4.1. This posture was most often noted on warm afternoons.

Plate 4.1. A *M. r. rufogriseus* individual lies on its side in the university enclosure.

Sitting

Sitting involved one of two postures. In the first position, individuals sat back on their haunches, with back curved into a semi-circle and tail emerging forwards between the hind limbs. The second position involved sitting upright with forelimbs held in against chest and frequently crossed and the tail either out behind or curled alongside the body. The former, shown in Plate 4.2 below, was more usually adopted during long rest periods, which could continue for periods of several hours, whereas the latter was more common during shorter breaks between feeding, lasting several minutes, or when more likely to be disturbed (e.g. when large groups of visitors were present in the vicinity).

Plate 4.2. A Bennett's wallaby sits back on its haunches.

Crouching down

During periods of poor weather the animals sat for long periods hunched very low, the body curled in a semi-circle and the head and limbs pulled in against the body. This posture was adopted whether under cover or in the open and during cold or rainy weather.

B. ALERT POSTURES

When disturbed the animals often raised the head from an upright, sitting or lying posture. They generally held still with head in the air and ears swiveling in all directions. This was a frequent occurrence during windy conditions. If browsing or moving when disturbed, individuals usually stood so that their whole body was erect. If sitting or lying, they would raise only the head and chest. Following the adoption of this posture, animals either resumed their prior activities or moved away rapidly. If disturbed, they occasionally assumed an alert posture and then returned to browsing regardless of whether or not the disturbing factor had moved away. Two distinct alert postures are described below.

Standing erect

Individuals stood with their backs at a 70-90° angle to the ground and heads held parallel to the ground, as can be seen in Plate 4.3. Ears were erect and mobile but otherwise the animal stood very still. The forelimbs retracted close to the chest and the tail extended straight out behind the body.

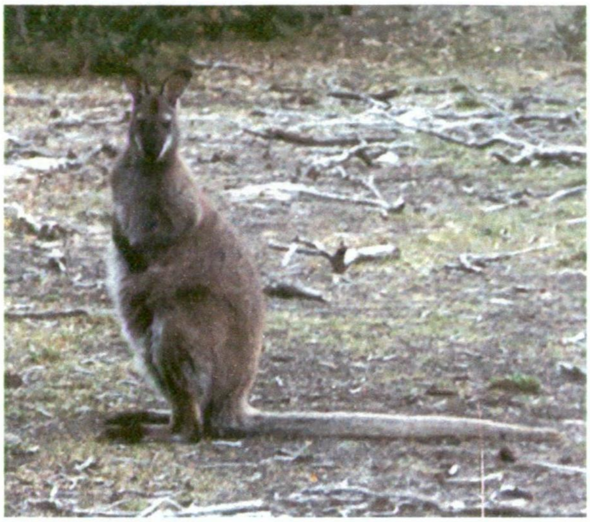


Plate 4.3 A wild Bennett's wallaby at the Coal Mines Nature Reserve in an upright alert posture.

Standing crouched

Individuals stood with their back at a 40-70° angle to the ground and the head held at shoulder height or above the body and parallel to the ground. Ears were again erect and mobile but the forelimbs were at times held out from the body. This posture, seen below in Plate 4.4, differed from the one above in that animals were more likely and quicker to return to their previous activity from the crouched position than the upright, but more likely to rapidly move away once having adopted an erect posture. Disturbances, such as another animal moving nearby or trees rustling in the wind, resulted in crouched stands, whereas voices or sudden loud and unexpected noises elicited the erect posture. During the reproductive season, males assuming this posture were frequently observed to extend their necks straight up in the air and sniff for periods of up to a minute.

Plate 4.4. Subadult *M. r. rufogriseus* female in a crouched alert posture.

Start up

If sufficiently disturbed, an animal that was lying would arise suddenly to an upright alert posture or else from lying to flight. After a few paces the animal sometimes paused and resumed the alert posture, followed by feeding or resting behaviour if no further disturbances ensued.

C. Locomotion

Two distinct gaits were employed by the wallabies: slow progression and bipedal hopping.

Slow progression

This was the most common type of locomotion seen, used to move around slowly, as when feeding, or when traveling only short distances. Animals moved on all four limbs but did not move the limbs in any particular order; the tail appeared to provide no additional support.

Bipedal hopping

Individuals employing this mode of locomotion held their forelimbs in against the chest and inclined their bodies forward. Powerful, synchronised movements of the hind limbs provided the propulsion. The speed of this gait varied from relatively slow (18 km/h) to a very fast top speed of 60 km/h. The angle of the body to the ground also varied from high angles up to 80° at slower velocities to 45° at high velocities.

D. Feeding & Drinking

Browsing

The animals browsed on grasses, herbs, shrubs and trees. When browsing on grasses and herbs, as seen in Plate 4.5, individuals moved around slowly on all fours while ripping and chewing. The chest and forepaws were held close to the ground. Legs were moved in no particular order. Wallabies also browsed on the lower branches of trees and shrubs, as well as on branches of eucalypt trees lying on the ground. The forefeet were used to manipulate branches and leaves and to grasp the branch firmly to allow leaves to be torn away and eaten. Wallabies ate wattle (*Acacia dealbata*) and casuarinas (*Casuarina stricta*) trees, as well as some eucalypts (*Eucalyptus viminalis, E. amydalina* and *E. pulchella*). The animals preferred to browse on juvenile, rather than adult, eucalypt leaves and would not browse at all on *E. globulus.*

Plate 4.5. A *M. r. rufogriseus* individual browsing on grass.

Merycism

Merycism, or regurgitation, was regularly observed and occurred both during feeding and some time after feeding had ceased (15 min or more). Food was rarely observed to be spilled during regurgitation and the bolus was masticated and swallowed.

Drinking

Both wild and captive individuals were observed lapping water from receptacles or pools of groundwater with their tongues.

E. Comfort Movements

Grooming

Animals groomed their limbs, backs, necks, heads, abdomens, pouches, sides, chests, tails and urogenital areas by scratching, biting and licking. Some of these activities can be seen in Plates 4.6, 4.7 and 4.8.

Plate 4.6. Subadult female *M. r. rufogriseus* individual grooming her forelimb.

Plate 4.7. Grooming actions directed toward the abdominal region.

Plate 4.8. Grooming the head and ears.

F. Vocal Communication

Growling

Individuals emitted a low growling sound when approached by other wallabies, whether resting, feeding, grooming or engaging in social interactions (e.g. a second male approaching a male inspecting a female). Growling also occurred during overt physical bouts. Both winners and losers emitted growls during interactions. On one occasion two wallabies feeding at a feeder moved away swiftly upon hearing the growling vocalizations of another animal approaching from their rear. Their sudden and swift departure from the feeder occurred before either animal had seen the approaching third wallaby but immediately after the growl was emitted. Shortly after this, another animal emitted a loud growl as it was chased away from a feeder.

Coughing

Coughing sounds were produced under similar circumstances to those described above.

G. Other Forms of Communication

Alarm foot thump

When an animal moved off at speed as a result of some disturbance, the first few hops were very heavy and the resulting thumps caused the wallabies in the area to assume alert postures. The most common result of this was for every wallaby in the area to rapidly move away out of sight.

Olfactory

Male *M. r. rufogriseus* used olfactory cues to ascertain the reproductive state of females. This will be discussed later in Section 4.3.2, which deals with sexual interactions.

Tactile

Tactile interactions were commonplace where wallabies were close together. Feeding wallabies would frequently be approached and nosed. Touching, scratching, pushing, kicking, biting, pawing and holding all occurred in a variety of contexts: agonistic, sexual and amicable. These will be elaborated upon in the appropriate sections below.

H. MISCELLANEOUS BEHAVIOURS

Fence running

Both males and females observed within the university enclosures were at times seen ambulating back and forth over short distances (< 4 m) along the fence line. Locomotory method varied from slow progression to rapid bipedal hopping; either type was periodically interrupted by the animal standing upright on its hind limbs and looking through the fence, as can be seen in Plate 4.9.

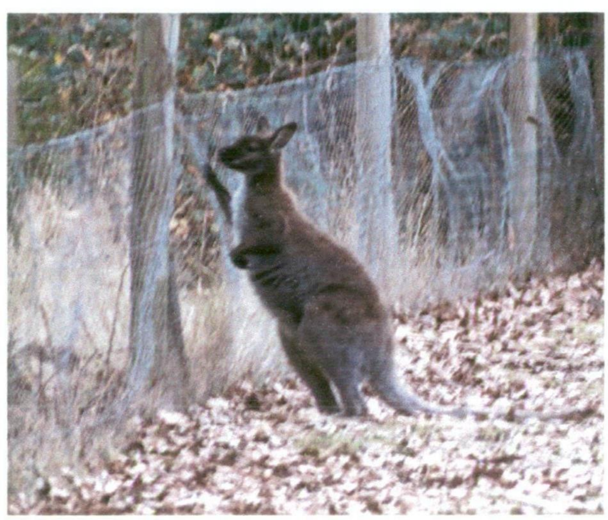


Plate 4.9. Fence running.

Escape

As described above, an animal that was disturbed while feeding or resting in a sitting posture might move swiftly away for a short distance before pausing. It may then move away again or return to feeding or resting. Alternatively, it then might flee.

Flee

Animals on occasion responded to disturbances by moving out of sight. In captivity, they would move swiftly to another area of an enclosure. In the wild, they would move from the open via a runway into the forest, or from a hiding position through the forest, away from the disturbance.

4.3.2 Types of Social Interactions

Types of interactions are divided into four categories for ease of discussion: maternal; sexual; agonistic & amicable. It is important to note that many behaviours have multiple functions which can be discerned from the context of the interactions.

A. Maternal Interactions

Very few direct interactions, apart from the suckling of offspring, were detected between females and their pouch young. Pouch young were often observed with head emergent from pouch browsing when their mothers bent low to the ground to browse. Females seemed to only interact directly with their offspring when it did not interfere with their other activities.

Feeding young-at-foot

Young at foot fed from the pouch whilst the females stood, sat or lay. Feeding was initiated by the young which approached and immediately began to feed by pushing the head into the pouch. The mother often terminated feeding when she either moved off or bent down to feed. Offspring would occasionally attempt to resume feeding. If the female moved into a resting position this was successful. If the young at foot was persistent, females frequently hopped away rapidly or responded with agonistic behaviour.

Play behaviour

Young-at-foot engaged in play fighting with adults. They predominantly interacted with their mothers, but at times attempted to initiate play bouts with other adults. Mothers either held still or wrestled gently with their own offspring. The responses of other adults varied. At times they responded aggressively, resulting in the immediate termination of the bout and the young-at-foot fleeing. This was particularly true of unrelated adult females. Adult males sometimes participated in play fighting bouts with male young-at-foot for several minutes, engaging in wrestling activities. At times, joeys would also kick and scratch with ferocity. Adult males responded with restraint, refraining from kicking or scratching on each occasion. Adult and subadult males engaged in wrestling but were never observed to kick.

One male joey was observed on one occasion to mount his mother and attempt to copulate with her. She remained seated throughout and did not respond to his activity. No intromission took place although copulatory behaviour (mounting and thrusting motions) continued for 1 or 2 minutes.

Crouch for young-at-foot

Females sometimes crouched to allow young to enter pouch. This usually occurred if a female was in a resting position.

When startled, young joeys sometimes rushed to their mothers and pushed into the pouch. Females then most often moved away rapidly themselves.

B. AGONISTIC INTERACTIONS

Tail lashing

Sinuous tail movements were observed during overt agonistic bouts, when one individual approached another, or when males were in a state of sexual excitement.

Stand beside

Individuals often approached and assumed a position next to and within a metre of others, usually animals that were feeding. That animal then often moved away. If it did not, further agonistic responses usually followed.

Stand upright

When approached, wallabies occasionally assumed an upright posture, rather than move away.

Crouch

When approached by dominant animals, individuals at times adopted a stationary crouched posture. The head and forelimbs were drawn in against the body and any actions by the approaching individual were tolerated without further response. Typically, the dominant individual would touch its nose to the crouching wallaby or scratch gently at the head, neck or forelimbs of the other wallaby before either moving away or commencing browsing or feeding. The subordinate individuals would then also either move slowly away or begin to feed or browse. This posture was also observed to be adopted by females when approached by males who engaged in preliminary copulatory activity, such as nosing their pouch or anogenital region or pawing their hindquarters. Copulation did not necessarily follow: females not in oestrus would crouch while inspected and then move away.

Kicking

Kicks were aimed at the head and chest region of opponents or else directed at the back while hopping over them. One young-at-foot was observed kicking its mother repeatedly on one occasion.

Biting

Both males and females were observed at times to aim bites at the head and ears. Males aimed bites at opponents during agonistic bouts with other males. Individuals of both sexes feeding in close proximity to one another were occasionally observed aiming bites at nearby animals.

Scratching/blows

These were typically directed toward the head, neck and chest of opponents during overt agonistic bouts.

Wrestling

Opponents adopted upright positions while grappling with their forelimbs. Their heads were usually held back with their noses directed upwards. More rarely they butted heads or bit one another. Wrestling extended over longer periods of time than any other type of interaction, with the exception of the occasional bouts of pursuit.

Approach

Individuals would move directly towards others that were in repose, grooming or feeding. They might then begin to feed themselves in close proximity, or nose, scratch or bite.

Move Away

A typical reaction by a subordinate individual to the approach and inspection of a more dominant individual was to remain in the same place but lean or turn the head and upper body away, as can be seen in Plate 4.10 below. At times no further interaction was observed. On other occasions further agonistic or sexual behaviours followed.

Plate 4.10. A male touches his nose to the head of a female, who leans away from him.

Arc

This involved one individual hopping directly towards another from a distance of more than 5 m and then swerving away when less than 0.5 m apart and moving away in another direction.

C. SEXUAL INTERACTIONS

Inspect pouch

Males approached females and sniffed the pouch region. They also on occasion nosed the chest region or nosed at the pouch to insert their head.

Inspect urine

Males sniffed the urine of females while the latter urinated or immediately after they had finished.

Inspect urogenital region

Males sniffed the urogenital regions of females by crouching in front of females which were sitting or standing, or by approaching from the rear or side of females which were feeding. The former of these can be seen in Plate 4.11.

Plate 4.11. A male Bennett's wallaby sniffs the urogenital area of a female.

Scratch tail

Males scratched the tails of females near the base, usually after initially inspecting the pouch.

Scratch hindquarters

Males pawed with their forelimbs the hindquarters of females.

Sternal rubbing

Males rubbed the top of their head or their face against the female's chest with some force.

Follow

The most common response of females to the above male behaviours was to move a short distance (typically around 1 m) away. Males frequently followed females and persisted in their activities until either they were disturbed or the female would move away to another area.

Escort

Males accompanied females while they fed, rested and slept. They usually performed the same activity as the female, and stayed within a few feet of her.

Compliance with inspection

Females approached by males would typically hold still to permit an initial inspection (a few seconds) before moving away. They might permit a pouch inspection, but move away if the male attempted to paw their tail or hindquarters. Alternatively, a male might progress from a pouch inspection to sternal rubbing to scratching before the female moved away.

Masturbate

On one occasion, two males were observed to each grasp vegetation in their forefeet and rubbed it against the penis.

Copulation

A male was observed to grasp a juvenile female from behind and hold her in position with his forelimbs around and under her hind limbs. During copulation, he leaned across her body and kept his head low with his nose butting her repeatedly. This kept the female very low to the ground. She made numerous attempts to escape and succeeded after about 20 sec of copulation. The male accompanied her for several minutes afterwards but made no attempt to again closely approach her. She appeared exhausted by the events and exhibited sweating, shaking and panting.

On another occasion, shortly after the one described above, an adult female was observed copulating with an adult male, probably the same one as the previous time. This time, the male grasped the female from behind and leaned low across her, holding her body close to the ground as before. However, the female made no attempt to escape and afterwards browsed and moved around the enclosure calmly. She was accompanied for at least 2 h by the male, who remained alert and at close range (within 2 m). Another male approached and was chased off. The female had a young-at-foot that approached several times to feed and was chased away before finally being allowed to feed from outside the pouch. The adult male watched the young-at-foot closely while it fed.

D. AMICABLE INTERACTIONS

Nose

Individuals were frequently observed to approach another wallaby and touch their nose to the second animal. At times both animals touched their noses together. On other occasions, a nose was touched to other parts of the body, especially to the hindquarters. Adult males and females of a similar size tended to touch noses, while an animal that was larger often touched noses to other areas of the body of a wallaby that it approached.

Look

Individuals often looked directly at another wallaby that came suddenly into sight, made a sudden movement or caused a sudden noise, but generally did not completely cease whatever activity they were pursuing.

4.3.3 Spatial Patterns

The frequencies with which individuals were recorded in any of the 14 marked sectors shown in Figure 2.2 were recorded and the results are presented in Figure 4.1. At times, when a recording fell due, focal animals were temporarily out of sight. These individuals were not simply too far away to see, but beneath or behind an object that formed a visual impediment. Trees, shrubs, feeding stations and the observation posts were typically the impediments to viewing focal individuals. On several occasions, when an individual was positioned so that it could not be seen from the observation post, the observer moved to other locations to visually assess the activities in which these animals were engaged. They were always in resting positions, occasionally grooming at the same time, and often gave the appearance of being asleep. This information is included with other data in all the descriptive statistics following because the proportion of time in which individuals were concealed from sight formed an important part of the total activity budget of Bennett's wallabies observed in this investigation and permits assumptions to be made about how time is apportioned between resting and more active pursuits.

The frequencies of recording individuals in each sector are shown in Figure 4.1, with frequencies adjusted to percentages of the total time observed. Frequently-used areas of the enclosure were sectors two, three, seven, eight and 12. All contained a feeding station or water receptacle, with the exception of sector eight. Sectors 10 and 11 were also relatively commonly used. These, along with sector eight, were areas close to a feeding station, with little cover but with relatively more browsing matter available. The frequency of recording a focal individual as out of sight was much higher during the evening period and much lower during the day.

A Kruskal Wallis one-way analysis of variance was used to test the hypothesis that the mean frequency of sighting focal individuals in each of the marked areas (1-14) the enclosure varied significantly between the daytime and nighttime periods. The results of these analyses are presented below in Table 4.1. The frequencies of the occupation of the various sectors differed significantly for three areas of the enclosure (sectors three, nine and 12).

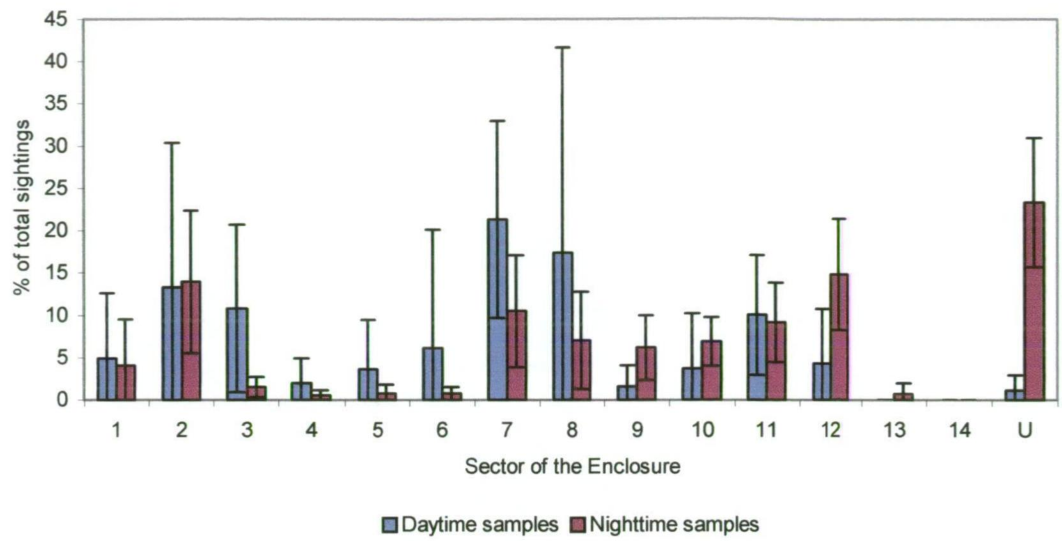


Figure 4.1. The mean percentages (± standard deviations) of overall sightings in which individuals were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when the focal animal was out of sight. N = 7 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 9 for the "night time" period (15:00 – 21:00, 146 h of observations).

Table 4.1: Results of a Kruskal-Wallis one way analysis of variance comparing the frequencies with which individuals were recorded in the various sectors of the university enclosure during the "day time" (9 a.m. – 3 p.m.) and the "night time" (3 p.m. – 9 p.m.). P values less than 0.05 were considered significant. . N = 7 for the "day time" period (09:00 – 15:00 h) and 9 for the "night time" period (15:00 – 21:00), degrees of freedom = 1. For a description of sectors, refer to section 2.1.4 and Figure 2.1.

Sector	H value	P value
3	7.013	0.008
9	5.844	0.016
10	4.390	0.036
12	6.826	0.009
13	4.394	0.036

4.3.4 Time Budgets

Initially, overall time budgets were examined by combining behaviours into categories. The frequencies of behaviours from particular categories during the periods designated as daytime and the nighttime are presented in Figure 4.2.

Feeding activities accounted for the greatest period of daytime observations, with individuals spending the majority of the remaining period resting. Grooming accounted for only 0.24% ± 0.73% of this period.

During the late afternoon and night, individuals again devoted the largest period of observed time to feeding activities. The next greatest period was accounted for by occasions when individuals were not sighted. The amount of time spent in alert postures and resting were similar. These activities accounted for over 93% of the observed time. The time spent grooming accounted for over half the remaining period, while social interactions only accounted for 0.70% ± 0.79% of the total observed time.

A Kruskal Wallis one-way analysis of variance was used to test the hypothesis that the frequency with which individuals were observed performing behavioural elements belonging to each category differed significantly between the daytime and nighttime periods. Miscellaneous behaviours were not examined as these occurred at very low frequencies. Similarly, mother-offspring interactions were not analysed as these also occurred at very low frequencies and can be expected to be influenced by the age of offspring to a degree that was not be controlled for due to time constraints. The results of those analyses that provided a significant P value are presented in Table 4.2.

Several significant differences were revealed by this analysis. The frequency of recording that an animal was not sighted was, of course, significantly greater during the night time period than the day time. Although the total amount of time that individuals spent feeding and drinking did not differ between day and nighttime, significantly different periods of time were devoted to locomotory and grooming activities and the adoption of alert (greater at night) and resting postures (greater during the day). The total amount of time that mothers and their offspring engaged in interactions during the day and nighttime observation periods was not statistically analysed, but other types of interactions occurred at significantly higher frequencies at night.

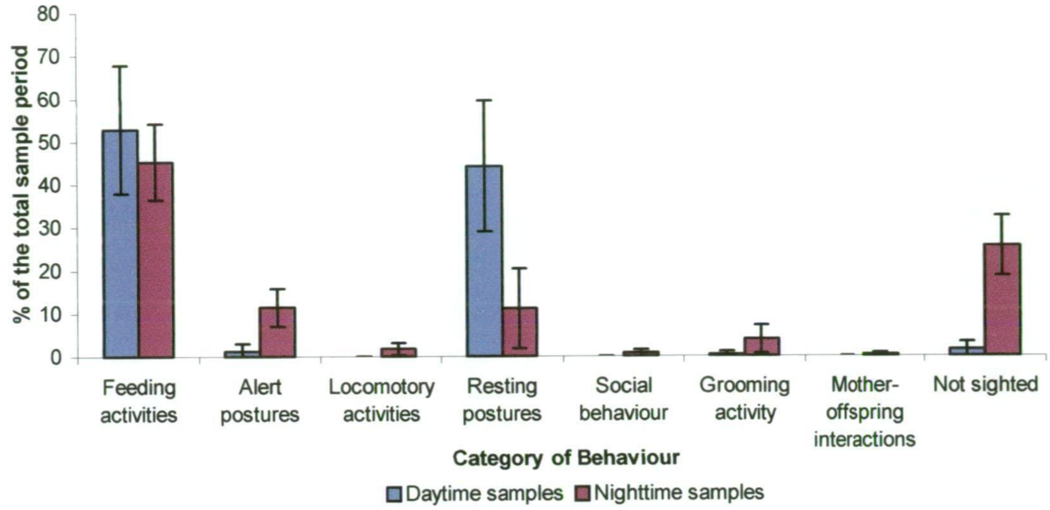


Figure 4.2. The mean percentages (± standard deviations) of overall sightings in which individuals were recorded performing acts belonging to each category of behaviour during the "day time" and "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

Table 4.2 Categories of behaviour for which there was a significant difference ($p < 0.05$) between the mean frequencies recorded during "day time" and "night time" observations (Kruskal-Wallis one way analysis of variance). N = 9 for the "day time" period and 7 for the "night time" period, d.f. = 1.

Behavioural Category	H ratio	P value
Alert Postures	10.05	0.002
Locomotion	13.52	0.001
Resting Postures	9.751	0.002
Social Behaviour	6.265	0.012
Grooming Activities	8.847	0.003
Not sighted	11.47	0.001

Next, a number of individual behavioural elements were selected for further examination, based on their desirability or otherwise and on their rates of occurrence. For example, both browsing about the enclosure and feeding at feeding stations were examined. The former involves the type of active behaviour that zoo visitors enjoy seeing (Croke, 1997), while the latter is a sedentary activity that may be less appealing. However, this type of feeding may be important in ensuring adequate nutrition is delivered, identified in Chapter 3 as one of the major concerns of current macropod managers. Individual resting postures and grooming actions were examined as well as alert postures. Finally, the two most common elements of social behaviour, looking towards another individual and approaching another, were examined. These behaviours again may involve activity that is appealing or unappealing to zoo visitors and may also provide a general indication of the motivational state of captive wallabies.

The frequencies with which individuals were observed performing individual behavioural elements associated with feeding activities during the day and the night are presented in Figure 4.3. Feeding activities comprised the largest proportion of time budgets. Of these activities, the largest proportion of time during the day was devoted to browsing on grasses and herbs growing throughout the enclosure, followed by time spent feeding at feeding stations. Similarly, during the late afternoon and evening, individuals spent the greatest amount of time browsing, followed by time spent attending feeding stations. However, during the daytime, the proportion of time spent browsing was far greater than the amount of time spent at feeding stations.

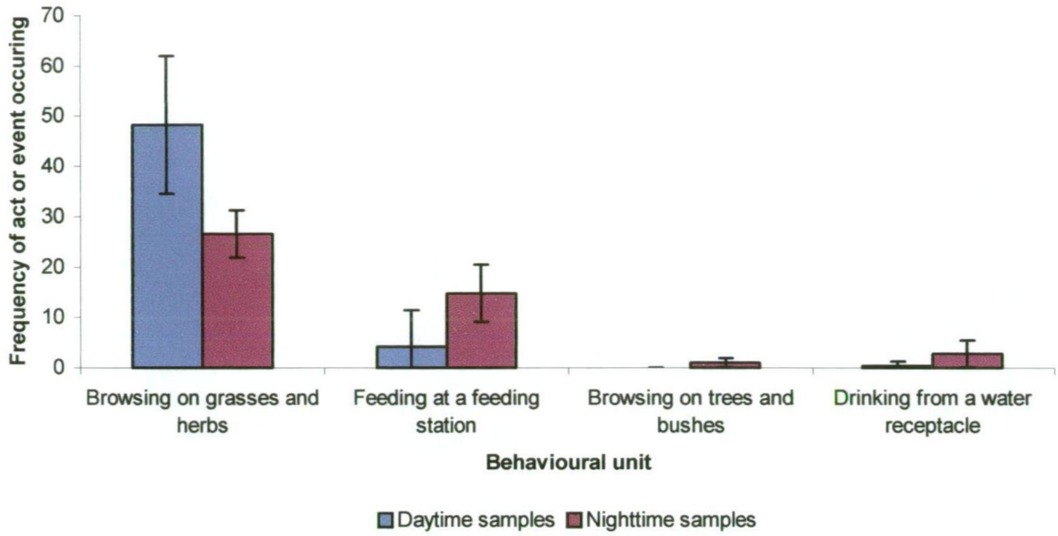


Figure 4.3: The mean percentages (± standard deviations) of recording the occurrence of acts related to eating and drinking during the "day time" and "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

No locomotory activity was recorded during the daytime periods. At night, the frequencies of wallabies hopping and walking were similar (walk: 0.78% ± 0.53%; hop: 0.96% ± 1.14%).

The frequencies with which individuals were recorded in the various alert postures are presented in Figure 4.4. Although upright alert postures were observed at similarly low frequencies in both trial conditions, the number of crouched alert postures recorded during the night time was far greater than that during the day.

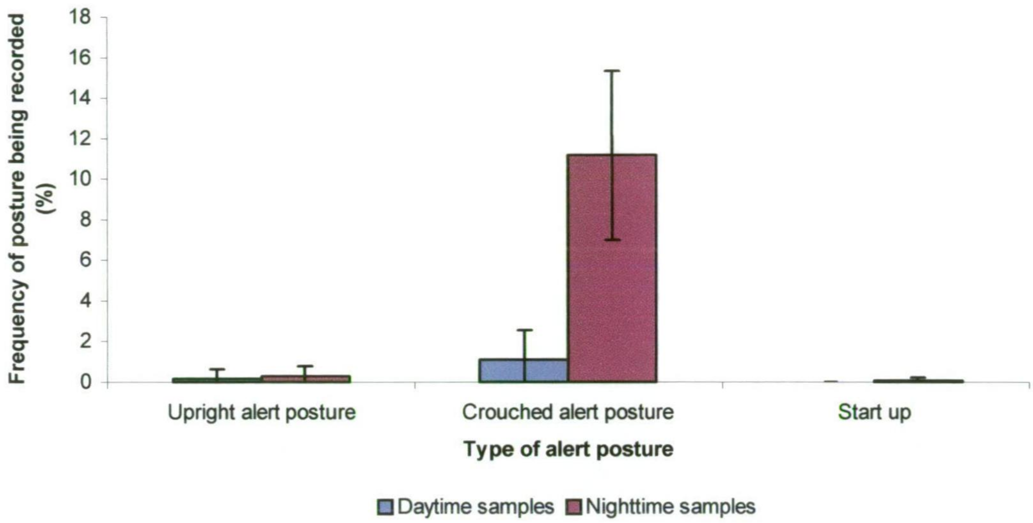


Figure 4.4: The mean percentages (± standard deviations) of recording the occurrence of the various alert postures during the "day time" and "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

Focal individuals at times adopted the various resting postures previously described. The proportion of the total observed time individuals were recorded in these postures is presented below in Figure 4.5, together with the frequencies of focal individuals being temporarily out of sight. When considering the daytime samples, the most frequently adopted resting postures were sitting either upright or on the hindquarters, with the hind limbs and tail extended forwards. During the late afternoon and evening, the frequencies of recording individuals sitting back on their haunches or lying down to rest, were similarly low compared to the frequency of recording the more upright posture.

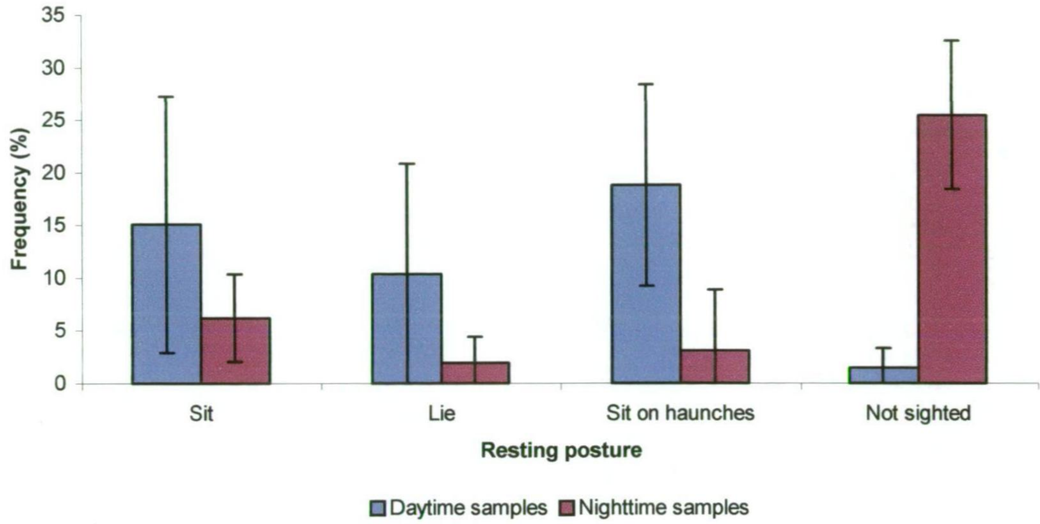


Figure 4.5: The mean percentages (± standard deviations) of recording the occurrence of resting postures (sit, lie, sit on haunches) during the "day time" and "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

The frequencies of recording focal animals engaged in social behaviour, including mother-offspring interactions, are presented in Figure 4.6. All recorded instances occurred during the nighttime period. The suckling of offspring by mothers was the most common type of interaction recorded during the total sampling period. The next most common interaction occurred when one wallaby looked at another individual, followed by approaches by one individual to another. A small number of instances of a wallaby touching its nose to, retreating from, shifting its body away from or following another individual were also seen.

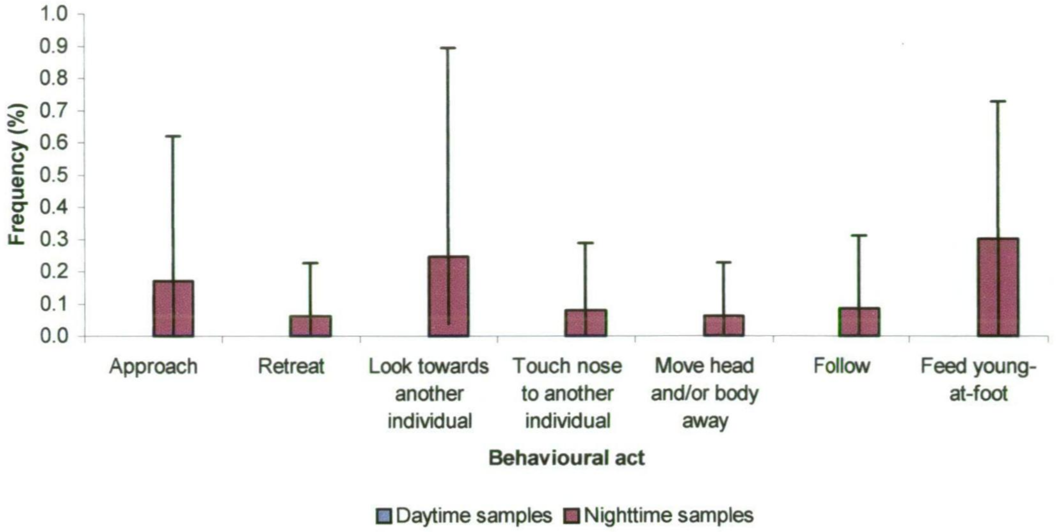


Figure 4.6: The mean percentages (± standard deviations) of recording the occurrence of the various elements of social behaviour during the "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

The percentage of grooming actions aimed at each of eight nominated regions of the body are presented in Figure 4.7. The majority of grooming actions were aimed at the head, neck and forelimbs, followed by the abdomen and hind limbs. Only two instances of grooming by individuals were observed during daytime sample periods: once an individual groomed its side and on the other occasion a wallaby groomed its hind limbs.

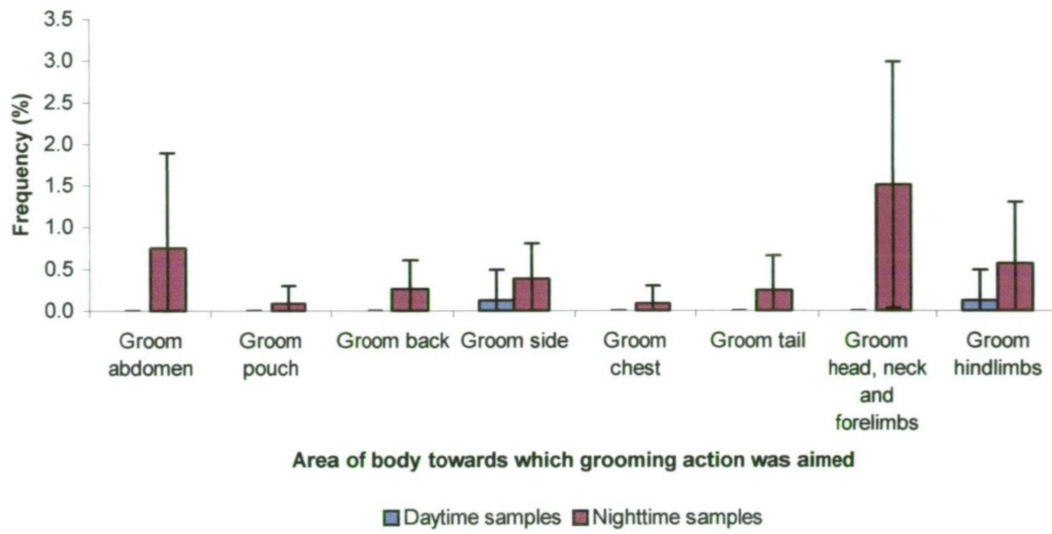


Figure 4.7: The mean percentages (± standard deviations) of recording the occurrence of the various grooming actions during the "day time" and "night time" periods. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations).

A Kruskal Wallis one-way analysis of variance was again employed to test whether the frequencies of individual elements of behaviour were significantly different between the day and nighttime periods. Those elements that yielded a significant result are presented in Table 4.3.

Although the total frequency of time spent on feeding and drinking did not significantly differ between day and nighttime periods, the amount of time devoted to different types of feeding activities did differ. Browsing occurred significantly more frequently during the day and attending feeding stations at night. The number of crouched alert postures recorded was also significantly greater during the nighttime, although the upright alert postures were adopted with similar frequencies. Grooming of the abdomen, back, head, neck and forelimbs all occurred significantly more frequently at night.

Table 4.3: Elements of behaviour for which there was a significant difference ($p < 0.05$) between the mean frequencies recorded during "day time" and "night time" observations (Kruskal-Wallis one way analysis of variance). N = 9 for the "day time" period and 7 for the "night time" period.

Behavioural Element	H value	P value
Browsing on grasses and herbs	10.42	0.001
Feeding at feeding stations	5.980	0.014
Crouching alert posture	10.74	0.001
Sitting on haunches	7.998	0.005
Grooming abdominal area	4.394	0.036
Grooming back	4.394	0.036
Grooming head, neck and forelimbs	8.385	0.004

The durations of elements of behaviour were also measured and the mean durations of each during day and night time observations are presented in Table 4.4. Behavioural events of the longest duration were those belonging to the categories of feeding, resting and alert postures, as well as those periods in which individuals were unsighted. Social interactions of any kind were very brief (usually 3 s or less per behavioural element), with the exception of periods when mothers fed their young at foot. These lasted for an average of 38 ± 27 s during the night. Instances in which grooming actions were aimed at particular areas of the body all lasted for less than 10 s on average, although grooming sessions lasted up 23 ± 30 s at night.

The durations of individual episodes of browsing and feeding at feeding stations were far greater during the morning and early afternoon than the late afternoon and evening.

The duration of the more intense erect alert posture was greater during morning and evening observations. However, the duration of crouched alert postures adopted during the daytime was more than twice as long on average as those from the nighttime period. Alert postures adopted from a position lying on the ground were sustained for much longer periods during the day than during the night.

The durations of periods of resting were far greater during the morning and early afternoon than during the late afternoon and nighttime. Individuals spent more time sitting on their haunches than sitting up or lying down.

Table 4.4: The mean durations in seconds (± standard deviations) of elements of behaviour recorded during all sampling periods during the day time (09:00 to 15:00 h) and night time periods (15:00 to 21:00 h). Data are drawn from the 150 half hour sample periods of focal animal observations. As these data are calculated using every instance that a behavioural element was observed and not every element of behaviour was recorded with the same frequencies, the number in brackets (n) is the number of focal individuals that performed that particular element of behaviour during the total of all observations.

Behavioural Unit	Day	Night
Browsing on grasses and herbs	1111 ± 553 (8)	162 ± 170 (7)
Feeding	400 ± 371 (4)	330 ± 163 (7)
Browsing on trees and shrubs		171 ± 149 (7)
Drinking	123 ± 76 (2)	131 ± 75 (6)
Regurgitation		27 ± 34 (5)
Erect alert	8 ± 7 (3)	20 ± 6 (6)
Crouched alert	56 ± 45 (8)	26 ± 4 (7)
Start up	63 (1)	16 ± 6 (3)
Sit	609 ± 452 (8)	141 ± 116 (7)
Lie	730 ± 513 (5)	124 ± 65 (5)
Sit on haunches	805 ± 529 (9)	178 ± 216 (4)
Sinusoidal tail movements	3 (1)	69 ± 93 (2)
Kick		3 (3)
Scratch	3 (1)	3 (2)
Wrestle		3 (1)
Approach	3 (1)	3 (5)
Retreat	3 (3)	3 (4)
Arc	2 ± 2 (2)	
Inspect pouch		3 (1)
Move away		3 (2)
Follow		3 (2)
Crouch		3 (1)
Look	3 (2)	4 ± 1 (6)
Touch nose to	3 (3)	3 ± 1 (5)
Groom abdomen	4 ± 5 (6)	8 ± 5 (6)
Groom pouch		9 ± 8 (3)
Groom back	2 ± 1 (5)	4 ± 1 (7)
Groom side	2 ± 1 (5)	4 ± 2 (7)
Groom chest	2 ± 2 (2)	3 ± 1 (5)
Groom tail	2 ± 1 (4)	4 ± 1 (6)
Groom head, neck and forelimbs	4 ± 2 (7)	8 ± 5 (7)
Groom hind limbs	2 ± 1 (6)	4 ± 2 (7)
Grooming session	8 ± 6 (9)	23 ± 30 (7)
Inspect trap		13 ± 9 (2)
Feed Young at foot		38 ± 27 (3)
Crouch for pouch young		3 (1)
Allogroom		3 (1)
Not sighted	123 ± 122 (4)	433 ± 31 (6)

Analyses of variance performed on the duration of individual behavioural elements revealed some significant differences between the durations of these performed in the day and nighttime observation periods. These are listed in Table 4.5.

The length of periods during which animals were recorded as temporarily out of sight differed significantly between the day and nighttime periods. The duration of browsing on grasses and herbs differed not only in the frequency of occurrence, but also in the duration of individual browsing episodes. The length of time that individuals held upright alert postures differed significantly between the two trial conditions, lasting longer during the afternoon and evening, although the frequency of occurrence was similar. The amount of time wallabies remained in the various resting postures also varied significantly between day and nighttime, lasting for longer periods during the day.

The duration of periods spent grooming various body areas was significantly briefer during the daytime observations (grooming the back, side and hind limbs during the day: each 2 ± 1 s, at night: 4 ± 1 s for the back and 4 ± 2 for the side and hind limbs). The length of time one individual looked directly at another also lengthened significantly during the nighttime (day: 3 s; night: 4 ± 1 s).

Table 4.5: Results of a Kruskal-Wallis one way analysis of variance comparing the durations of elements of behaviour performed by focal individuals during the "day time" and the "night time" periods. P values less than 0.05 were considered significant. N = 9 for the "day time" period (09:00 – 15:00 h, 71 h of observations) and 7 for the "night time" period (15:00 – 21:00 h, 141 h of observations), degrees of freedom = 1.

Behavioural Element	F value	P value
Browsing on grasses and herbs	19.91	0.001
Upright alert posture	13.91	0.007
Start Up	125.32	0.008
Sitting down	7.43	0.017
Lying on the ground	10.77	0.011
Sitting on haunches	7.16	0.022
Looking towards another individual	11.68	0.014
Grooming the back	9.75	0.011
Grooming the side	5.13	0.047
Grooming the hind limbs	7.09	0.022
Not sighted	61.26	0.001

4.4 Discussion

The primary aim of this section of this project was to provide a comprehensive inventory of behavioural elements performed by *M. r. rufogriseus* individuals. This can then be employed in comparative studies considering the importance of particular aspects of the captivity environment. This inventory also expands on the previous studies undertaken by Murböck (1977, 1979) and LaFollette (1971) that provided information on aspects of the behaviour of members of this subspecies in enclosure environments.

Aspects of the agonistic behaviour of Bennett's wallabies have previously been examined by LaFollette (1971) and Murböck (1975) and facets of the reproductive behaviour of the subspecies briefly described by Fleming *et al.* (1983). Murböck (1977) also examined agonistic interactions that males engaged in, including playfighting between juvenile males and the mothers. The same author provided further information about the general behaviour and social interactions of Bennett's wallabies in captivity in three zoos (Murböck, 1979). However, this information was by no means comprehensive and Murböck (1979) noted that the variability of the behaviour of subjects observed under different conditions should encourage further research to permit a greater understanding of the behavioural repertoire of this subspecies. A number of behavioural elements and interactions observed to be performed by Bennett's wallabies in this study are detailed here from observations of both wild and captive individuals and expand on these earlier studies to provide a greater understanding of the behaviour of Bennett's wallabies.

Bennett's wallabies may spend up to 15 h per day browsing and the time devoted to this activity increases for lactating females (Clarke and Loudon, 1985). Browsing within an enclosure environment can place a strain on the availability of a sufficient food resource. The provision of supplemental feed may be used to ensure the delivery of adequate nutrition, although it is recommended that this is provided using containers that hold feed above the ground where it will not be contaminated by faecal matter (Calaby and Poole, 1971; Poole, 1982). *M. r. rufogriseus* individuals at the enclosure at the University of Tasmania were frequently recorded in areas that contained either a feeding station or a water receptacle. In this study, activities associated with eating and drinking occupied the largest amount of the daytime period for these individuals. Typically, this involved lengthy intervals of browsing about the enclosure. Less frequently, individuals spent periods of time attending feeding stations. Wallabies, particularly juveniles and subadults, appeared to queue around feeders until more dominant individuals finished feeding and moved away. This contrasts with what has previously been suggested for members of this subspecies: that they do not assert dominance in order to gain priority of access to a food source (Hutchins *et al.,* 1991). Feeding activities were alternated with long and frequent periods of resting. Wallabies rarely interrupted either feeding or resting to assume alert postures. Despite this, once a crouched alert posture was assumed, a focal individual would maintain this for significantly longer periods than at night.

Bennett's wallabies utilise refuges within the dense vegetative understorey of the forests they inhabit to rest (Calaby, 1984; Cronin, 1991). The number of times captive individuals at the university enclosure were recorded as temporarily out of sight significantly increased at night. This was at least partially attributable to the greater success in viewing wallabies in the more heavily vegetated areas of the enclosure prior to sunset. It is also related to the apparent temporal shift in activities resulting in the day-use of these areas for resting. During the day individuals were observed sitting and lying at similar frequencies. At night, wallabies were rarely recorded lying. Lying postures may have been adopted once in these cryptic positions.

Alert postures can be identified in the behavioural repertoires of all macropod species. They provide visual alarm cues to other macropods. Bennett's wallabies, like other macropod species, employ a foot thump as an additional alarm signal (Croft, 1989; Jarman, 1991). These animals, although not forming social groups, do form large feeding aggregations where the ability of individuals to signal members of the larger group about potential threats is advantageous to all (Croft, 1989). In this study, the majority of alert postures were recorded during the late afternoon and evening. The vast majority of these comprised a crouched posture, the average duration of which, at night, was half that recorded during the day. This is related to the reduced frequency and duration of episodes of browsing and an increase in the amount of time spent attending feeders in the same period. During the day, when sources of disturbance were easier to view, prolonged periods of watchfulness were followed by a resumption of browsing. After nightfall, briefer periods of watchfulness were followed by a cessation in browsing and a return to cover. Similarly, animals became noticeably anxious during periods of windy weather.

Alert postures were frequently adopted and animals often fled suddenly only seconds after emerging from cover to browse.

Autogrooming typically involves comfort or cleaning activities. The frequency of pouch grooming has been related to the presence and age of pouch young; as the pouch young increases in body size and excretory output, pouch grooming increases (Clancy, 1982). It may also play a role in thermoregulation and thus be related to variations in temperature. Grooming actions have been reported to be incorporated into ritualised displays in the repertoires of some large macropods. Clancy (1982) reported that red-bellied pademelons (*Thylogale billardierii*) groomed at similar frequencies throughout the day and night and that grooming was associated with other activities. In this study, most grooming activities were recorded at night. Those less frequently recorded, such as grooming actions directed towards the back, sides and hind limbs, were often observed to be performed by wallabies during the course of browsing. Grooming of the abdominal region, head, neck and forelimbs occurred more frequently but often occurred when the individual had finished feeding and adopted a resting posture.

Visual and olfactory methods of communication are more common among macropods than auditory or tactile forms. Visual signals can assist in the determination of gender, with males being larger and having more muscular shoulders and forelimbs. Intent can also be visually signaled through the adoption of postures flagging an intention to approach, retreat, submit or attack (Jarman, 1991). Nasonasal touching between members of macropod species has previously been related to mouth and nasal odours that play an important role in social interactions (Heathcote, 1989). In this study, as anticipated, maternal, sexual, agonistic and amicable interactions accounted for only an extremely small proportion of all observations and all were recorded during the night time period. Interactions of any kind generally occurred over very short periods of time. Typical interactions consisted of one individual looking towards another emerging into open ground or approaching an individual to touch a nose to them. Interruptions to activities from these types of interactions were brief; individuals resumed feeding, resting or grooming almost immediately.

Olfactory cues provided by glandular secretions assist in the identification of social and reproductive status and identity (Coulson, 1989; Heathcote, 1989). *M. dorsalis* individuals direct sniffing actions towards the general body areas (Heathcote, 1989).

Both wild and captive *M. r. rufogriseus* individuals were observed to participate in these types of interactions, with sniffing directed both at the head and the general body areas. The inspection of the cloacal and pouch areas of females is a common practice amongst male members of the Macropodidae, who rely on olfactory cues to help determine the reproductive status of females (Heathcote, 1989). Females advertise their oestrus with olfactory cues over a prolonged period of time. Males, with considerably larger home ranges, are encouraged by this system to locate and accompany females in oestrus and compete with other accompanying males (Jarman, 1991). Larger males who are successful in agonistic interactions have an increased probability of achieving mating success (Gansloßer, 1989). As anticipated, male Bennett's wallabies in the university enclosure opportunistically and frequently approached females and inspected either the pouch or anogenital region.

Male macropods often approach females and stand in front of them. From this position they paw at the head and shoulders of the female or grasp her head and perform sternal rubbing (Coulson, 1989). By contrast, male Bennett's wallabies observed during this project usually approached females from behind or a lateral position and nosed the anogenital region and pouch area. They often followed this by pawing at the females' tail or lower body, or less frequently pawed at the top of the head. These activities were not mutually exclusive, although females generally moved a short distance away if this activity persisted for more than a few seconds. Male red-necked wallabies (*M. r. banksianus*) vigorously rub their chins on their mate's back when mounting. Although this activity was not observed during this study, sternal rubbing was seen on occasion. Males also demonstrated their sexual arousal by the erection of their penis and tail lashing, behaviours that are common among members of the Macropodoidea (Coulson, 1989). Masturbation has also been previously reported among members of the Macropodoidea (Coulson, 1989) and was observed to be performed by male Bennett's wallabies at Bonorong Wildlife Park, using tree branches as an aid. These acts may have actually been a display aimed at another male present and were probably stimulated by the presence of a female in oestrus.

Bennett's wallabies belong to Croft's (1989) Type 3 species with regard to their social behaviour. Males do not defend either a resource or a harem. Rather, high ranking males respond to a degree of predictability in the presence of females in feeding aggregations by maintaining large home ranges that encompass these areas and exclusively consorting with oestrous females and gain a disproportionate number of matings (Croft, 1989). Adult males in the university enclosure were frequently observed escorting recently weaned females as they browsed about the enclosure. Males repeatedly approached and touched their nose to or pawed these young females, who crouched and submitted to these approaches. Juvenile females benefited from these escorts; they moved freely throughout the enclosure and fed at feeding stations unmolested. It is more difficult to determine what benefit accrued to the consort males; no copulatory activity ever occurred. Benefits may accrue to males engaging in these activities, resulting from the experience gained in escorting females.

The mating system of Bennett's wallabies generally follows that described by Jarman (1991) for larger wallabies that display sex related size dimorphism. However, some aspects of the sexual interactions observed during this project differed from those previously reported for this subspecies. Previous observations of attempted and successful matings between Bennett's wallabies have suggested that females remain in a crouched and passive position while the consort male attempts copulation or fends off competitors. After a period of time, the female generally moved away, followed by the competing males in line behind the consort male (Fleming *et al.*, 1983). Several matings within the university enclosure were observed during the process of undertaking observations. It was noted that experienced, adult females did remain passive during copulation and accepted most attempts to mount by the consort male, browsing and grooming in the intermittent periods. The successful male escorted the oestrous female during this period and discouraged approaches by all other individuals, male or female, including the young at foot of the oestrus female. This was achieved through a variety of agonistic interactions varying from an approach resulting in the third individual moving away, to overt bouts of varying lengths.

By contrast, younger and less experienced females attempted repeatedly and unsuccessfully to elude males, resulting in prolonged chases, during which females appeared to become physically distressed. Many males became involved in these chases and, although one male usually remained dominant in these circumstances, as evidenced by its sole, close proximity to the oestrous female, multiple agonistic interactions between accompanying males commonly occurred. These were typified by rapid and very violent acts, especially kicking to the body. This occurred most frequently when the dominant male attempted copulation; other males present repeatedly kicked the dominant male until copulation was interrupted, at which stage the female and all accompanying males moved on again. Males took advantage of raised areas within the enclosure such as boulders and fallen trees to leap onto the back of the male engaged in copulation and deliver kicks. During the incident reported by Fleming *et al.* (1983), a consort male attempted to mate with an oestrus female but was repeatedly and violently attacked by several other males. However, unlike the incidents described by Fleming *et al.* (1983), competing males did not follow the oestrus female and consort male in line. Rather, unritualised attacks from behind or to the side of a successful male were seen, similar to those previously reported by Johnson (1989b) for red-necked wallabies and Gansloßer (1989) for Bennett's wallabies.

Agonistic interactions between male Bennett's wallabies have previously been noted to be brief in duration (15.5 s mean duration) and unritualised in nature, characterised by wrestling, pawing at the head and upper body and kicking towards the chest (Gansloßer, 1989). In this study agonistic encounters on occasions other than those when an oestous female was present were generally briefer and less intense than those described above. More frequently, one individual approached another, which moved away immediately or angled its head and upper body away. More overt interactions generally led to the subordinate individual moving away rapidly and, in these instances, the dominant animal rarely pursued it, even within the confines of the university enclosures, where the fleeing animal often remained in sight. This is typical of macropod species, which tend to form dominance hierarchies rather than exclusive territories and which do not generally drive away members of particular classes (Jarman, 1991).

Although overt agonistic interactions are more common among small to medium sized macropods, the type of agonistic interactions in which female Bennett's wallabies have been reported to engage in are typical of the less social macropod species (Jarman, 1991). In this study, overt bouts were occasionally seen between females, especially when one individual approached another who was feeding at a feeding station. Adult females occasionally drove away subadult and juvenile females away by repeatedly scratching and growling. Adult females less frequently engaged each other in these types of interactions. One subadult female was seen to repeatedly harass a conspecific who was in oestrus and being pursued by several males; eventually the males drove her away.

It has previously been reported that body size is a determining factor in the outcome of agonistic interactions between males of this subspecies (Fleming *et al.,* 1983). In this study, covert interactions were far more common than overt agonistic bouts. These types of interactions were difficult to detect as, usually, neither animal looked directly at the other. However, these covert interactions are important in determining the spatial distribution of group members (Jarman, 1991).

Mother-offspring interactions were similarly brief and typically terminated by the mothers. Mothers and their offspring engaged in allogrooming, a common feature of maternal interactions in the Macropodidae (Heathcote, 1989). Grooming actions were directed from both individuals towards each other. Female Bennett's wallabies engage in playful interactions with their male offspring that encompass sexual and agonistic acts (Murböck, 1977). Mothers in this study were observed to engage in play fighting with offspring for relatively prolonged periods of time; this was particularly true of male offspring, although female offspring also engaged in play fighting. Juvenile males also honed their fighting skills in bouts of play fighting with each other, subadult males and adult males, as previously described by Murböck (1977). An interesting observation was made regarding the nature of these interactions: adult males exercised considerable restraint in the face of the considerable enthusiasm of juveniles. This restraint was not apparent when subadults were engaged in overt bouts with adults males. Juveniles engaged in the most aggressive types of behaviour, including kicking and scratching. In response, adults males generally restricted their behaviour to wrestling and juveniles were never seen to suffer injury from these interactions.

Murböck (1977) suggested that observations of captive individuals undertaken by himself should form the basis of a consideration of the behaviour of these animals in the wild. The idea that captive studies can assist in gaining an understanding the behaviour of wild counterparts, providing proper weight is given to the specific conditions of captivity and their affect on behaviour, seems particularly pertinent. As previously mentioned, Bennett's wallabies stay hidden in refuges within dense vegetation during the day and emerge late in the day to feed (Calaby, 1984; Cronin, 1991). Observations of wild Bennett's wallabies prior to emergence could not be made, due to the cryptic habits of these animals. During those periods when observations could be made, individuals were seen engaging in those activities associated with eating, drinking, resting and grooming described in section 4.3.1 of this chapter. However, interactions, particularly between mothers and offspring, were rarely seen. In this regard, studies of captive individuals can assist in gaining a more complete understanding of the behavioural repertoire of a species.

As well as forming a qualitative behavioural inventory from observations of wild and captive individuals, the identification and description of elements of the behaviour of Bennett's wallabies, together with an understanding of how these individuals interact and how they apportion their activities, permits the undertaking of comparative studies aimed at producing a management plan for captive Bennett's wallabies that will provide standards of best practice.

Chapter 5 The Provision of Feeding Stations

5.1 Introduction

Clarke and Louden (1985) reported that Bennett's wallabies can spend 15 hours per day browsing, particularly when lactating. Wallabies that grazed on swards of varying lengths were observed to reduce their bite rate and increase search time per bite in response to increased sward length. Wallabies that grazed on short swards browsed for longer portions of the day, extending browsing time into the middle of the day. This contrasted with the reduced levels of browsing activity at midday recorded for individuals on swards with a greater herbage mass and suggests a degree of plasticity in the response of *M. r. rufogriseus* individuals to different herbage conditions (Clarke and Loudon, 1985).

The results of the survey of current managers of captive macropods, reported in Chapter 3, highlighted several priorities in caring for these animals. Fourteen out of 22 respondents cited various aspects of managing feeding regimes to ensure the delivery of adequate nutrition to meet the needs of all individuals as issues of key importance in their roles as managers of captive macropods.

Poole (1982) and Calaby and Poole (1971) noted the importance to the health of captive macropods, including Bennett's and red-necked wallabies, of providing high quality supplemental feed in addition to pasture. This feed is more efficiently utilised by captive macropods and less likely to become contaminated and produce health risks if it is placed in hoppers or on racks suspended above the ground. By utilising large feeders, the frequency of replenishing these can be reduced and feeding operations made more efficient (Poole, 1982). Large feeders provide economic benefits, but do they meet the feeding requirements of all captive individuals?

The provision of a number of alternative feeding stations was identified as a key factor in the successful management of captive quokkas, *Setonix brachyurus*, particularly with regard to minimising male aggression (Crebbin, 1982). Crebbin (1982) provided multiple feeding stations to a group of captive swamp wallabies, *Wallabia bicolour* (Desmarest), and reported that the number of agonistic interactions between members of different age and sex classes changed in response to the number of individuals accessing a food source and spacing of wallabies as they fed; the more individuals at a feeding station or browsing in close proximity to one another, the higher the probability of agonistic interactions.

In the Chapter 4 of this thesis, it was suggested that captive wallabies within the university enclosure exercised a priority of access to feeding stations, so that subordinate individuals "queued" in areas close to feeding stations while awaiting the departure of more dominant individuals. Dominant animals were seen to drive their subordinates away by growling and scratching. Under these circumstances, failing to provide a number of alternative feeding stations may lead to increased agonistic interactions and exclusion from food sources for some individuals. However, positioning a number of feeding stations in close proximity to one another may also give rise to undesirable interactions and may lead to increases in environmental stress and injuries suffered by captive Bennett's wallabies.

In response to respondents to the questionnaire in Chapter 3 identifying feeding regimes as a key management issue, this chapter describes the effect of manipulating one aspect of the enclosure environment of Bennett's wallabies at the university: the availability of feeding stations. Both the number and position of feeding stations available was varied to investigate whether this would significantly alter the frequencies of focal individuals, as well as members of each sex and age class:

1. occupying each of the sectors of the enclosure;
2. performing any element from each category of behaviour; and
3. performing specific individual behavioural elements.

5.2 Materials and Methods

5.2.1 Experimental Methods

Captive subjects were observed in the enclosure at the University of Tasmania's Hobart campus under three trial conditions represented in Figure 5.1. These were –

1) Trial 1: Four feeding stations were utilised in sectors one, two, three and seven, positioned within the sectors so that feeding stations were spaced throughout the enclosure.

2) Trial 2: Feed was only provided at the feeding stations in sectors two and seven, at diagonally opposite ends of the enclosure.

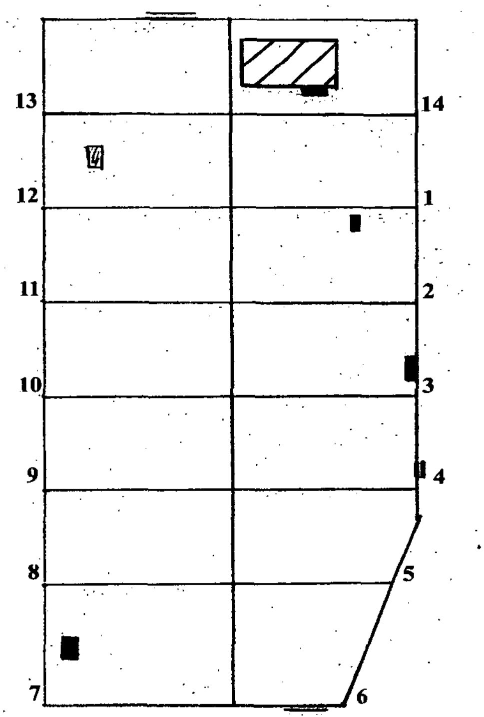
3) Trial 3: Four feeding stations were positioned in sectors one, two and three, all within close proximity of one another.

A mixture of wallaby pellets and lucerne chaff was provided at feeding stations *ad lib.* and browse matter was always available in the form of grass, trees and shrubs throughout the enclosure.

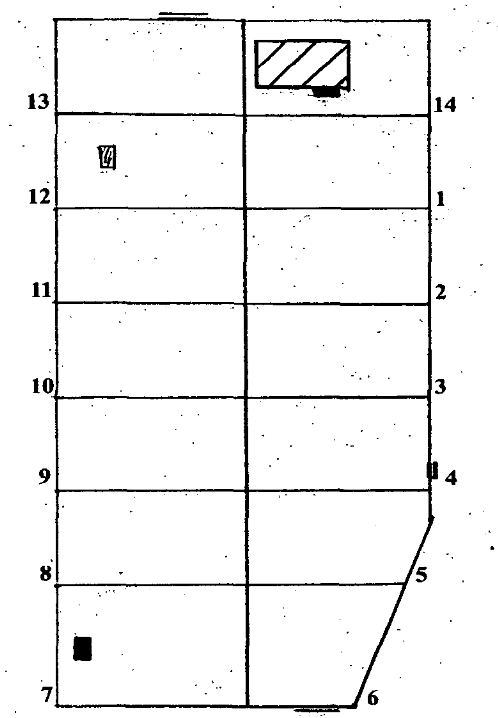
Observations were conducted between 15:00 and 21:00 h over the period between the end of April and the start of September in 1997. Wallabies were observed after dark by utilising the spotlights permanently mounted throughout the enclosure. Spotlights were turned on at least half an hour prior to sunset so that this event did not disturb the wallabies. All observations were taken from the observation post inside the shed previously described in Section 2.1.4. Upon entering the enclosure, the feeders currently being utilised were checked to ensure feed was still available. A period of at least 30 min was then allowed to elapse before recordings were commenced, in order to permit the wallabies to recover from the disturbance.

Wallabies were observed over 30 min sample periods by employing the focal animal technique described by Altmann (1974). Fifty-one hours of observations were recorded for each trial condition, yielding a total of 153 h. Individuals were visually identified using the coloured ear tags previously described so that their identity, sex and age class could be recorded. Initially, six wallabies were held in the 1000 m^2 of the enclosure. This group comprised a subadult and a juvenile male, three adult females and one subadult female. Because the behaviour of each individual in the captive group can reasonably be expected to effect the behaviour of other group members, and as all group members were required to be included in the sampling, the observed behaviour of focal individuals cannot be said to be independent without taking additional steps. In order to increase the independence of observations of behaviour, one adult female was substituted into the enclosure from the holding group when half the recordings for each trial condition had been achieved.

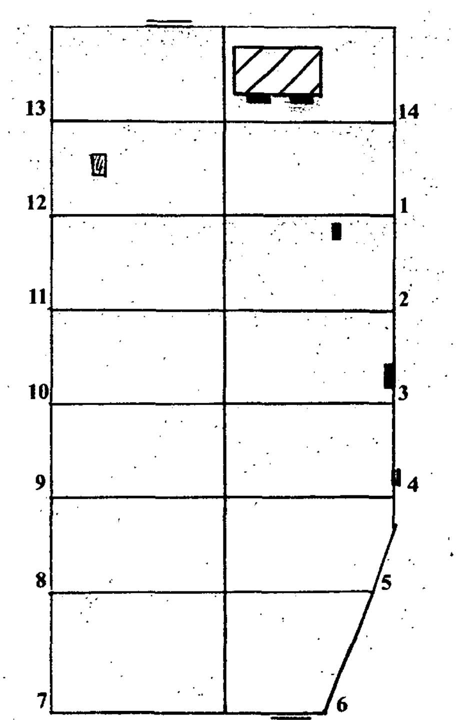
During the sample period, all activities in which the focal animal was engaged were recorded. Any interactions with other wallabies were recorded, including acts performed by all participants from instigation to cessation. Finally, a record was made every 5 min, starting at zero minutes, of the sector of the enclosure occupied by the focal animal.



a) Trial 1 Four feeding stations spaced throughout the enclosure



b) Trial 2 Two feeders spaced apart



b) Trial 3 Four feeding stations clumped together

Figure 5.1: Positioning of feeding stations during Trials 1, 2 and 3.

5.2.2 Data Treatment

Data collected from focal animal observations were used to produce descriptive statistics. In order to do this, data collected on the frequencies of the occupation of each of sector of the enclosure, and the occurrence of each of the behavioural elements and categories of behaviour, were converted to percentage values. During each half hour observation period, seven separate recordings were made of the location and activity of the focal individual. Each half hour sample of seven recordings was tallied into count data (for example, three recordings of the focal individual in sector 1 and 4 in sector 11) and these counts were then tallied into percentage frequencies. From this, both mean frequencies and standard deviations could be calculated. This process was utilised for all data for each trial condition. Data for each sex and age class were then separated out and treated in the same manner.

5.2.3 Statistical analyses

Kruskal-Wallis tests were utilised to identify any significant differences in the frequencies of the occupation of each sector of the enclosure, the frequency of the performances of acts and events belonging to behavioural categories and the performance of specific individual behavioural elements between the three trial conditions. The categories of miscellaneous behaviour and mother-offspring interactions were again excluded from consideration, the former because of the low frequencies of occurrence and the latter because of time restraints that prevented controlling for the age of the offspring. The individual elements of behaviour that were statistically analysed were those examined in Chapter 4, as they occurred relatively frequently and allowed consideration of issues such as aggression, the attractiveness of the exhibit stemming from activity and individual comfort withinth the enclosure environment. Initially, data for all focal individuals were pooled and analysed. Next, data were separated by sex and age class and each tested in the same manner. Where a significant difference was identified, a post-hoc Mann-Whitney U test was then performed on pairs of trials to identify which trials gave rise to this difference. P values of <0.05 were considered to be significant in all instances.

5.3 Results

5.3.1 Spatial Patterns

5.3.1 (i) Group Spatial Patterns

The percentages of the total observation time for which individuals were recorded in each sector of the enclosure are presented in Figure 5.2. In Trial 1, focal animals were recorded in most sectors, with the exception of sectors three to six, which were the most heavily vegetated areas furthest from the observer's post. In Trial 2, a sharp increase in the occupation of sector seven occurred and sectors eight to eleven, grassy areas where browsing matter was available, were less frequently occupied. Although feed was also provided in sector two, occupation of this area did not increase in line with the increase in sector seven; in fact, it decreased. However, during Trial 3, the occupation of sectors one and two increased to their greatest levels.

Several significant differences in the use of some sectors during the three trial conditions occurred; these are shown in Table 5.1. As previously noted, during Trial 3, the occupation of sectors one, two and 13 (adjacent to sector two and providing an access route to the feeder) significantly increased, while utilisation of sector seven decreased. By comparison, during Trial 2, only the use of sector seven increased significantly when compared to Trial 1. Use of sectors three and four, where feed was no longer available, decreased, while sectors four and six were more frequented.

The greatest difference in the patterns of utilisation of the enclosure occurred between the Trials 2 and 3. Sectors one and two were more frequently utilised and a corresponding decrease in the use of sector seven occurred during Trial 3. Sectors three and 13 were visited more frequently during Trial 3. By comparison, sectors four and six were more often occupied by focal animals during Trial 2.

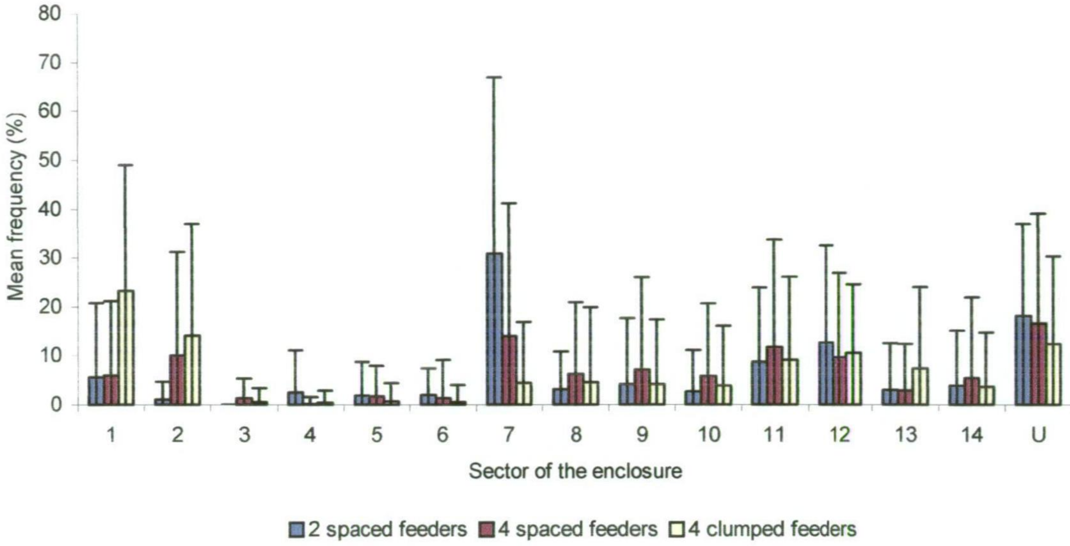


Figure 5.2: The mean percentages (± standard deviations) of overall sightings in which focal individuals were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=100 observation periods for each trial condition.

Table 5.1: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of occupation of sectors 1-14 had been identified. Differences were considered significant if $p<0.05$. Trial 1 = four feeders distributed in sectors one, two, three and seven. Trial 2 = two feeders distributed so that one each is in sectors two and seven. Trial 3 = four feeders in sectors one, two and three. N = 100 observation periods for each trial condition.

Sector	Trial 1 vs. Trial 3		Trial 1 vs. Trial 2		Trial 2 vs. Trial 3	
	H value	P value	H value	P value	H value	P value
1	40.57	0.001	-	-	40.57	0.001
2	15.52	0.045	15.52	0.001	15.52	0.001
3	-	-	1.216	0.002	1.216	0.044
4	-	-	1.360	0.005	1.360	0.042
6	-	-	1.754	0.027	1.754	0.010
7	27.34	0.024	27.34	0.001	27.34	0.001
13	2.842	0.030	-	-	2.842	0.033

5.3.1 (ii) Patterns of Spatial Utilisation by Each Sex

Females

The mean frequencies of the occupation of sectors of the enclosure by female Bennett's wallabies in the three trial conditions are presented in Figure 5.3. These frequencies varied between the trial conditions in line with that previously described in Figure 5.2. The use of the open areas of the enclosure increased during Trial 1, when four feeders were spaced throughout the enclosure. During Trial 2, when two feeding stations were utilised at opposite corners of the enclosure, use of sector seven, containing the feeding station furthest from the observer's post, greatly increased. By contrast, when feeders were positioned close together (Trial 3) use of sector seven decreased and females were more frequently recorded in sectors one and two.

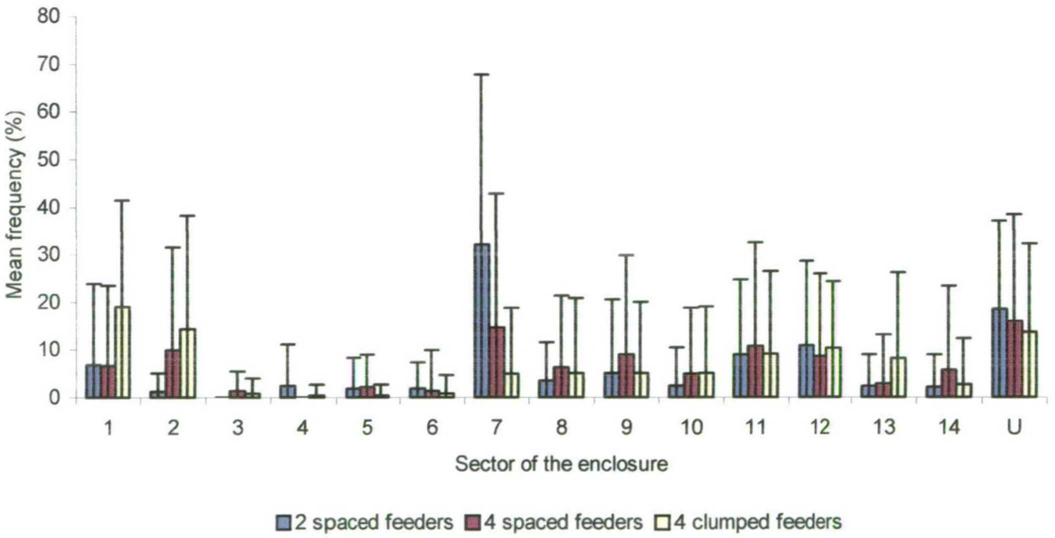


Figure 5.3: The mean percentages (± standard deviations) of overall sightings in which females were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. Sector 15 represents those occasions when a focal animal was not in sight at the time a recording fell due. N=75 observation periods for each trial condition.

Males

The frequencies of recording males in each sector of the enclosure during the three trials are shown in Figure 5.4. The patterns of occupation of the sectors of the enclosure by males in each of the trials were similar to that described for females. However, some differences can be seen. When feeding stations were available in other sectors (Trials 1 and 2), males utilised those in sectors one and two at lower rates than females. When only two stations were available (Trial 2), males occupied sector seven even more frequently than females. However, when feeding stations were clumped together in sectors one and two (Trial 3), the frequency of recording males here was greater than that of females.

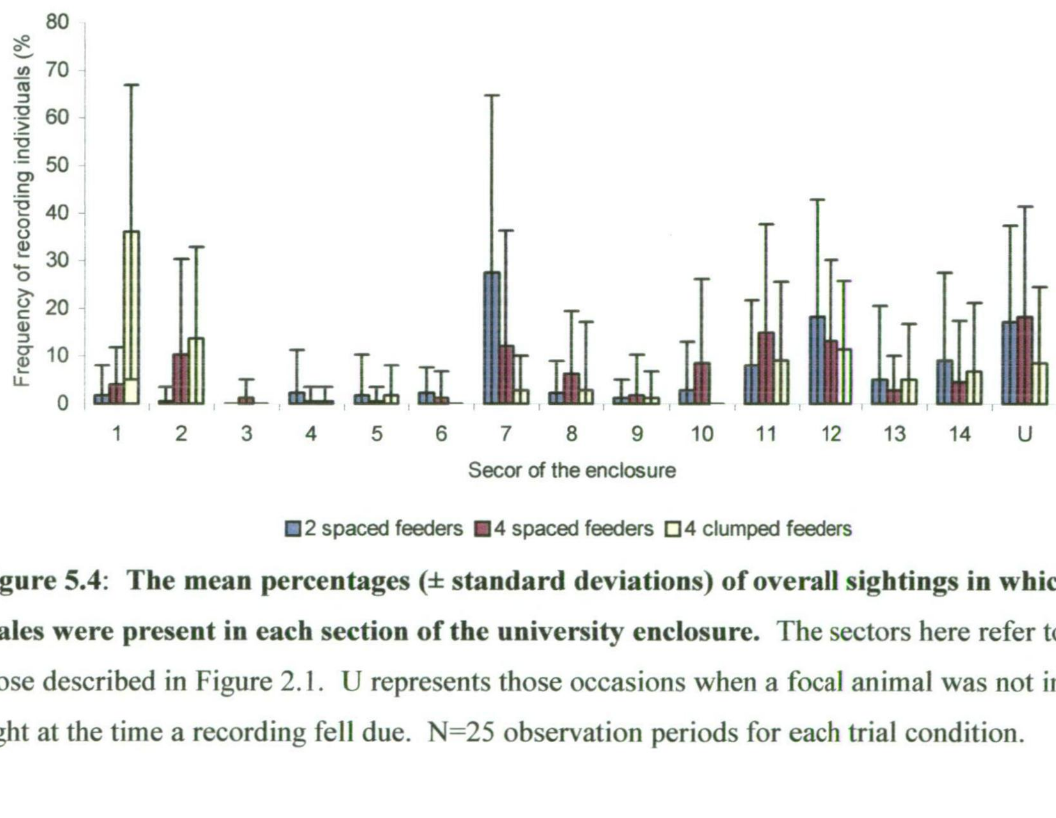


Figure 5.4: The mean percentages (± standard deviations) of overall sightings in which males were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=25 observation periods for each trial condition.

5.3.1 (iii) Patterns of Spatial Utilisation by Each Age Class

Adults

The percentages of the total time adult focal animals were recorded in each sector of the enclosure are presented in Figure 5.5.

Adult Bennett's wallabies were less frequently recorded in sectors one and two during Trial 3, when feeding stations were clumped together in this area, than when considering all individuals together. However, their occupation of sector one at other times was greater than when considering all focal individuals. During Trial 3, the occupation of sectors one and two was greater than at other times. The use of sectors four and five, shrubby areas, also varied between trials, with the occupation rates of the former at their lowest in Trial 2, while the opposite is true of the latter.

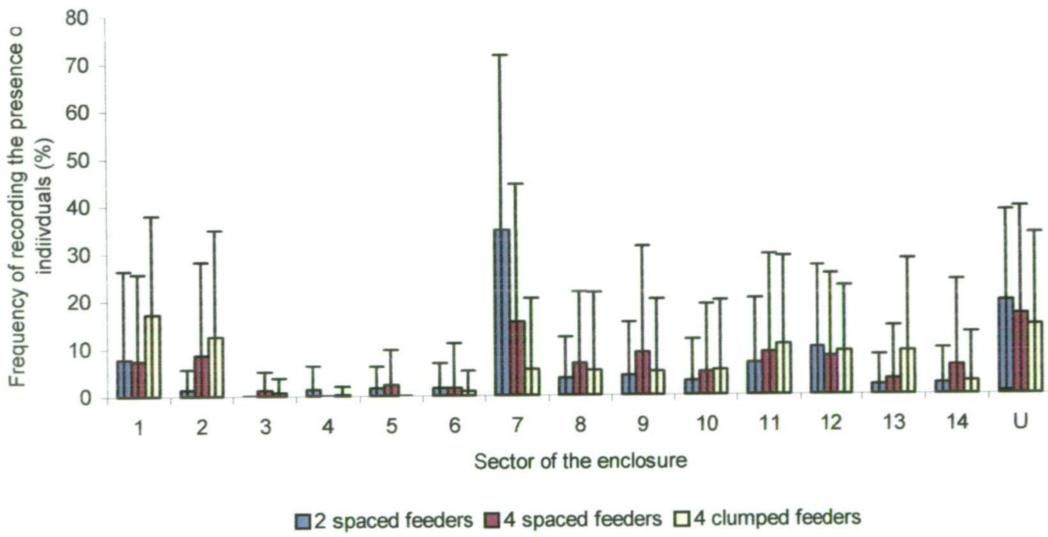


Figure 5.5: The mean percentages (± standard deviations) of overall sightings in which adults were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=62 observation periods for each trial condition.

Subadults

The patterns of the occupation of sectors by subadult individuals are presented in Figure 5.6. Subadults were recorded in sector one more frequently than adults when feeding stations were clumped here (Trial 3). At other times, they were far less frequently seen in this area. When four feeding stations were being utilised (Trial 3), the occupation of sector two by subadults was greater than for adults. However, when only two feeders were available (Trial 2), sector two was hardly visited. Sector seven was occupied far less by subadults in this circumstance than by adults. Subadults were more frequently recorded in the more heavily vegetated areas of the enclosure than adults, with the exception of sector six. Subadult Bennett's wallabies were sighted in sectors 11 and 12 more frequently than their adult counterparts.

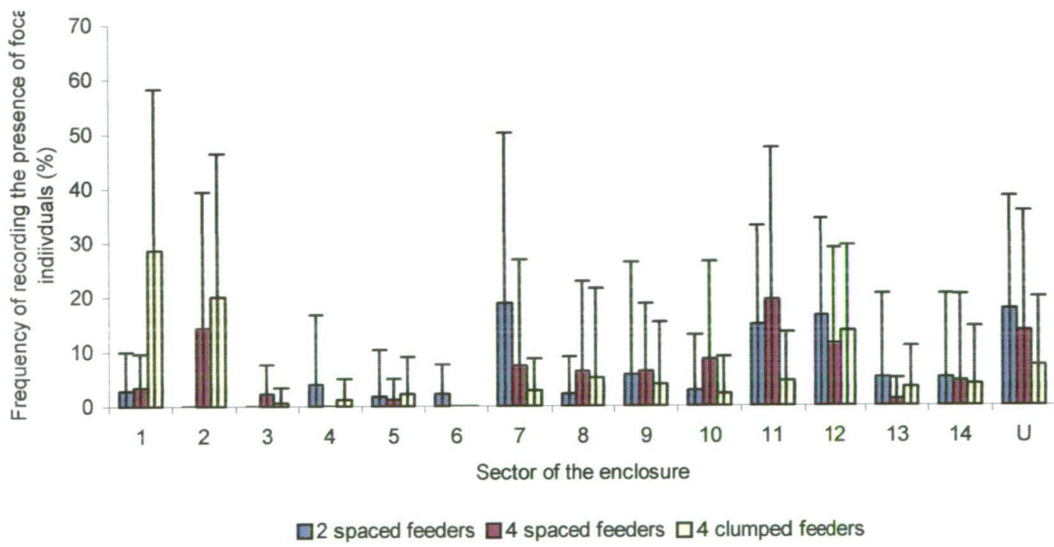


Figure 5.6: The mean percentages (± standard deviations) of overall sightings in which subadults were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=25 observation periods for each trial condition.

Juveniles

The frequencies of occupation of each sector of the enclosure by juvenile Bennett's wallabies are presented in Figure 5.7. These individuals were sighted in the more open areas of the enclosure represented by sectors eight, nine and ten far less often than either adults or subadults. When feeding stations were only available in sectors one, two and three (Trial 3), juveniles greatly increased the amount of time spent in sector one but had relatively low rates of occupation of sector two. Conversely, sector seven was far more frequently occupied when only two feeding stations were available (Trial 2) than when four were clumped together (Trial 3).

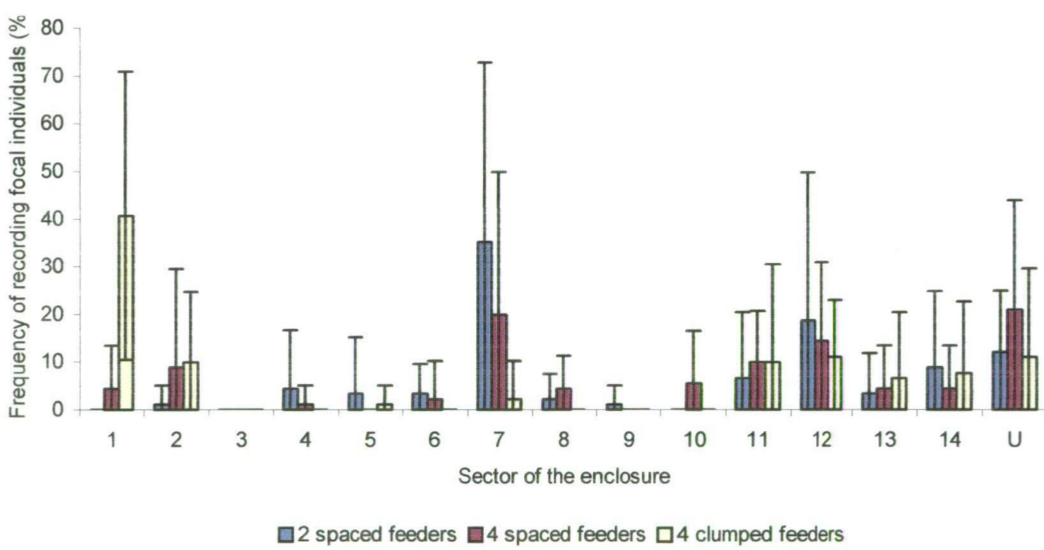


Figure 5.7: The mean percentages (± standard deviations) of overall sightings in which juveniles were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=13 observation periods for each trial condition.

5.3.2 Frequencies of Observations of Acts from Categories of Behaviour

5.3.2 (i) Group Frequencies of Observations of Acts from Categories of Behaviour

The various elements of behaviour recorded for focal individuals were grouped together into categories of behaviour and the mean frequency of acts from each of these categories are summarised in Figure 5.8. In each trial, wallabies devoted the greatest amount of time to feeding activities. Focal animals were out of sight for the next longest period of time. When feeding stations were clumped together in close proximity to the observer's position (Trial 3), the period of time devoted to feeding activities increased and individuals were less frequently recorded as out of sight. Wallabies were most frequently recorded as unsighted when feeding stations were placed in locations throughout the enclosure (Trial 1).

The total amount of time for which wallabies were recorded as having adopted alert postures also varied between the three trials. The lowest frequencies of these acts were recorded when feeding stations were spaced apart (Trial 1). When the number was reduced from four to two (Trial 2), almost half again the number of alert postures were recorded. This difference further increased when the feeders were clumped together (Trial 3), so that alert postures were adopted almost twice as frequently in this trial as when the same number of feeding stations were spaced apart (Trial 1).

The frequencies of acts belonging to each of these behavioural categories were tested to see if significant variations occurred between the various trials. Some differences were discovered and these are reported in Table 5.2.

The total amount of time devoted to feeding activities was significantly shorter when feeding stations were spaced throughout the enclosure (Trial 1) than in either of the other two conditions. The number of alert postures increased as feeding stations were removed (Trial 2) and was higher again when feeders were positioned closer to each other (Trial 3). By contrast, the number of occasions in which individuals were recorded as not sighted was significantly greater when four spaced feeding stations were employed (Trial 1) than when the same number were clumped together (Trial 3). Similarly, the frequencies with which individuals were recorded either walking or hopping across the enclosure was significantly greater when four feeders were spaced throughout the enclosure (Trial 1) than in either of the other trials. The greatest number of social interactions was recorded during Trial 2 and this was significantly higher than the number recorded during Trial 3.

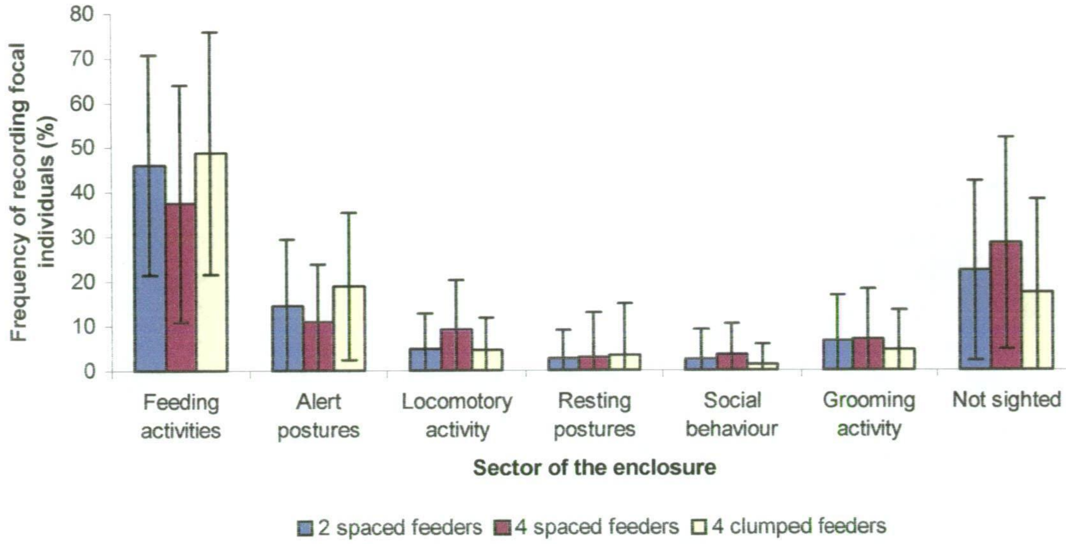


Figure 5.8: The mean percentages (± standard deviations) of overall sightings in which focal individuals were recorded performing any of the acts from categories of behaviour. N=100 observation periods for each trial condition.

Table 5.2: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing any of the acts from each category of behaviour. Differences were considered significant if $p<0.05$. Trial 1 = four feeders distributed in sectors one, two, three and seven. Trial 2 = two feeders distributed so that one each is in sectors two and seven. Trial 3 = four feeders in sectors one, two and three. N = 100 observation periods for each trial condition. H values provided are from the Kruskal-Wallis one-way analysis of variance.

Category of behaviour	Trial 1 vs. Trial 3		Trial 1 vs. Trial 2		Trial 2 vs. Trial 3	
	H value	P value	H value	P value	H value	P value
Feeding activities	10.35	0.013	10.35	0.012	-	-
Alert postures	11.96	0.001	11.96	0.013	11.96	0.050
Locomotory activities	8.622	0.003	8.622	0.004	-	-
Elements of social behaviour	3.300	0.004	-	-	-	-
Not sighted	11.55	0.001	-	-	-	-

5.3.2 (ii) Frequencies of Observing Members of Each Sex Performing Acts from Each of the Categories of Behaviour

Frequency data derived from recordings of focal individuals were divided by sex and each was considered separately. The way that female wallabies apportioned their time between each of the categories of behaviour is presented in Figure 5.9 and that of males in Figure 5.10.

Females

Females apportioned the largest amount of time to activities associated with eating and drinking in all three trials. When four feeders were clumped together (Trial 3), females were more frequently sighted in alert postures than in either of the other two trials. When four feeders were positioned throughout the enclosure (Trial 1), females moved about more and spent more time grooming themselves. Social interactions were also more common in these circumstances.

The number of alert postures recorded for females was significantly less when four feeders were spaced throughout the enclosure (Trial 1) than in either of the other trials. However, grooming activity increased at this time.

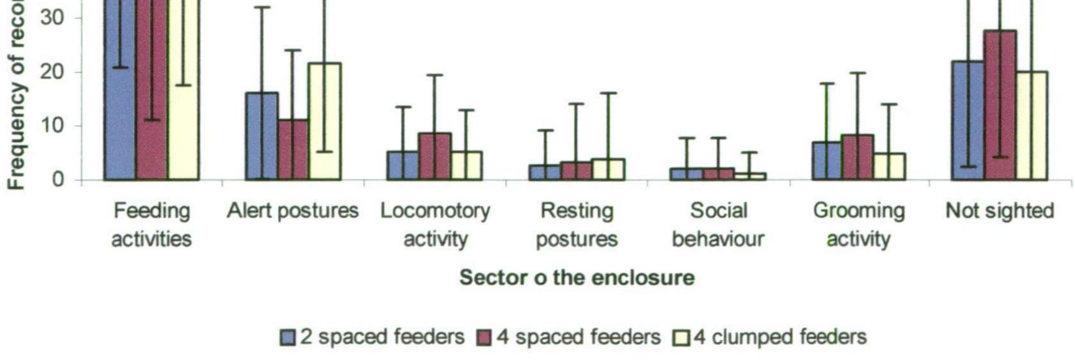


Figure 5.9: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing any of the acts from categories of behaviour. N=75 observation periods for each trial condition.

Males

Male Bennett's wallabies also devoted the largest proportion of time to feeding activities. The amount of time males devoted to feeding activities varied between all conditions, with this activity occurring most frequently when feeding stations were clumped together (Trial 3) or reduced in number (Trial 2). When four feeding stations were spaced throughout the enclosure (Trial 1), males moved around more and were recording eating and drinking less frequently than at other times. Males also engaged in relatively frequent social interactions and periods of grooming. The frequencies of adopting alert postures were similar in each of the three trials. Males were recorded as out of sight less frequently when four feeders were clumped together (Trial 3) than in either of the other trials.

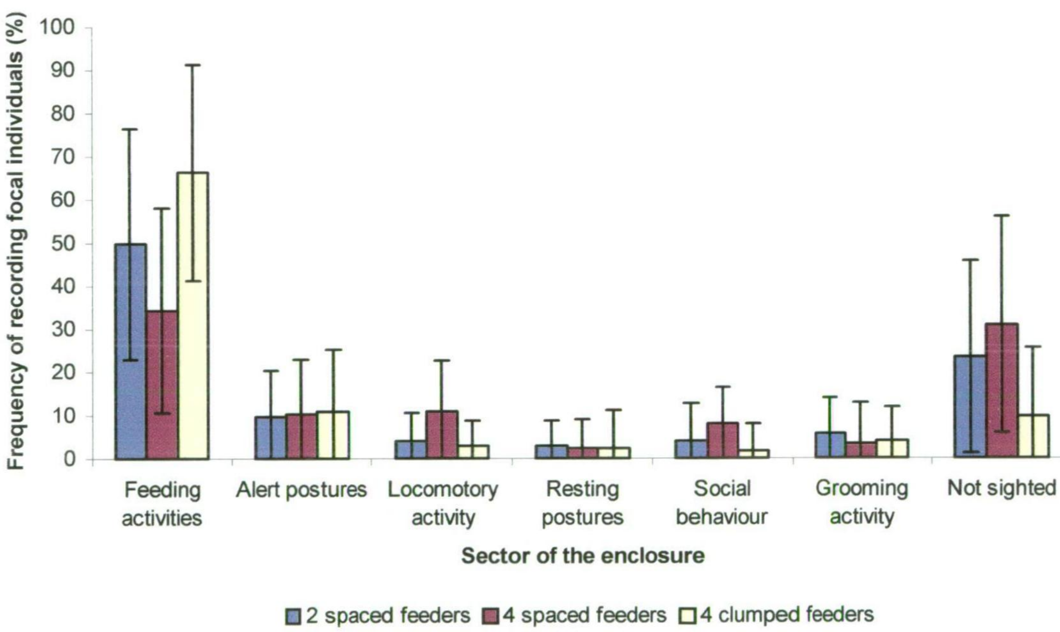


Figure 5.10: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing any of the acts from categories of behaviour. N=25 observation periods for each trial condition.

5.3.2 (iii) Frequencies of Behaviour Categories for Each Age Class

Frequency data derived from recordings of focal individuals performing any act from each of the categories of behaviour were divided by age class and each was considered separately. The way that adult wallabies apportioned their time between each of the categories of behaviour is presented in Figure 5.11, that of subadults in 5.12 and juveniles in 5.13.

Adults

Adult Bennett's wallabies spent similarly large periods engaged in feeding activities in all trials. Periods during which adults were out of sight were also similar in each of the three trials. When four feeding stations were clumped together (Trial 3), alert postures were more commonly adopted, particularly compared to adults presented with the same number of feeding stations spread throughout the enclosure (Trial 1). Adults moved through the enclosure and groomed more during Trial 2.

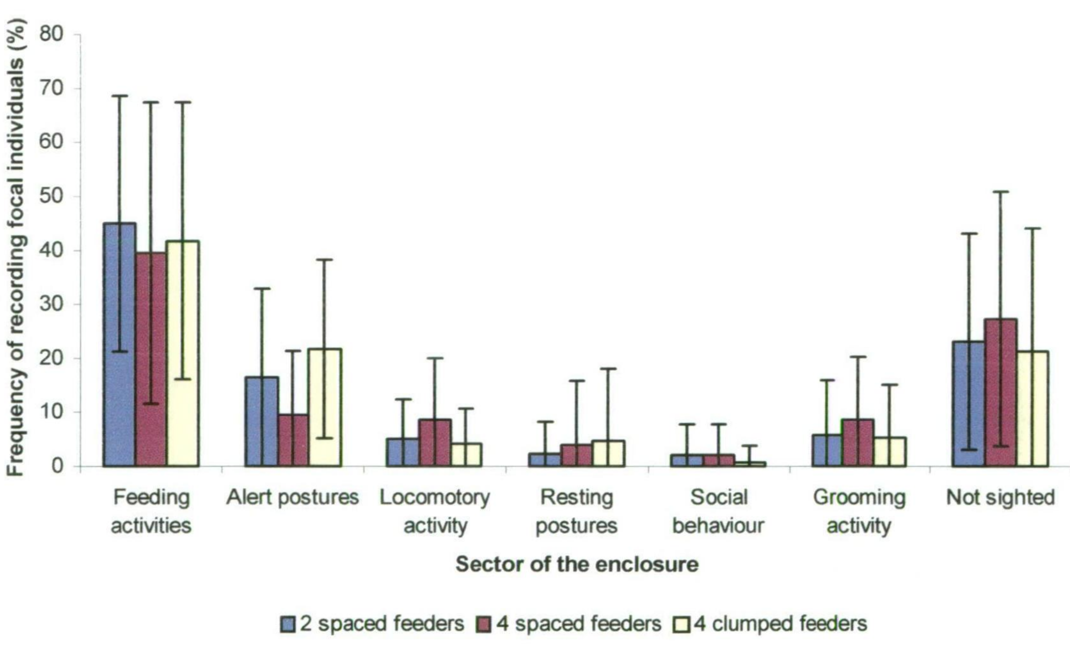


Table 5.11: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing any of the acts from categories of behaviour. N=62 observation periods for each trial condition.

Subadults

Subadult Bennett's wallabies, by contrast, spent more time eating and drinking when four feeding stations were positioned near to each other (Trial 3) than at other times, while the least amount of time was apportioned to these activities when these feeders were spaced apart (Trial 1). The same pattern was seen for the adoption of alert postures, which were most commonly seen when feeders were clumped (Trial 3) and least when four feeders were spread out (Trial 1). When only two feeding stations were stocked with feed, subadults remained in vegetative refuges and grooming was more common.

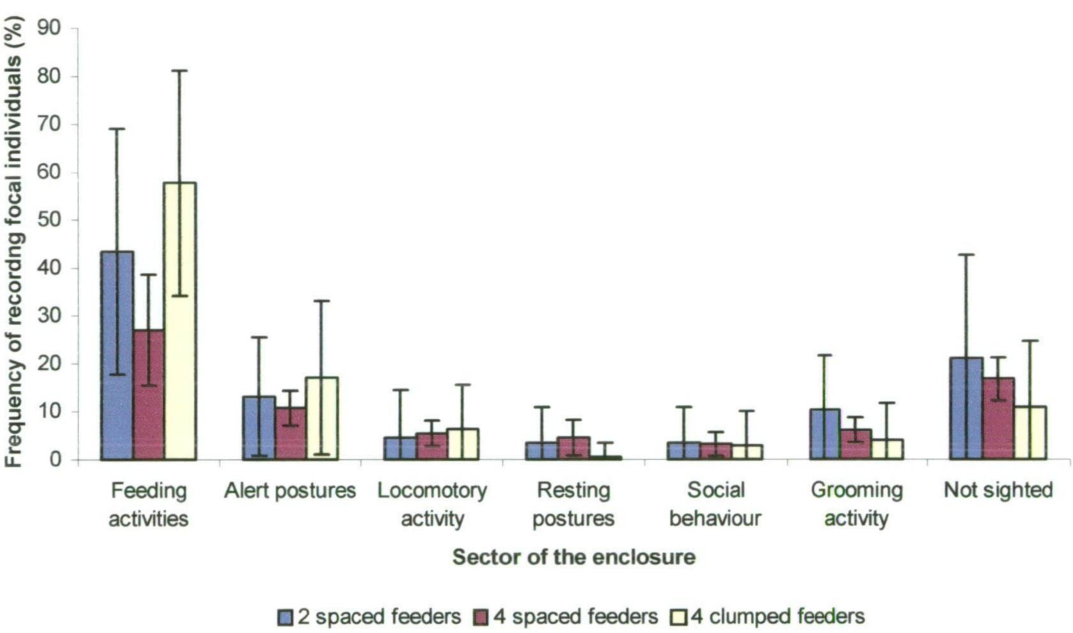


Table 5.12: The mean percentages (± standard deviations) of overall sightings in which subadults were recorded performing any of the acts from categories of behaviour. N=25 observation periods for each trial condition.

Juveniles

Juveniles devoted large portions of time to eating and drinking when only two feeding stations were available (Trial 2) or when four were clumped together (Trial 3). However, less than half this time was spent feeding when four feeding stations were spaced apart. Instead, wallabies were hidden from view more often and were more often recorded moving about the enclosure and social interactions were relatively common.

The amount of time devoted to feeding activities by the younger age classes was greatest in Trial 3, although juveniles were also recorded feeding more of the time when the number of feeders was reduced from four (Trial 1) to two (Trial 2).

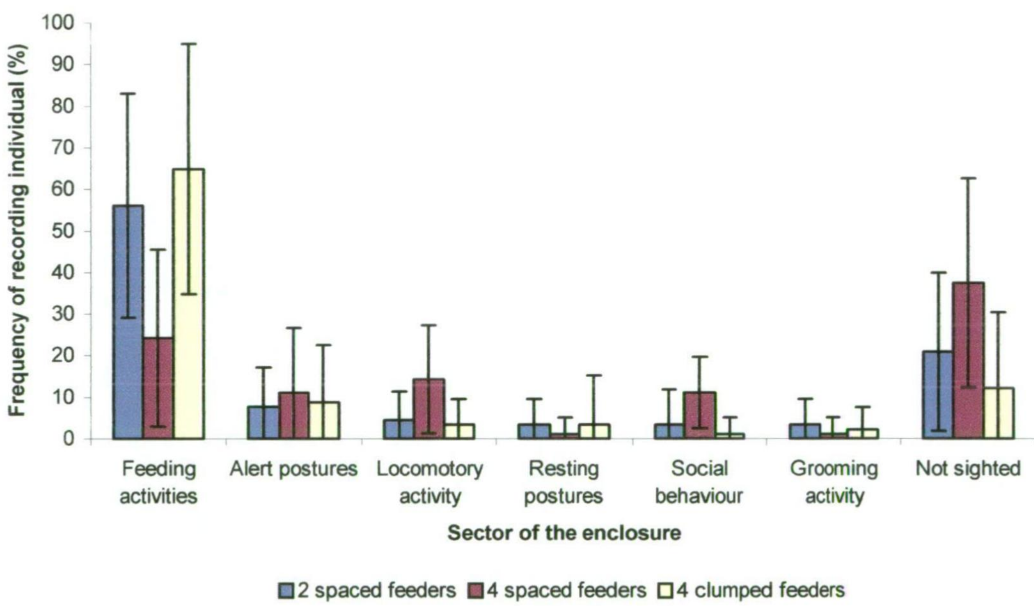


Figure 5.13: The mean percentages (± standard deviations) of overall sightings in which juveniles were recorded performing any of the acts from categories of behaviour. N=13 observation periods for each trial condition.

5.3.3 Frequency of Behavioural Elements and Events

5.3.3 (i) Group Frequencies of Behavioural Elements and Events

The frequencies with which focal animals performed individual behavioural elements in each of the trial conditions are presented in Figures 5.14 and 5.15. The results of post-hoc Mann-Whitney U tests performed on these data are presented in Table 5.3.

The type of feeding activities engaged in varied between each trial condition. Less time was devoted to browsing when four feeders were clumped together (Trial 3) compared to the other trials, while twice as much time was devoted to feeding at the feeding stations during Trial 3 than at other times, with the lowest frequency occurring during Trial 2.

The total number of crouched and upright alert postures adopted in each trial also varied. As the number of feeders were reduced (Trial 1) and then clumped together (Trial 3), the number of crouched alert postures increased. In contrast, the number of upright alert postures decreased as crouched postures increased.

The different resting postures were recorded at similar frequencies in each of the three trials. Lying was most frequently recorded during Trial 2, while sitting back on the haunches was most common during Trial 3.

Individual rarely looked directly at another during Trial 3, but this behaviour increased in frequency during Trial 1. A relatively high number of approaches were recorded in the Trial 2.

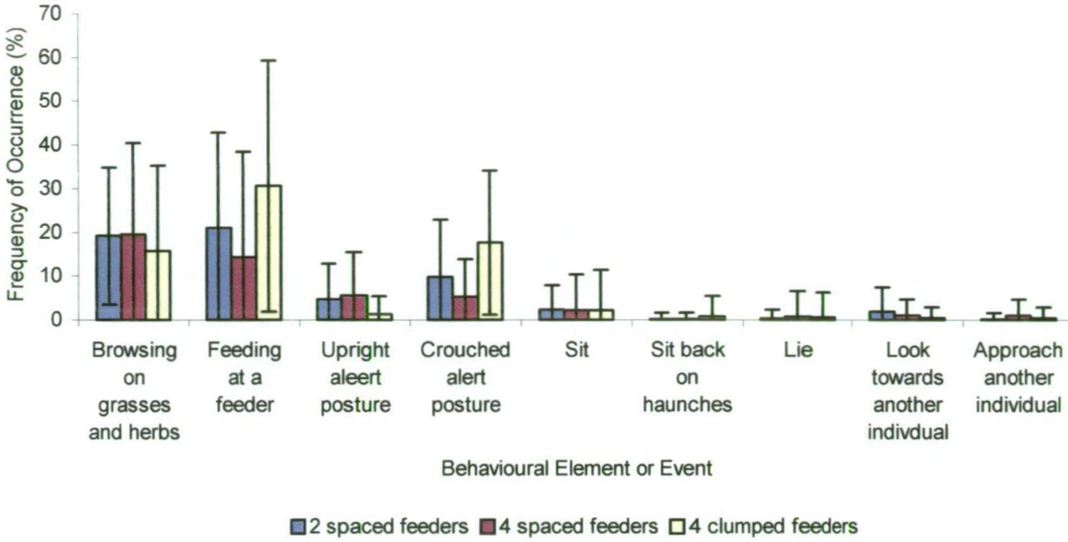


Figure 5.14: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing the key elements of behaviour. N=100 observation periods for each trial condition.

Grooming generally occurred at similar levels in all three trials. Grooming of the hind limbs was less frequent during Trial 2, while grooming the sides increased during the same trial.

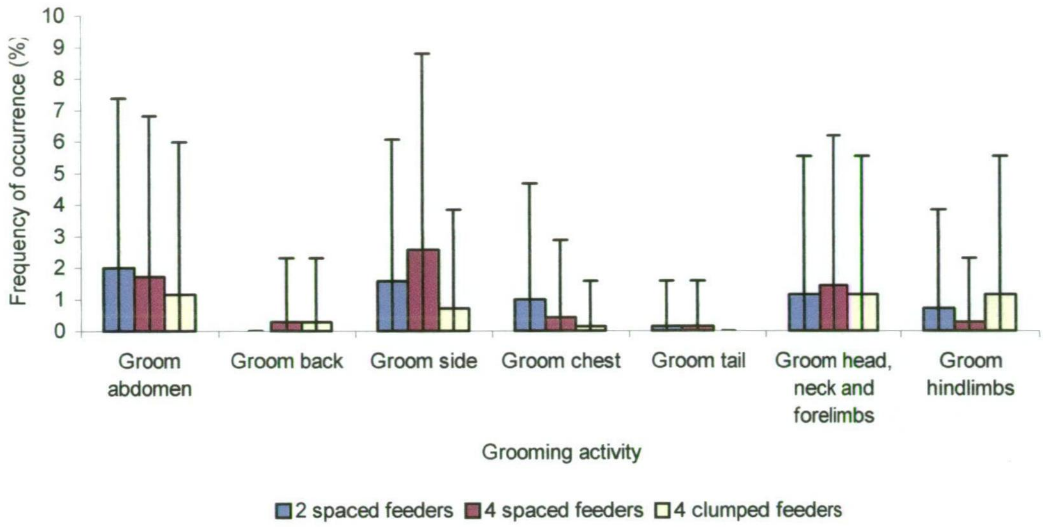


Figure 5.15: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing grooming actions. N=100 observation periods for each trial condition.

The greatest variation occurred between the two trials 1 and 3. Crouched alert postures were adopted significantly less frequently when four feeders were spaced apart (Trial 1) than in either of the other two trials and less when two feeders were spaced apart (Trial 2) than when four were clumped together (Trial 3). The number of upright alert postures did not differ significantly between the two conditions where feeding stations were spaced apart (Trials 1 and 2), but the number adopted when four feeders were spaced apart (Trial 1) was significantly higher than seen for Trial 3 and higher during Trial 3 than for Trial 2.

The differences in time apportioned to feeding from a feeding station described above varied significantly between the three trials when compared to each other.

Although grooming activity accounted for a very minor proportion of the day's activities, the number of times focal animals were recorded directing grooming actions towards their sides was significantly greater during Trial 1 than during Trial 3.

Table 5.3: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing elements of behaviour. Differences were considered significant if $p<0.05$. Trial 1 = four feeders distributed in sectors one, two, three and seven. Trial 2 = two feeders distributed so that one each is in sectors two and seven. Trial 3 = four feeders in sectors one, two and three. N = 100 observation periods for each trial condition. H values provided are from the Kruskal-Wallis one-way analysis of variance.

Behavioural element or event	**Trial 1 vs. Trial 3**		**Trial 1 vs. Trial 2**		**Trial 2 vs. Trial 3**	
	H value	**P value**	**H value**	**P value**	**H value**	**P value**
Crouched alert posture	31.03	0.001	31.03	0.013	31.03	0.001
Upright alert posture	8.084	0.001	-	-	8.084	0.001
Feeding from a feeding station	22.57	0.001	22.57	0.001	22.57	0.028
Groom side	1.858	0.011	-	-	-	-

5.3.3 (ii) Frequencies of Observing Members of Each Sex Performing Behavioural Elements

Frequency data derived from recordings of focal individuals were divided by sex and each was considered separately. The frequencies with which female wallabies performed each behavioural element are presented in Figures 5.16 and 5.17 and that of males in Figures 5.18 and 5.19.

Females

The amounts of time females spent browsing about the enclosure were similar in each trial, although lower when the feeders were positioned in close proximity (Trial 3). In this latter trial condition the time spent attending feeding stations was greater than at other times.

Females rarely adopted the upright alert posture when feeding stations were clumped together. The crouched alert posture was relatively common; these were recorded more frequently in Trial 3 compared to the other trials.

Females looked directly at other individuals most frequently when only two feeders were available.

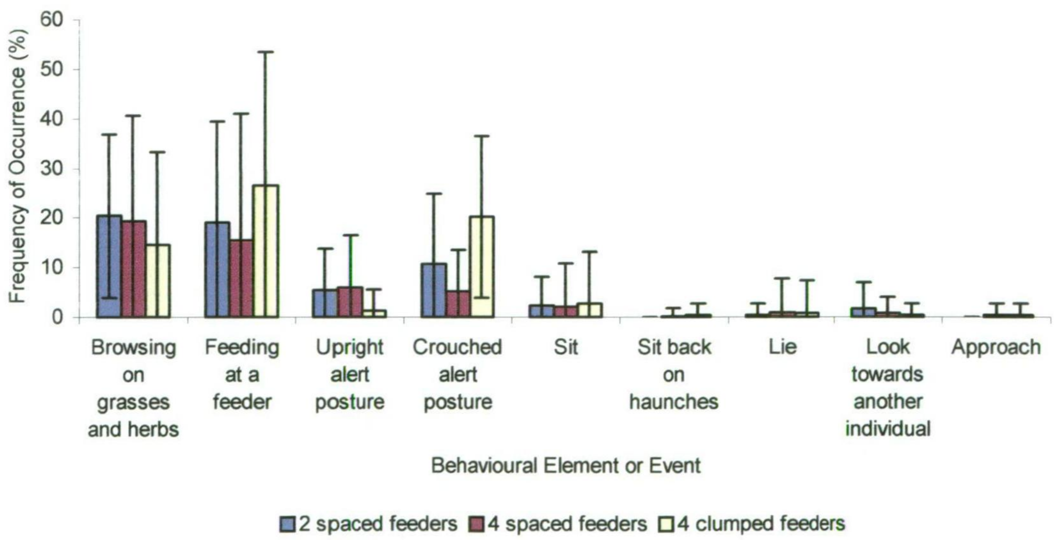


Figure 5.16: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing the key elements of behaviour. N=75 observation periods for each trial condition.

Females groomed their sides more frequently during Trial 2, but were almost never recorded grooming their hind limbs during the same trial. The frequency of grooming actions being directed towards the chest was greatest when two feeders were spaced apart and least when four feeders were clumped together.

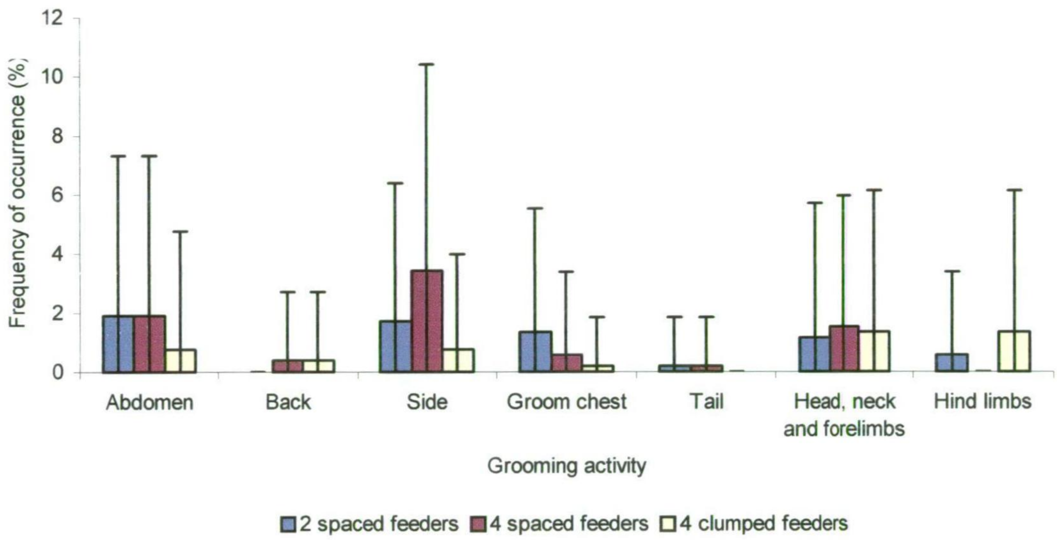


Figure 5.17 : The mean percentages (± standard deviations) of overall sightings in which females were recording performing grooming actions. N=75 observation periods for each trial condition.

Males

Although males spent similar amounts of time browsing about the enclosure compared to females, the time spent attending feeding stations varied to a greater degree between the three trials. Males fed from feeders for the greatest periods when these were clumped together (Trial 3) and the least when four were spaced apart (Trial 1). Males were rarely seen in resting postures in any of the trials.

Male subjects approached other wallabies more often when four feeders were spaced throughout the enclosure but looked directly at others more frequently when two feeders were spaced apart.

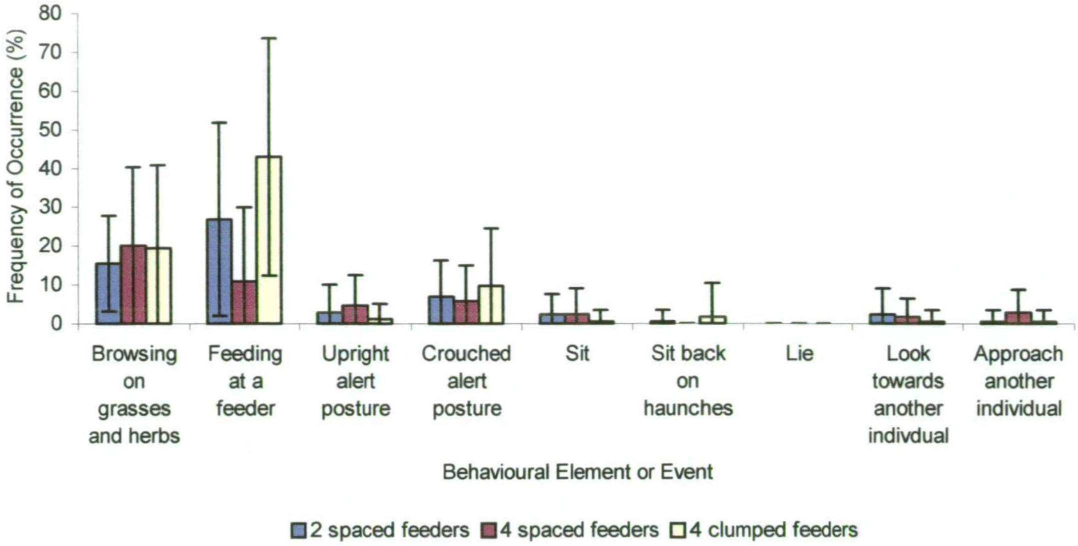


Figure 5.18: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing the key elements of behaviour. N=25 observation periods for each trial condition.

In contrast to females, males were not recorded grooming their sides during Trial 2 and rarely groomed their abdomens at this time.

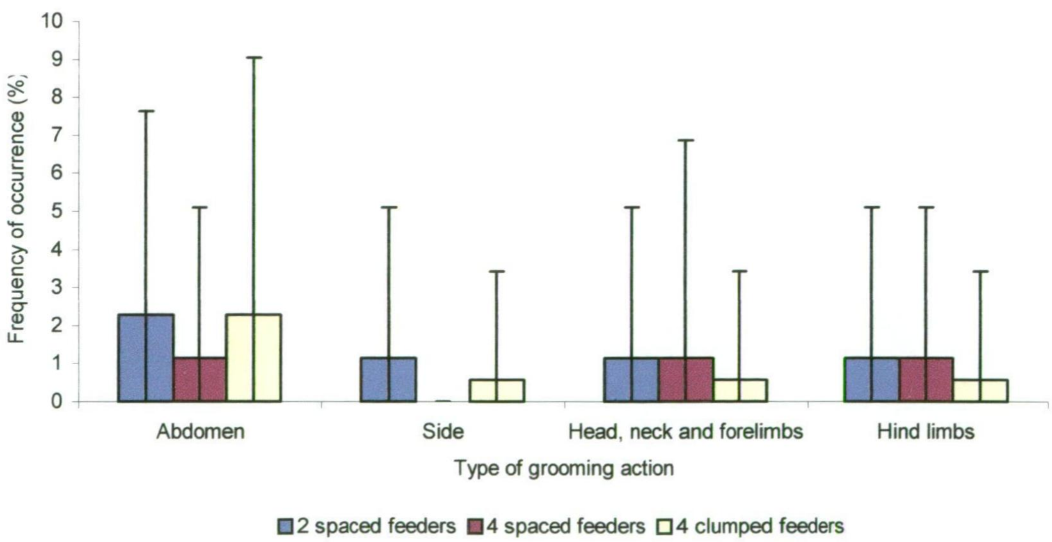


Figure 5.19: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing grooming actions. N=25 observation periods for each trial condition.

5.3.3 (iii) Frequencies of Behavioural Elements and Events for Each Age Class

Frequency data derived from recordings of focal individuals were divided into the three age classes and each considered separately. The frequencies with which adults wallabies performed each behavioural element are presented in Figures 5.20 and 5.21, that of subadults in Figures 5.22 and 5.23 and that of juveniles in Figures 5.24 and 5.25.

Adults

Adults browsed about the enclosure with similar frequencies when feeding stations were spaced apart (Trials 1 and 2) and slightly less often during Trial 3. In this latter case, more time was spent attending feeding stations.

Crouched alert postures were recorded far more commonly than the upright postures during Trial 3 and occurred more commonly at that time than in the other trials. The frequencies of adults adopting crouched alert postures differed between each of the trials, being most common in Trial 3 and least in Trial 2. When feeders were spaced apart (Trials 1 and 2), adults assumed upright alert postures at similarly low frequencies, but this posture was recorded least often during Trial 3 compared with the other trials.

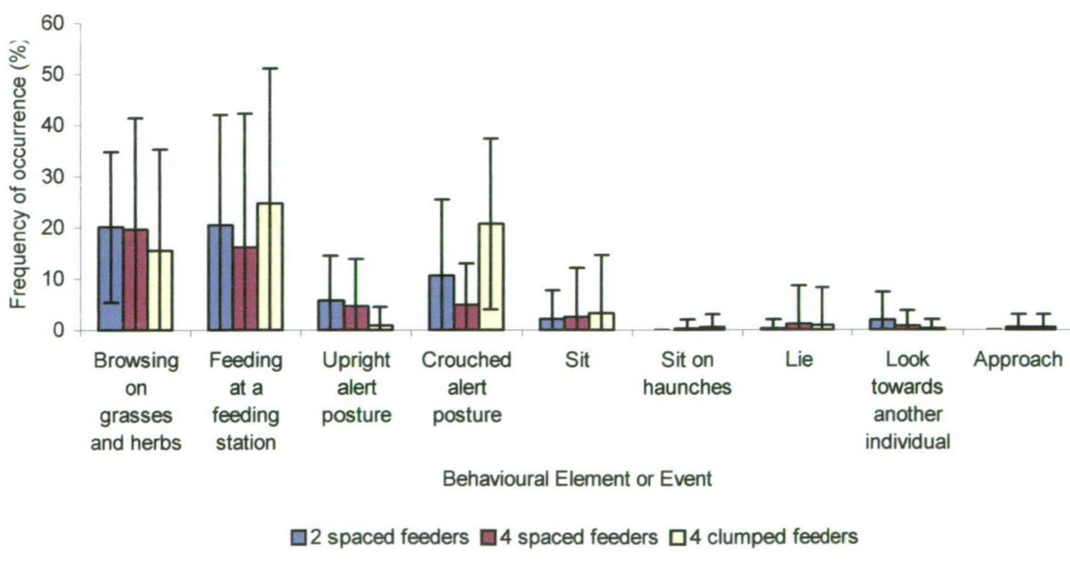


Figure 5.20: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing the key elements of behaviour. N=62 observation periods for each trial condition.

Adults were the only age group to spend more time grooming their sides in any of the trial conditions; more time was devoted to this when four feeders were spaced (Trial 1) than when the same number were clumped together (Trial 3).

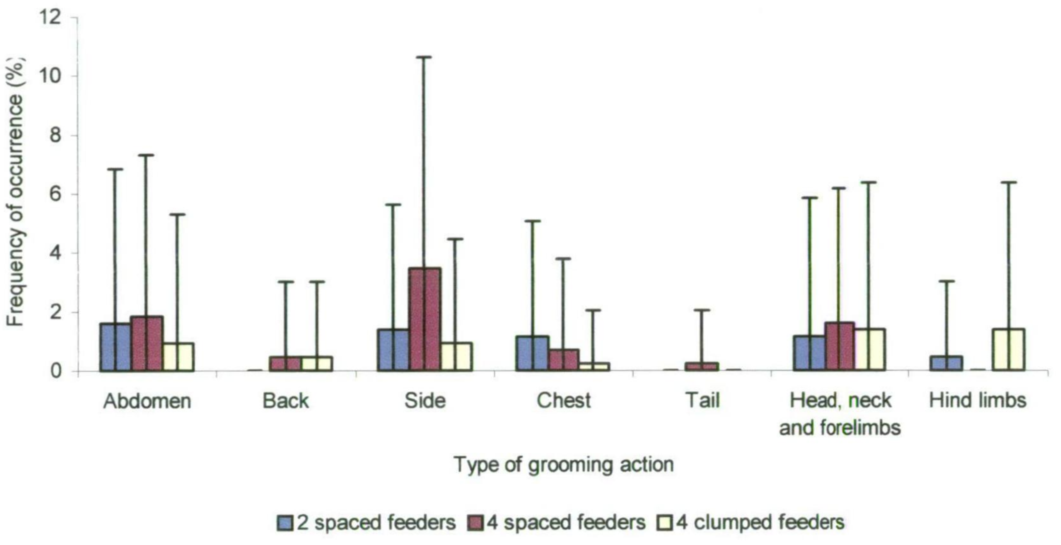


Figure 5.21 : The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing grooming actions. N=62 observation periods for each trial condition.

Subadults

Subadults apportioned time spent browsing and attending feeding stations in a similar manner to that seen for adults, except that a far greater amount of time was spent at feeding stations during Trial 3. All age classes spent longer feeding from a feeding station when during Trial 3 than during Trials 1 and 2. Subadults also spent more time at feeding stations when these were clumped together (Trial 3) than when they were reduced to utilising two spaced feeders (Trial 2).

Subadults assumed upright alert postures more often when four feeding stations were spaced apart and crouched alert postures when feeders were clumped together.

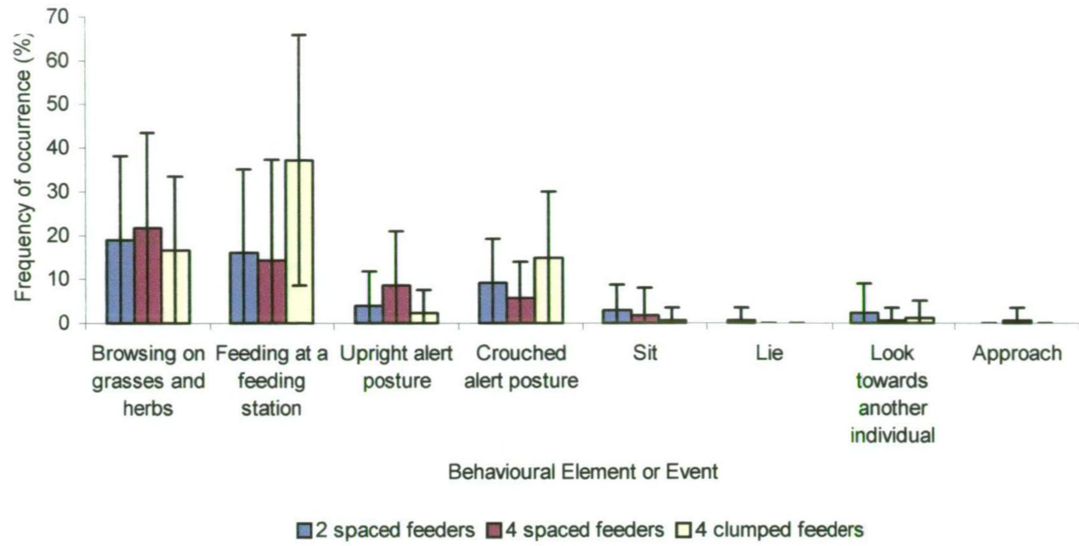


Figure 5.22: The mean percentages (± standard deviations) of overall sightings in which subadults were recorded performing the key elements of behaviour. N=25 observation periods for each trial condition.

Grooming actions were directed towards the abdomen, side, chest and tail relatively frequently during Trial 1 and at similarly low levels during the other trials.

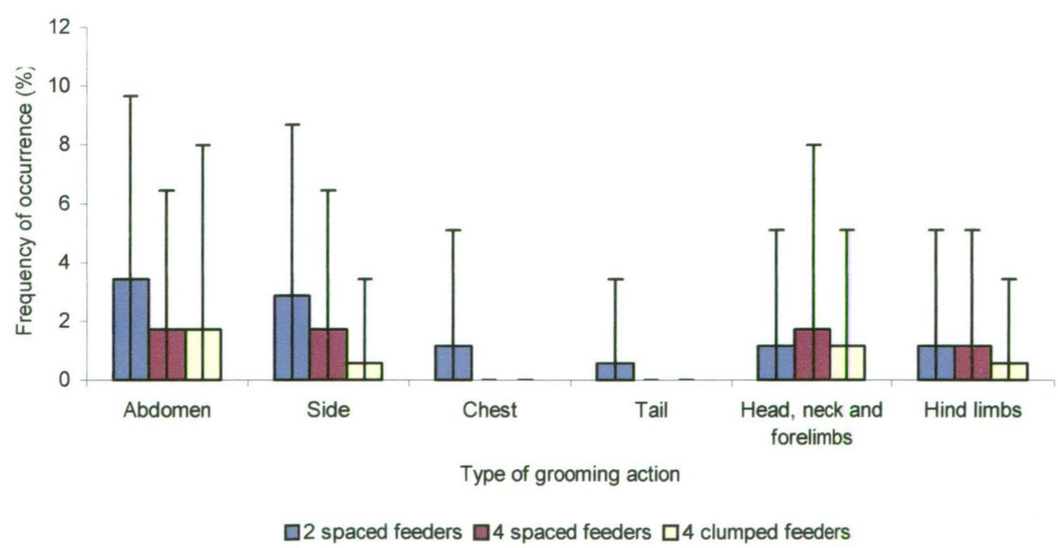


Figure 5.23: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing grooming actions. N=25 observation periods for each trial condition.

Juveniles

When four feeders were spaced apart, juveniles spent a relatively small amount of time attending them, particularly when compared to the amount of time spent feeding from clumped feeders. Juveniles utilised the two feeding stations provided more frequently than when four spaced feeders were provided.

Juveniles adopted crouched alert postures at similar frequencies in all three trial conditions, whilst upright postures were far more common during Trial 1. These animals engaged in social interactions more than members of other age classes in this latter trial.

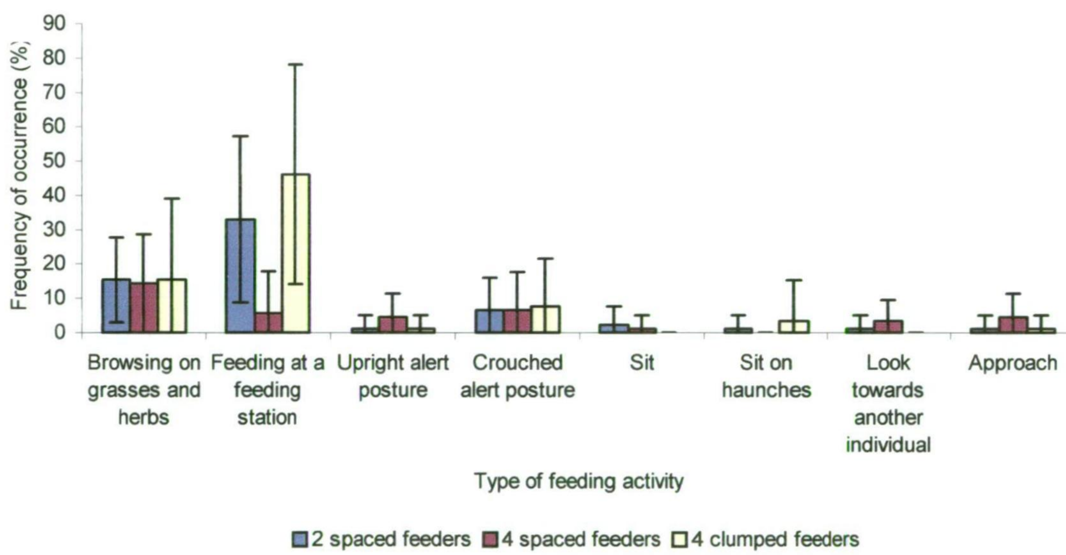


Figure 5.24: The mean percentages (± standard deviations) of overall sightings in which juveniles were recorded performing the key elements of behaviour. N=13 observation periods for each trial condition.

Grooming actions were rarely recorded during the three trials but occurred slightly more frequently during Trial 1.

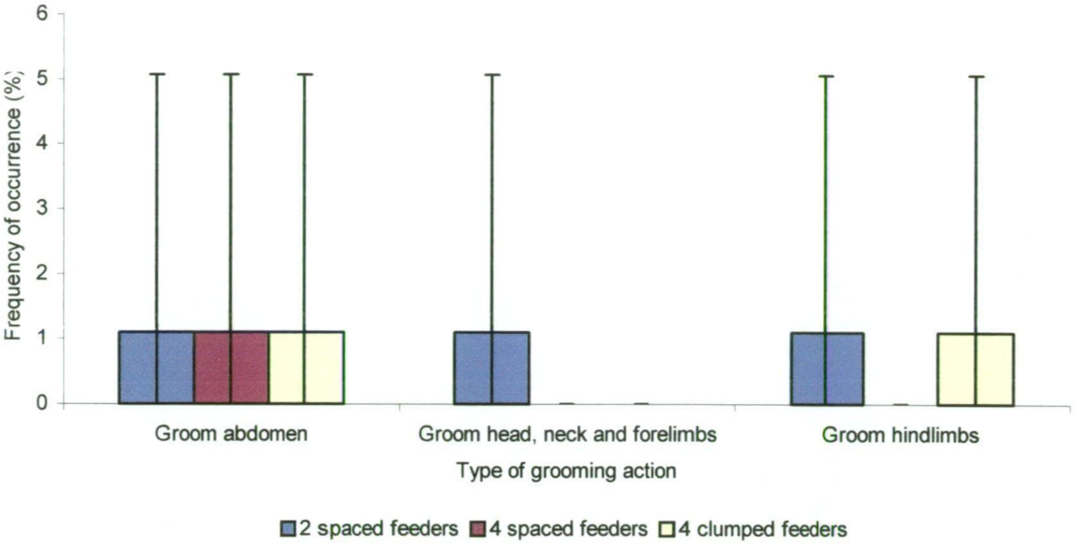


Figure 5.25: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing grooming actions. N=13 observation periods for each trial condition.

5.4 Discussion

Previous studies have suggested that Bennett's wallabies demonstrate a plasticity of browsing responses, compensating for decreases in herbage mass with increased bite rates and extended periods of browsing (Clarke and Louden, 1985). Other macropodoids have been reported to demonstrate similar changes in browsing behaviour. Rangeland herbivores, including red kangaroos, alter their food intake on different vegetation types (Short, 1987). The amount of food intake is also affected by the quality and palatability of the food, the structure of the vegetation and the well-being of the animal. Feeding behaviour of red kangaroos vary in another way; when food resources are limited, kangaroos dig into the ground for stems. The bridled nailtail wallaby, *Onychogalea fraenata,* is a medium-sized, nocturnal edge specialist, characteristics it shares with the Bennett's wallaby. Fisher (2000) reported that bridled nailtail wallabies browsing in Taunton National Park in both cleared and non-cleared areas, with a range of herbage mass, demonstrated a degree of plasticity in their browsing response, increasing their home ranges in response to decreasing herbage mass. In the present study, the ability to alter browsing behaviour in response to environmental and competitive pressures was assessed to include the use of feeding stations.

The provision of supplemental feed to captive macropods is important to the health of these animals (Calaby and Poole, 1971; Poole, 1982). In all three trials in this study, focal animals were more frequently recorded in sectors of the enclosure containing a feeding station with feed available. The frequency of occupation of sectors with feeding stations reduced or increased respectively as use of these stations commenced or was discontinued. However, this pattern was not as pronounced when four feeding stations were spaced throughout the enclosure as it became when the feeders were clumped together or reduced in numbers. The amount of time devoted to feeding activities significantly increased when feeding stations were clumped together or reduced. Specifically, wallabies fed at feeding stations more frequently when the number of these was reduced or they were positioned near to each other. Although the same total amount of supplemental feed was available, Bennett's wallabies in the university enclosure responded to these conditions in a similar manner to those described by Clarke and Louden (1985) that were browsed on relatively poorer quality herbage, increasing the amount of time devoted to feeding.

When the number of feeding stations was reduced to two, wallabies appeared to feed preferentially from the station in sector seven, although feed was also available in sector two. The feeding station in sector seven had some vegetative cover around it and was furthest from where observations were recorded. Wallabies may have been expressing a preference for feeding at a site with more cover available and less disturbance from people, despite the fact that the number of feeding stations had already been reduced and the effect of preferentially utilising this feeder was to further increase the numbers of individuals using it.

Bennett's wallabies in the wild rest during the day in refuges within dense vegetation (Calaby, 1983; Cronin, 1991). Wallabies in this study were recorded at the lowest frequencies in sectors three to six, a shrubby area with relatively extensive vegetative cover providing refuges. One obvious explanation for fewer sightings is the increased difficulty of viewing individuals in this area. However, another possible explanation is that this area is primarily a "day use" area that is less frequently utilised by members of this subspecies, when they are more active during the midafternoon and through the night time. When considering the patterns of spatial utilisation reported in the previous chapter, this trend for increased use of this area during the less active period of the day, compared to the more active period, can also be seen. Periodic spot checks of wallabies that were out of the line of vision of the observer during earlier sampling periods revealed that animals in more sheltered positions were often resting or grooming.

Patterns of use of these shrubby sections of the enclosure varied when feeding regimes were altered. The use of most of the heavily-vegetated sectors neighbouring those where feeders were stationed increased when these feeders were employed. The difficulty of sighting focal individuals was greatest when they entered sector five, suggesting that if reliable sightings could have been made, patterns of the occupancy of this sector are likely to have varied in response to varying the positions of feeders also. Sector 13, a more open area with browsing matter available, was also more frequented when feeders were clumped together nearby than when they were spaced apart. Those areas more frequented by individuals in each feeding regime were near to feeding stations employed at that time. This same non-random occupation of grid regions has previously been reported for Brush-tailed rock wallabies, *Petrogale pencillata*, at the Jenolan Caves Reserve in New South Wales (Bulinski *et al.,* 1997). Members of this species preferentially occupied grid cells with high quality resting sites. Previous studies on brush tailed rock wallabies by Batchelor (1980), Joblin (1983) and Scholz (1980) reported that dominant individuals defended areas containing preferred shelter sites. Bridled nailtail wallabies in Taunton National Park preferentially selected shelter sites that provided the highest degree of concealment. Individuals remained faithful to shelter sites in varying conditions but altered browsing habits in response to environmental conditions (Pople *et al.*, 2001). In this study, the probability of various areas of the enclosure being occupied by Bennett's wallabies, particularly females, varied according to the positioning of feeding stations. These different sections of the enclosure provided various resources including the feeding stations themselves, refuges and areas where wallabies could browse.

Johnson (1987b) reported that red-necked wallabies at Wallaby Creek extended their home ranges over winter when browsing conditions were more severe but remained faithful to shelter sites. The home ranges of males differed from those of females and between the age classes of males. Adult males maintained home ranges in close proximity to the greatest densities of adult females, while medium sized males appeared to be displaced into peripheral areas (Johnson, 1987b). In this study the liklihood of various areas of the enclosure being occupied by female Bennett's wallabies varied according to the positioning of feeding stations. Male Bennett's wallabies, however, preferentially fed from the feeder in sector seven whenever it was stocked and were sighted less frequently in sector one in those trials where feeders were available in other areas. The occupation of the more heavily-vegetated sectors of the enclosure by males did not differ to a large degree. However, the behaviour of males could be very cryptic and those individuals were often hard to observe for long enough periods to complete a 30 min observation sample. They were most easily observed when they emerged to feed and gained priority of access to feeding stations through both covert and overt intimidation. Once they had entered a feeding station, they remained for longer periods. This translated into relatively higher samples of feeding and lower of resting males than might be the case if all positions within the enclosure were equally visible. In fact, rather than suggesting that males were unsighted more infrequently and occupied relatively open areas, the opposite is the case. Males occupied sector five and other heavily-vegetated areas, where visibility was relatively poor, and emerged for sustained periods during which they browsed or fed at feeding stations uninterrupted by other members of the group. Similar observations were made of grey kangaroos free ranging within an enclosure at the University of New South Wales (Grant, 1973). These individuals associated with one another within the structures of a hierarchy. Individuals occupying high-ranking positions within the hierarchy appeared to gain preferential status at feeding stations within this enclosure, which may have advantaged them if subjected to stressful conditions. Male grey kangaroos were more commonly seen at the observation post near the prime feeding site if they held dominant positions within the group: one of these was twice seen driving another male away from this site (Grant, 1973). The patterns of occupation of the enclosure by male Bennett's wallabies at the university enclosure in this study were generally similar in each trial. This may have been because these individuals maintained the holding the prime positions in terms of refuges and shelter sites in each instance. Male Bennett's wallabies range widely over relatively large home ranges in order to maximise their contact with potential mates (Croft, 1989) and this may equally explain why they did not utilise different shelter sites in response to movements of the feeders, as seen for females.

LaFollette (1971) reported from observations of captive Bennett's wallabies that individuals did not assert dominance over food through agonistic interactions. In this study, however, subadults and juveniles tended to occupy sectors bordering on those containing feeding stations and these shifted with alterations to the feeding regimes. Subadults and juveniles were subordinate to adults in almost all encounters and were often observed browsing in close proximity to feeding stations while waiting their turn to enter or were chased away from feeders by approaching adults. They also spent proportionally more time in less open areas or out of sight completely. Some temporal separation appeared to result from this, with subadult and juvenile individuals accessing feeders when adults were resting in concealed positions. However, in stressful conditions, these individuals would be most vulnerable to competition for limited resources, either in the wild during drought conditions or in captivity with an inadequate feeding regime (Grant, 1973).

In this study, both the number and type of alert postures adopted by Bennett's wallabies varied when the numbers and positions of feeding stations were varied. Alert postures were recorded more frequently for all animals, particularly adults and females, when feeding stations were clumped together or reduced. Wallabies adopted more crouched alert postures when feeders were clumped together and individuals were in close proximity of one another as they fed. However, the opposite is true of the upright alert posture, adopted more frequently when four feeding stations were separated. These results may reflect the expression of vigilance. The amount of time in which grazing macropods maintain vigilance for predators has been related to group size (Colagross and Cockburn, 1993; Wahungu *et al.,* 2001). Vigilance employed against potential predators is at a cost to time available for feeding as vigilant individuals must hold their heads up, a posture that prevents feeding with the head lowered to the ground. In the university enclosure used for this study, wallabies were most vigilant when feeding stations were in close proximity to one another. The increase in crouched alert postures may have been a response to limiting food resources and increasing the density of individuals around feeders; that is, vigilance was directed towards potential competitors for food or aggressors, rather than predators. Upright alert postures, by contrast, were generally adopted in response to an external source of disturbance, such as loud bird noises from nearby bush. These postures were sometimes followed by flight into cover, terminating observations and reducing the frequencies of recordings included here. Thus, the reduced numbers of these postures seen during Trial 1 reflected a greater probability that individuals would resume feeding rather than flee from sight.

Wallabies moved about the enclosure more when the feeding stations were spaced throughout the available area. One obvious explanation for this result is that individuals had to travel further to feeding stations when these were spaced throughout the enclosure. However, this may have instead indicated that individuals subjected to a less stressful environment spent more time browsing about the open areas of the enclosure or near to feeding stations while awaiting their turns. Males, in particular, tended to move directly to feeding stations when they were clumped together or reduced in number, browsing for shorter periods, displacing individuals rather than queuing.

A number of elements of social behaviour were observed in each of the three trial conditions. Female and adult wallabies were recorded more commonly engaging in amicable interactions such as nasonasal touching, while males and members of the younger age classes engaged in more aggressive interactions, approaching other wallabies and engaging in bouts of kicking and wrestling. Social interactions involving females or adults occurred significantly more frequently when four feeders were spaced apart than clumped together. The same was true of males, which also engaged in more frequent interactions when a greater number of feeders were spread throughout the enclosure. As previously noted, wallabies moved and browsed about the enclosure more when a greater number of feeders were spread apart; this is probably an important contributing factor to changes in social behaviour. Where feeders were either positioned in closer proximity to one another or the availability was reduced, males responded by spending less time in the open areas and emerging primarily to feed at feeding stations before returning to cover. Subordinate individuals were displaced from feeders, or shifted their times of feeding, in response to the presence of males at feeding stations. Crebbin (1982) reported that for captive swamp wallabies, the more individuals feeding from a feeding station, the more likely agonistic interactions were to occur. In this study, situations likely to produce this effect were avoided through general changes in activity patterns resulting in temporal separation of feeding.

Although the total proportion of all grooming activity did not differ significantly between trials, the frequency with which individuals directed grooming actions towards their sides was significantly greater when four feeders were spaced apart than when they were clumped together. Other grooming actions, such as grooming of the abdominal area, chest, tail, head, neck and forelimbs, were more common when feeders were spaced apart than when they were clumped together. In Chapter 4, these grooming actions occurred more frequently when individuals were more relaxed. Although the frequency of each type of resting posture adopted did not differ significantly during these feeding trials, the differences in grooming activity may provide further evidence that wallabies were generally more relaxed when feeding stations were spaced throughout the enclosure.

This project aims to improve management practices for captive Bennett's wallabies, particularly with regard to undesirable interactions and environmental stress. With regard to the latter, this occurs when stressors arising from specific aspects of the captive environment, such as an inability to escape or terminate interactions, overcrowding and limiting available feed, result in physiological changes that, if persistent, may result in serious illness or even death (Manning, 1968). The timing of observation periods during those times of the day likely to yield the most useful and informative results cannot normally be achieved in a zoo where studies are often undertaken during opening hours (Hosey, 1997). The observation periods covered those hours of the day when the probability of sighting focal animals was greatest, coinciding with peaks in daily activity. Although the behaviour of focal animals was only sampled during part of each day, this accounted for the most active part, when interactions were more likely to occur. Although it must be borne in mind that the experimental group contained only six individuals, comprising a limited representative sample of both sexes and each of the three age classes, nonetheless, this does represent the type of exhibits commonly seen in zoos and wildlife parks, where a small number of individuals are held together in an enclosure (refer Appendices 5, 6 and 8; Hosey, 1997). Varying the number and position of the available feeding stations did impact the patterns of occupation of the enclosure by these captive Bennett's wallabies, as well as the patterns of activity.

Manipulating the number and position of feeding stations available to captive individuals at the university enclosure did result in changes in the type of activities engaged in and the patterns of utilisation of various sectors of the enclosure. When considering managing captive Bennett's wallabies within a zoo or wildlife park to meet the goals of these organisations, consideration should be given to providing a number of feeding stations positioned throughout the front half of an enclosure. This should result in reduced environmental stress for captive individuals and a reduction in undesirable agonistic interactions or displacement of subordinate individuals from feeding stations. It also increases locomotory activity; zoo visitors prefer exhibits where animals are active and preferably young (Croke, 1997). Subadult and juvenile individuals in the type of enclosure suggested should spend more time browsing about in the open while awaiting a turn at the feeder, bringing them into the visitor's view. Finally, all captive animals should be able to access appropriate levels of nutrition for good health to be maintained.

Chapter 6 The Effects of Varying Stocking Rates

6.1 Introduction

In the survey reported in Chapter 3, current managers of captive macropods identified a number of key issues in the management of their animals. As well as the provision of adequate nutrition, another common concern of wildlife park and zoo managers was maintaining stocking rates at levels that minimised undesirable interactions and environmental stress. Thirteen of the 22 respondents to the questionnaire nominated this as one of the key issues that they faced.

Bennett's wallabies are commonly held as an exhibited species in wildlife parks and zoos throughout Australia. Members of this subspecies breed successfully at many of these facilities. They are also frequently held together within enclosures with members of other species, effectively increasing the stocking rates. More than half of the zoos and parks that responded to the questionnaire stated that additional stock were gained from donations of injured or orphaned wildlife, including five of the nine parks that held Bennett's wallabies. Successful breeding outcomes and stock donations from members of the public place further pressure on management strategies.

Murböck (1977) noted that ritualised fighting between captive male Bennett's wallabies occurs constantly as dominant males confirm their rank, but that these interactions become more intense and overt as the density of wallabies in the enclosure increases. Density significantly affected the frequency of social interactions, including agonistic, maternal and reproductive interactions, of captive swamp wallabies at the University of New South Wales (Crebbin, 1982). As stocking rates increased, interactions occurred more frequently. However, the intensity and type of interaction as well as the age and sex class of the initiator did not change. Animals in captivity have limited opportunities to escape when stocking rates are higher. Aggressive interactions between captive grey kangaroos have been attributed to enforced close proximity preventing subordinates from avoiding aggressors (Grant, 1973). In larger enclosures, Bennett's wallabies disperse until they achieve the maximum possible nearest-neighbour distance. Under these circumstances, the rates of agonistic interactions reduce to zero (Murböck, 1977).

Stress arising from overcrowding may have other impacts on captive individuals besides increased rates of injuries from fighting. Animals subjected to long-term environmental stressors may suffer from pathological changes, including the suppression of the immune system and nerve damage as well as reduced reproductive success (Davies, 1996). Managers of captive macropodoids must consider strategies that minimise stress and agonistic interactions resulting from overcrowding within a confined area where opportunities to escape or disperse are limited.

This chapter describes the effect of manipulating a second aspect of the enclosure environment of Bennett's wallabies at the university: the stocking rate. The number of individuals in the 1000 m^2 of the enclosure was varied to investigate whether this would significantly alter the frequencies of focal individuals:

1. occupying each of the sectors of the enclosure;
2. performing any element from each category of behaviour; and
3. performing individual behavioural elements.

6.2 Materials and Methods

6.2.1 Experimental Methods

Captive subjects were again observed in the enclosure at the University of Tasmania's Hobart campus under three trial conditions, which were selected based on stocking rates of captive wallabies in wildlife parks and zoos that responded to the questionnaire. In the first of these conditions, wallabies were stocked at a rate of six animals/1000 m^2. The group comprised one adult male, one subadult male, three adult females and one subadult female. The stocking rate was then altered to nine animals/1000 m^2 with the group formed of one adult, one subadult and one juvenile male, three adult females, two subadult females and one juvenile female. Finally, a stocking rate of three animals/1000 m^2, with the group comprising one adult male, one adult female and one subadult female, formed the third trial condition. These trials are referred to throughout as follows –

- Trial 1 = 3 animals per 1000 m^2
- Trial 2 = 6 animals per 1000 m^2
- Trial 3 = 9 animals per 1000 m^2

It was originally intended that the three trial conditions would consist of groups stocked at six, nine and 12 wallabies per 1000 m^2. However, during another phase of experimental manipulations involving a group of eight wallabies, of which four were males, one wallaby died suddenly and unexpectedly and indications of physiological stress (weight loss, elevated blood glucose levels) were recorded in several others. As a consequence, the experimental design was altered to include a third stocking rate of three wallabies rather than 12 and the total number of hours of data collected was reduced from 75 to 51 for each trial condition, yielding a total of 153 hours of focal animal sampling.

Further practical difficulties were associated with the lowest stocking rate of three animals only. Although the same total numbers of hours of observations were collected for analysis, a greater total period of time was needed to collect these than required for the completion of the other trials. Wallabies at the low stocking rate exhibited signs of extreme nervousness, emerging infrequently to browse for brief periods of time, usually terminating browsing activity because of some small noise causing general alarm. Focal animal observations could only be recorded successfully on those occasions when wallabies remained visible for longer periods than were typical in this condition; this must be borne in mind when interpreting these data.

Observations were conducted between 16:00 and 20:00 h over three non-consecutive periods. The first of these ran between September and December 1998, yielding 75 h of observations, of which 51 hours were used for analyses. Wallabies were stocked at nine animals/1000 m^2 over the period April to May 2000 and then reduced to three animals/1000m^2 from May to July 2000. During each of these periods, a further 51 h of observations were collected. All observations were taken from the observation post inside the shed previously described. A mixture of wallaby pellets and lucerne chaff was always provided at the four feeding stations positioned in sectors one, two, three and seven. Browse matter was also available throughout the enclosure. Upon entering the enclosure, the observer verified that feeders were well stocked and then waited for a period of at least 30 min before recordings commenced.

During each of these trial conditions, substitutions of some individuals were again made after half of the observations had been collected. One of the three wallabies in the lowest density group was substituted, two of the six in the medium and three of the nine in the highest density group. Focal animals were sampled in subgroups in each trial. In Trial 1, subgroups contained two wallabies, in Trial 2 four wallabies and in Trial 3 six wallabies. In each trial, the numbers of samples were divided amongst members of each subgroup as evenly as possible. For example, during Trial 2, two members of subgroup one were sampled four times each, while the third was sampled five times. Each subgroup contained a different grouping of individuals.

During the sample period, all activities that the focal animal engaged in were recorded. Any interactions with other wallabies were recorded, including acts performed by all participants from instigation to cessation. A record was also made every 5 m, starting at 0 m, of the sector of the enclosure occupied by the focal animal. Finally, the duration of each behavioural element performed by the focal individual was recorded, with the exception of those acts that lasted less than 3 s; these were recorded as lasting for three seconds.

6.2.2 Data Treatment

Data collected from focal animal observations were used to produce descriptive statistics. As a preliminary step, average scores were calculated per focal animal. Data were then converted into percentage values in the same manner as previously described in section 5.2.2. The mean frequencies of the occupation of each sector of the enclosure, the performance of any behavioural element from each category of behaviour and the occurrence of individual behavioural elements, as well as their durations were calculated. This process was utilised for all data for each trial condition. Data for each sex and age class were then separated out and treated in the same manner. Data collected from observations of juvenile and subadult individuals in each trial condition were pooled due to the otherwise low number of individuals sampled.

6.2.3 Statistical analyses

Kruskal-Wallis tests were utilised to identify any significant differences in the frequencies of the occupation of each sector of the enclosure, the frequency of the performance of acts and events belonging to each behavioural category and the performance of specific individual behavioural elements between the three trial conditions. Initially, data for all focal individuals were pooled and analysed. The elements considered here are the same as those selected for analyses in Chapter 5.

Where a significant difference was identified, a post-hoc Mann-Whitney U test was then performed on pairs of trials to identify which trials gave rise to this difference. P values of <0.05 were considered to be significant in all instances.

A one-way analysis of variance was utilised to test whether the duration of individual behavioural acts varied significantly between the three trial conditions. P values <0.05 were again considered to be significant.

6.3 Results

6.3.1 Spatial Patterns

6.3.1 (i) Group Spatial Patterns

The percentages of observations of focal individuals in each sector of the enclosure at each of the three stocking rates can be seen in Figure 6.1. There were several significant differences in the use of the various sectors between the three trial conditions (Table 6.1). The patterns of the occupation of the various sectors of the enclosure in each trial did differ significantly. At the lowest stocking rate (Trial 1), focal animals were significantly less frequently recorded in the more open sectors 11 and 12 and were more often hidden from sight at the time recordings fell due. These individuals were also recorded in the sectors with the more secluded feeding stations (three and seven) more frequently than individuals in the other trials. Sector one, containing a less well concealed feeding station, was more frequently occupied during trials 2 and 3 (medium and high stocking rates). Wallabies were observed in the more heavily vegetated sectors five and six significantly less frequently during Trial 3 when compared to Trial 2.

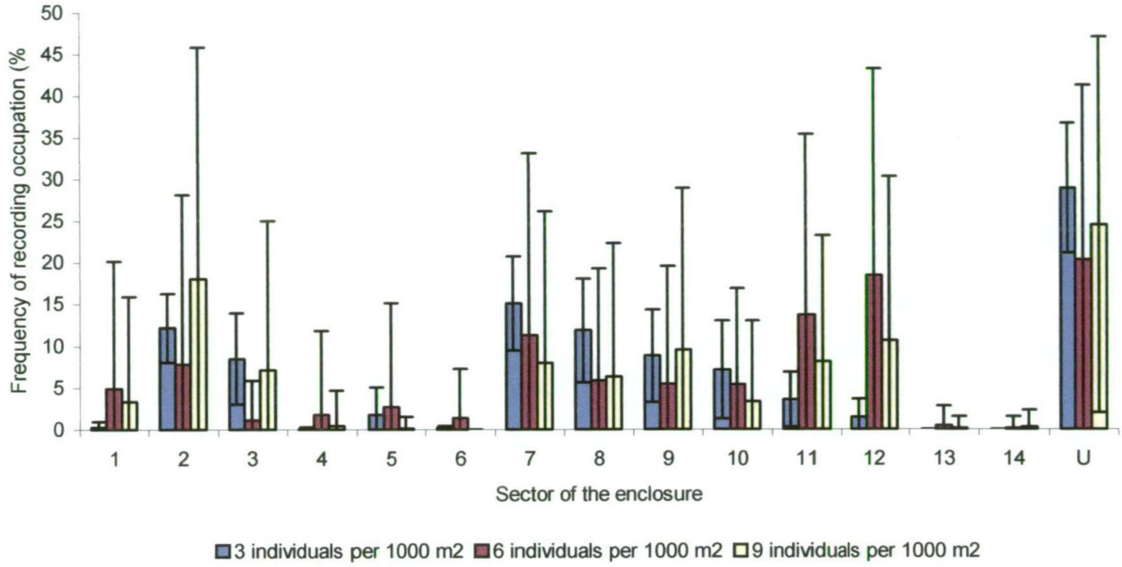


Figure 6.1: The mean percentages (± standard deviations) of overall sightings in which focal individuals were present in each section of the university enclosure. N = 4 in Trial 1, 7 in Trial 2 and 12 in Trial 3. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due.

Table 6.1: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of sector occupation had been identified. Differences were considered significant if $p<0.05$. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 4 in Trial 1, 7 in Trial 2 and 12 in Trial 3. H values provided are from the Kruskal-Wallis one-way analysis of variance.

Sector		Trial 1 vs. Trial 2	Trial 2 vs. Trial 3	Trial 1 vs. Trial 3
	H value	P value	P value	P value
3	7.444	0.028	0.028	-
5	8.116	-	0.017	-
6	8.763	-	0.045	-
11	8.131	0.028	0.028	-
12	8.347	0.020	-	0.020

6.3.1 (ii) Patterns of Spatial Utilisation by Each Sex

The mean frequencies of the occupation of each sector of the enclosure by males and females in each trial condition are presented in Figures 6.2 and 6.3.

Females

The frequency at which females occupied sector one, an area that contained the feeder with the least cover, was relatively low during Trial 1 compared to either of the other two trials. Sectors 11 and 12, relatively open areas close to the other feeding stations, were less frequently occupied by females during Trial 1 compared to each of the other two trials. The more heavily vegetated sectors five and six were relatively infrequently occupied when the stocking rate greatest.

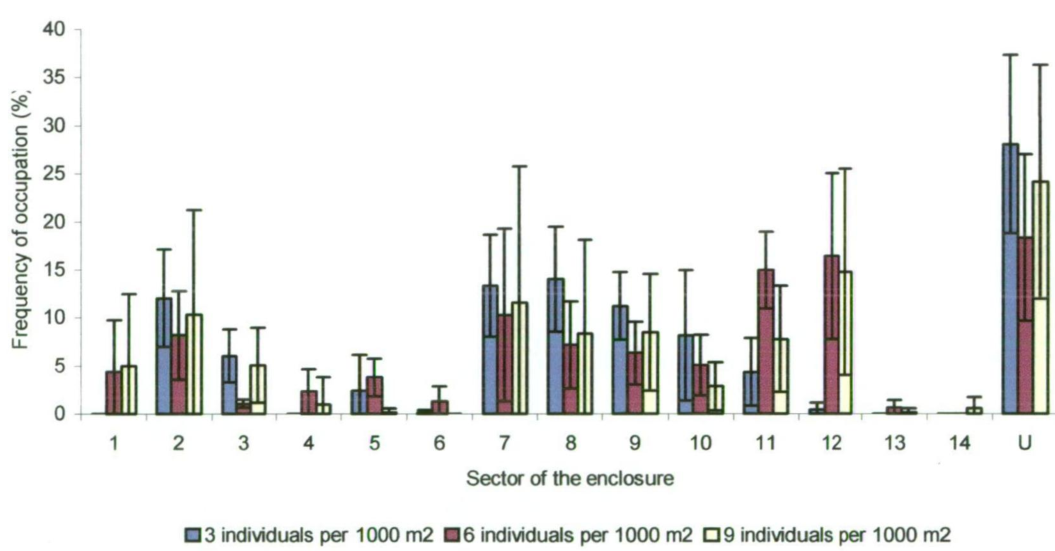


Figure 6.2: The mean percentages (± standard deviations) of overall sightings in which females were present in each section of the university enclosure. N = 3 in Trial 1, 4 in Trial 2 and 9 in Trial 3. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due.

Males

In contrast to females, males occupied sector two, with a better concealed feeder, at greater frequencies during Trial 3 than at other times. Males were recorded in sector three, also containing a better concealed feeding station, more frequently in the lowest (Trial 1) and highest (Trial 3) stocking rates than the medium (Trial 2) rate. These animals were less frequently sighted in sector seven, containing the feeding station furthest from the observer's post, when stocked at the highest rate, compared to the other two stocking rates. Males occupied sector 12 at far greater rates during Trial 2 than in either of the other trials.

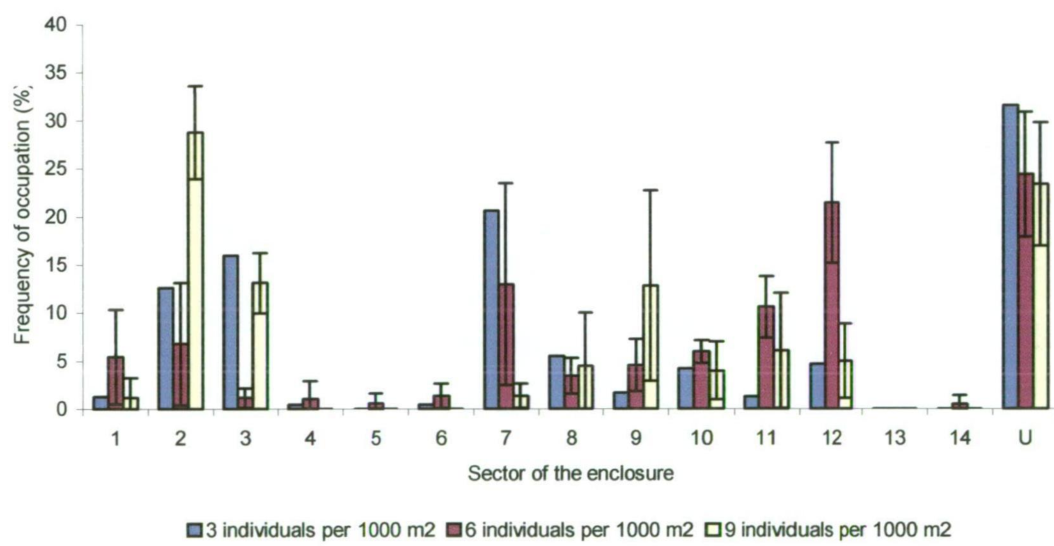


Figure 6.3: The mean percentages (± standard deviations) of overall sightings in which males were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=1 in Trial 1, 3 in Trial 2 and 3 in Trial 3.

6.3.1 (iii) Patterns of Spatial Utilisation by Each Age Class

The frequencies with which members of each age class occupied sectors of the enclosure are presented in Figures 6.4 and 6.5.

Adults

Adult wallabies were generally more visible at the medium stocking rate. They spent more time in sectors containing feeding stations with more vegetative cover (three and seven) in general than younger animals, while the reverse was true of the sectors with more exposed feeders in sectors one and two. Sectors 11 and 12 were occupied most frequently by adults at the medium stocking rate (Trial 2) and least at the lowest stocking rate (Trial 3).

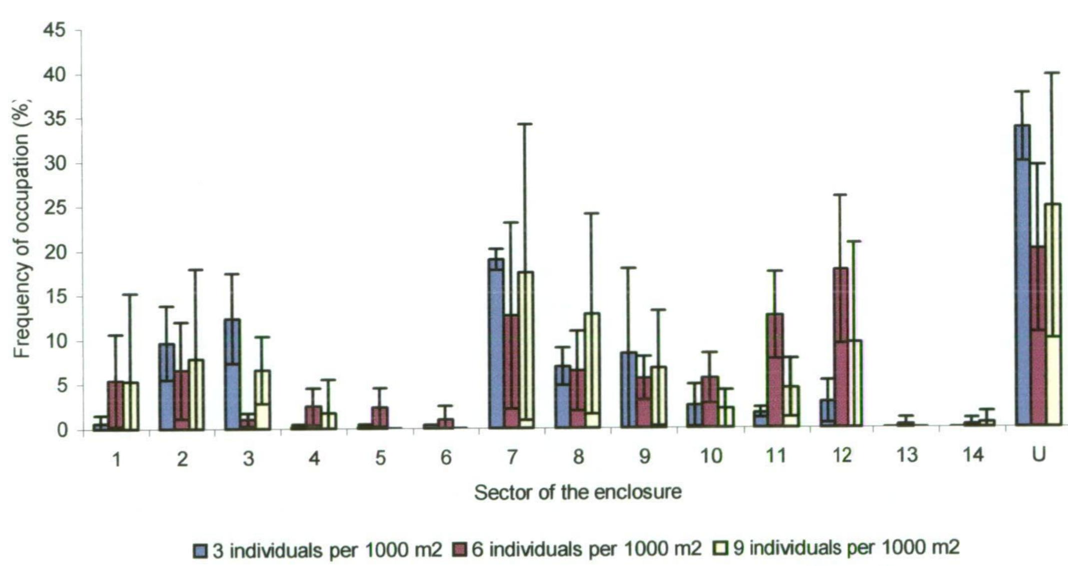


Figure 6.4: The mean percentages (± standard deviations) of overall sightings in which adults were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N= 2 for Trial 1 and 5 for Trials 2 and 3.

Subadults and Juveniles

Subadults and juveniles were sighted more frequently in sectors 11 and 12 at the medium and high stocking rates. Subadults remained visible at imilar frequencies during each trial. They occupied sectors six, 11 and 12 more frequently at the medium stocking rate. The latter two sectors were the relatively open areas where browsing material was available. Another such area, sector eight, was occupied at relatively high levels during Trial 1.

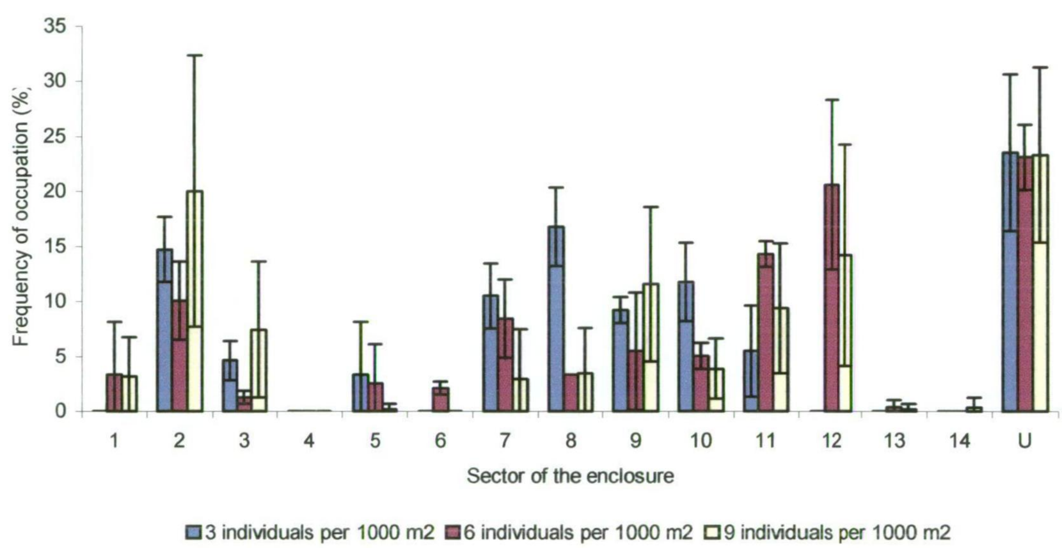


Figure 6.5: The mean percentages (± standard deviations) of overall sightings in which subadults and juveniles were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=2 for Trials 1 and 2 and 7 for Trial 3.

6.3.2 Frequency of Behavioural Categories

6.3.2 (i) Group Frequencies of Observations of Acts from Categories of Behaviour

The percentage of time devoted to acts belonging to each category of behaviour is shown in Figure 6.6. The greatest percentage of time was again devoted to activities associated with eating and drinking. However, this amount was lowest in animals held at the medium stocking rate (Trial 2) and at similar, relatively higher levels in the other two trials. Focal animals were recorded as unsighted most often in Trial 1 and the lowest frequencies of alert postures were seen in this trial. Resting postures were also less frequently seen at the lowest (Trial 1) and most frequently at the medium stocking rates (Trial 2). Wallabies were recorded interacting and grooming at similarly low levels during each of the experimental conditions.

Statistical analyses of all observational samples collected under the three trial conditions revealed some significant differences, which can be seen in Table 6.2. When comparing wallabies in Trials 1 and 3, no significant differences were found in the amounts of time focal animals engaged in different types of activities. However, when comparing individuals in Trial 2 to those in either of the other trials, a number of differences were noted in the way that focal animals apportioned their activities. Feeding activities accounted for a greater proportion of time at the highest stocking rate (Trial 3), while alert postures were more frequently recorded during Trial 2. When comparing the focal animals maintained at the lowest and medium stocking rates, significantly more of the latter were seen to adopt alert postures.

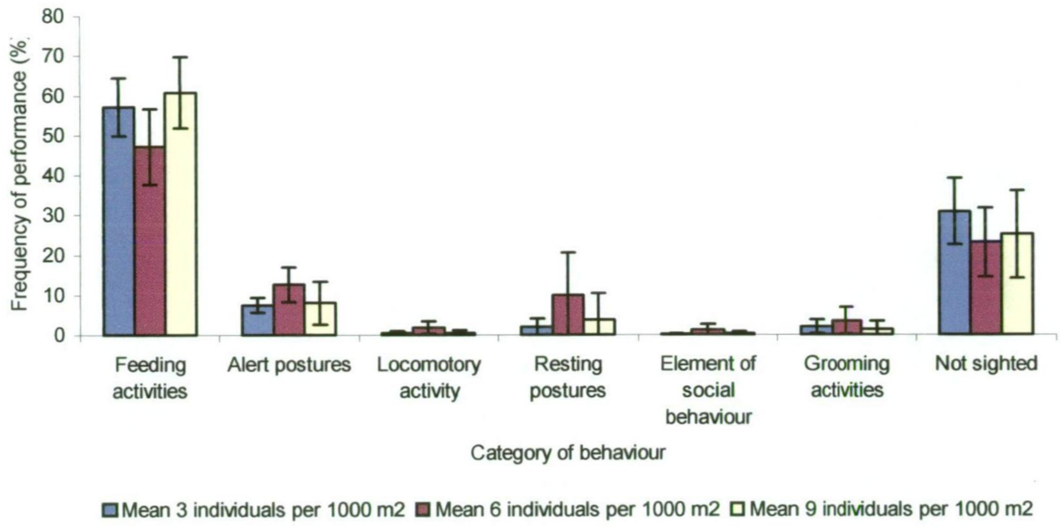


Figure 6.6: The mean percentages (± standard deviations) of overall sightings in which focal individuals were recorded performing any of the acts from categories of behaviour. N=4 for Trial 1, 7 for Trial 2 and 12 for Trial 3.

Table 6.2: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing any of the acts from each category of behaviour. Differences were considered significant if $p<0.05$. N=4 for Trial 1, 7 for Trial 2 and 12 for Trial 3. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2.

Category of behaviour		**Trial 1 vs. Trial 2**	**Trial 2 vs. Trial 3**	**Trial 1 vs. Trial 3**
	H value	**P value**	**P value**	**P value**
Feeding activities	7.037	0.012	-	-
Alert postures	6.440	-	-	0.010
Locomotory activities	6.003	-	0.028	-

6.3.2 (ii) Frequencies of Observing Members of Each Sex Performing Acts from Each of the Categories of Behaviour

The mean frequencies with which female and male Bennett's wallabies in the university enclosure engaged in activities from each category of behaviour are presented in Figures 6.7 and 6.8.

Females

Females in the group stocked at six individuals per 1000 m^2 (Trial 2) spent significantly more time resting, grooming and moving about the enclosure than those in either of the other trials, but spent more time in feeding activities in the highest density group (Trial 3). Alert postures were also relatively common during Trial 2.

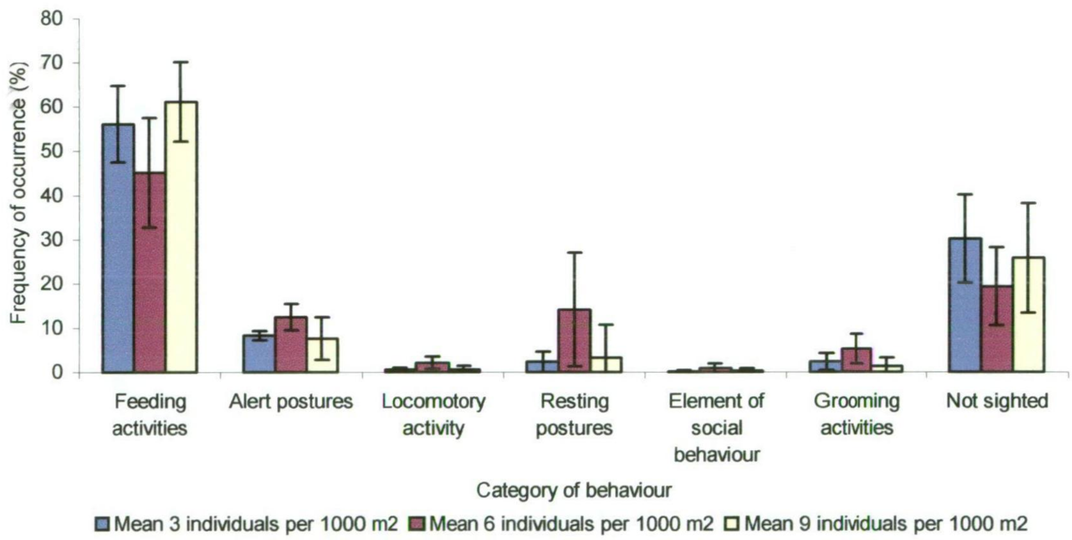


Figure 6.7: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing any of the acts from categories of behaviour. N=3 for Trial 1, 4 for Trial 2 and 9 Trial 3.

Males

Males spent more time moving about the enclosure and resting during Trial 2. In that trial, males also adopted a greater number of alert postures when compared to either of the others.

Males included in the groups stocked at three (Trial 1) or six (Trial 2) wallabies per 1000 m^2 devoted more time to feeding activities than females, while the reverse is true of those in Trial 3. Males in Trials 1 and 2 rested in view and groomed less than females. Males devoted the greatest amount of time to resting at the highest stocking rate (Trial 1).

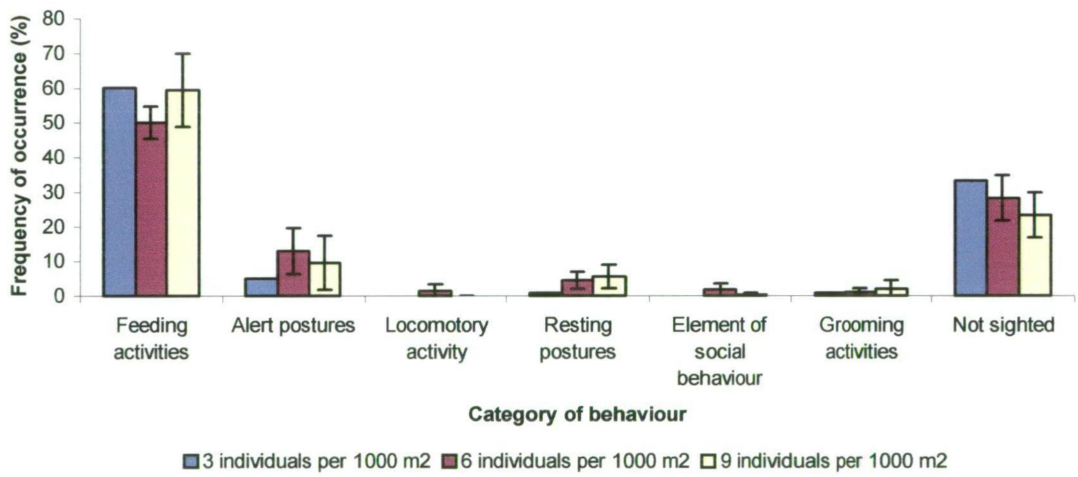


Figure 6.8: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing any of the acts from categories of behaviour. N=1 for Trial and 3 for Trials 2 and 3.

6.3.2 (iii) Frequencies of Observing Members of Each Age Class Performing Acts from Each of the Categories of Behaviour

The frequencies of acts belonging to each category of behaviour performed by the two nominated age groups of Bennett's wallabies are presented in Figures 6.9 and 6.10.

Adults

Adults apportioned their time differently when comparing the medium stocking rate (Trial 2) to either of the others. The total time spent feeding was least when wallabies were stocked at the medium rate (Trial 2). The number of occasions in which individuals were out of view when a recording was due was also greater during both Trials 1 and 3 compared to the medium density condition. The frequencies of wallabies adopting alert postures, moving about the enclosure, grooming and resting were greatest during Trial 2.

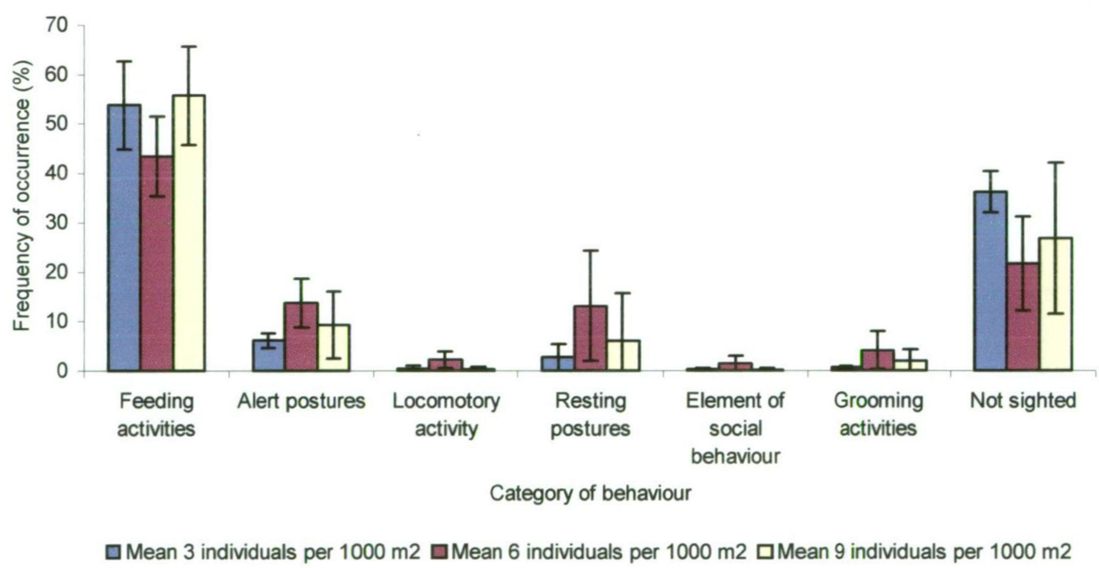


Figure 6.9: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing any of the acts from categories of behaviour. N= 2 for Trials 1 and 5 for Trials 2 and 3.

Subadults and Juveniles

Members of the younger age classes did not differ greatly with regard to the amount of time apportioned to activities from each of the categories of behaviour. The vast majority of time in each trial was devoted to feeding activities, with alert postures adopted occasionally (Figure 6.10). These animals were generally hidden from view within the vegetation at other times.

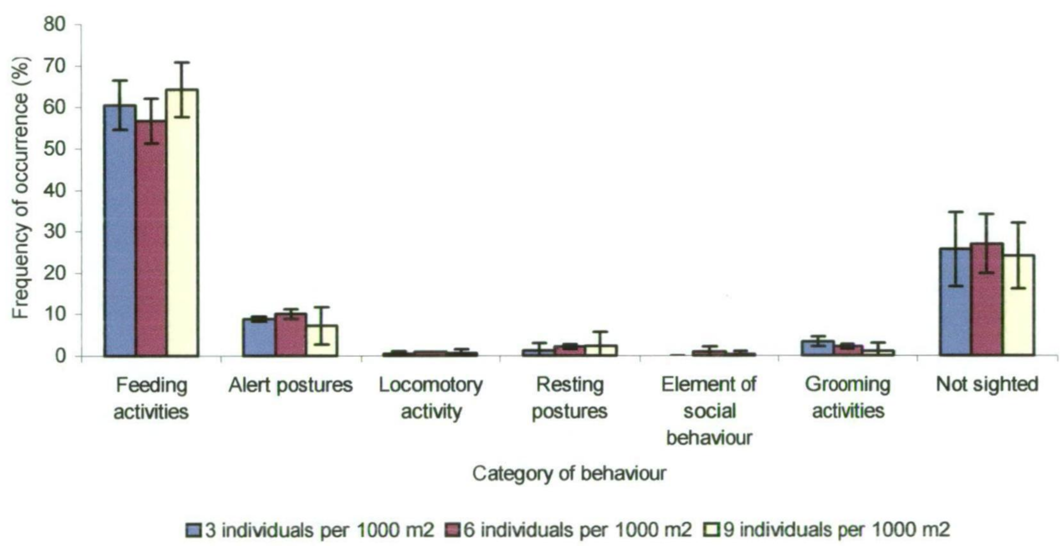


Figure 6.10: The mean percentages (± standard deviations) of overall sightings in which subadults and juveniles were recorded performing any of the acts from categories of behaviour. N=2 for Trials 1 and 2 and 7 for Trial 3.

6.3.3 Frequency of Behavioural Elements and Events

6.3.3 (i) Group Frequencies of Observations of Acts from Categories of Behaviour

The frequencies with which animals at each of the three stocking rates performed specific behavioural acts are shown in Figures 6.11 and 6.12.

Wallabies were seen to browse on grasses and herbs throughout the enclosure at similar frequencies at the highest and lowest stocking rates, while this activity was less frequent at the medium stocking rate. Feeding from a feeding station was most common during Trial 3.

The upright alert posture was recorded at similar levels in all trials. However, the crouched alert posture was most common among wallabies stocked at the medium density (Trial 2) and least frequently seen at the lowest density (Trial 1).

The frequency of recording focal animals sitting back on their haunches was similar in each of the trial conditions. By contrast, the amount of time spent sitting upright was greatest in the medium stocking rate (Trial 2) and half as common in other trials. Wallabies were rarely seen lying except during Trial 2.

Wallabies in Trial 1 rarely interacted and this is also true of those in Trial 3. Wallabies occasionally looked towards one another or approached others at the medium-stocking rate.

Significant differences in the frequencies of the various behavioural elements and acts in the three trials are presented in Table 6.3. The frequency of adopting alert postures was significantly greater in Trial 2 than Trial 1. Wallabies browsed about the enclosure significantly less frequently during Trial 2, when compared to Trial 3.

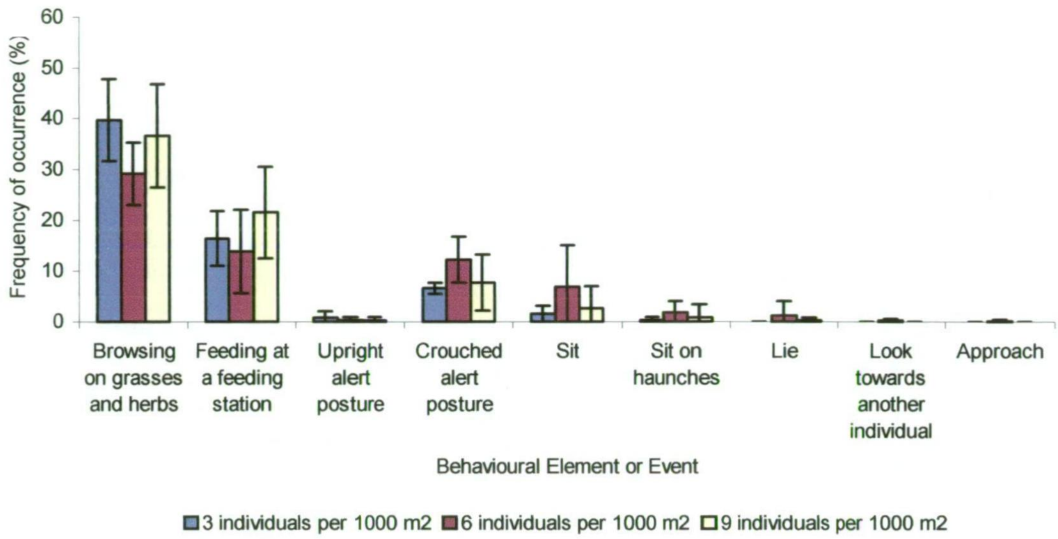


Figure 6.11: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing the key elements of behaviour. N=4 for Trial 1, 7 for Trial 2 and 12 for Trial 3.

Grooming actions directed towards the abdomen, tail, chest, head, neck and fore limbs was relatively common when wallabies were stocked at the medium rate. By comparison, wallabies groomed their hind limbs more frequently at the lowest stocking rates.

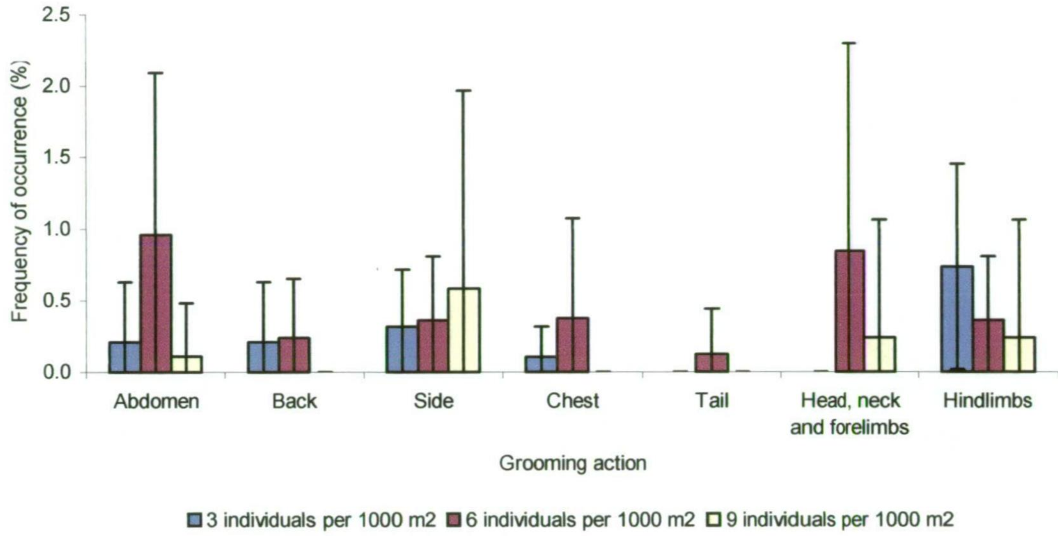


Figure 6.12: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing grooming actions. N=4 for Trial 1, 7 for Trial 2 and 12 for Trial 3.

Table 6.3: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing elements of behaviour. Differences were considered significant if $p<0.05$. N=4 for Trial 1, 7 for Trial 2 and 12 for Trial 3. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. H values provide are from the Kruskal-Wallis one-way analysis of variance.

Behavioural element or event	H value	Trial 1 vs. Trial 2 P value	Trial 2 vs. Trial 3 P value	Trial 1 vs. Trial 3 P value
Browsing on grasses and herbs	5.527	-	0.045	-
Crouched alert posture	6.539	0.005	-	-
Groom abdominal region	7.213	-	0.036	-

6.3.3 (ii) Frequencies of Observing Members of Each Sex Performing Each of the Elements of Behaviour

The frequencies with which male and female Bennett's wallabies performed individual units of behaviour were examined separately and the results of these examinations are presented in Figures 6.13 – 6.16.

Females

Females browsed about the enclosure at relatively lower frequencies during Trial 2, compared to the other trials. These animals spent similar amounts of time at feeding stations during Trials 1 and 2, but this increased during Trial 3. Resting postures were more commonly recorded during Trial 2, as was the crouched alert posture.

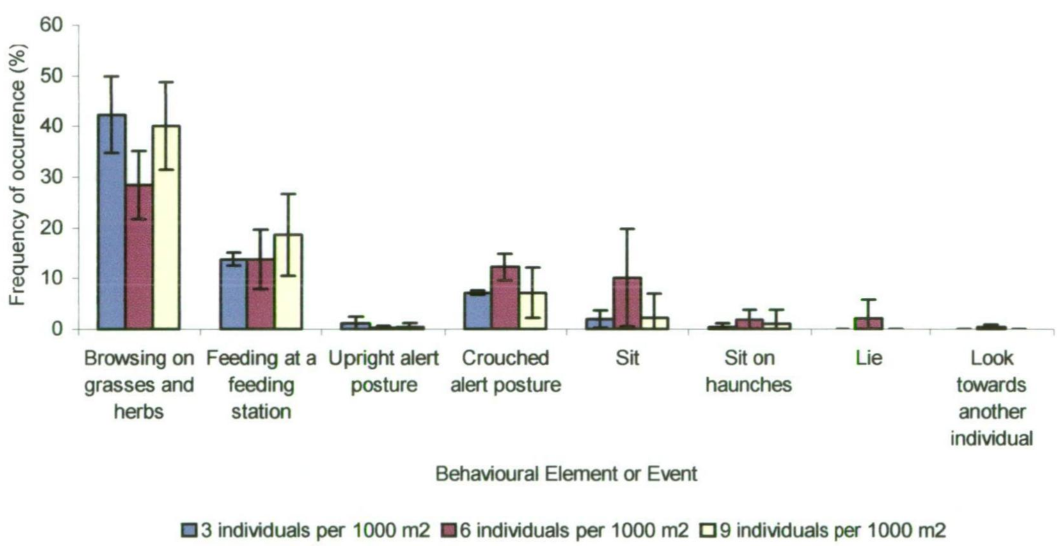


Figure 6.13: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing the key elements of behaviour. N=3 for Trial 1, 4 for Trial 2 and 9 for Trial 3.

Most grooming actions were recorded at the highest frequencies during Trial 2, with the exception of grooming actions directed towards the hind limbs, which were relatively common during Trial 1.

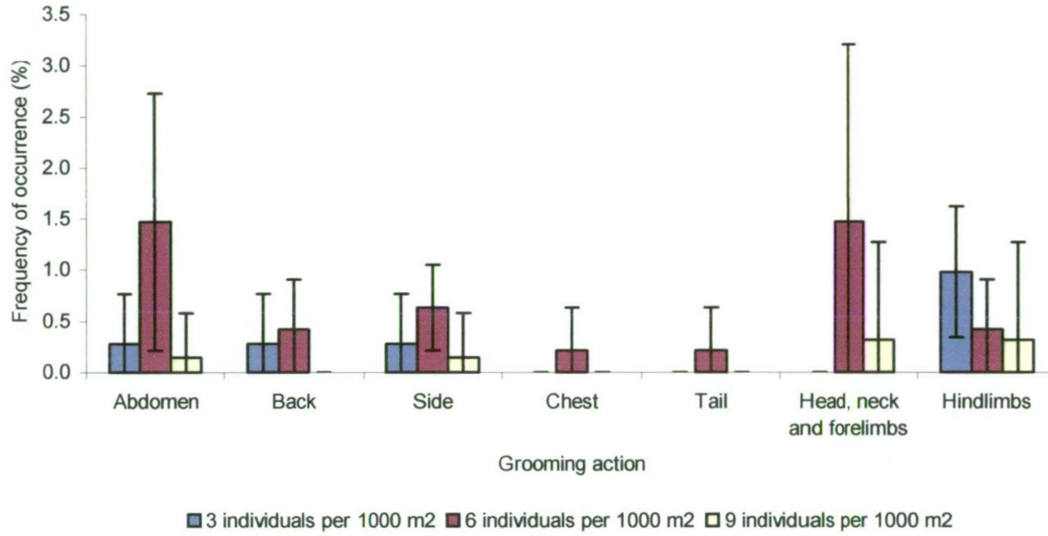


Figure 6.14: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing grooming actions. N=3 for Trial 1, 4 for Trial 2 and 9 for Trial 3.

Males

Males differed with regard to the number of crouched alert postures they adopted, a lesser number being recorded under the lowest stocking rate than either of the other regimes. Male Bennett's wallabies appeared to spend less time feeding at feeding stations at the medium density, although the amounts of time devoted to browsing were similar in each trial.

Males were rarely recorded in resting postures. These animals sat upright or lay in view more often at the highest stocking rate, but sat back on their haunches more during trial 2.

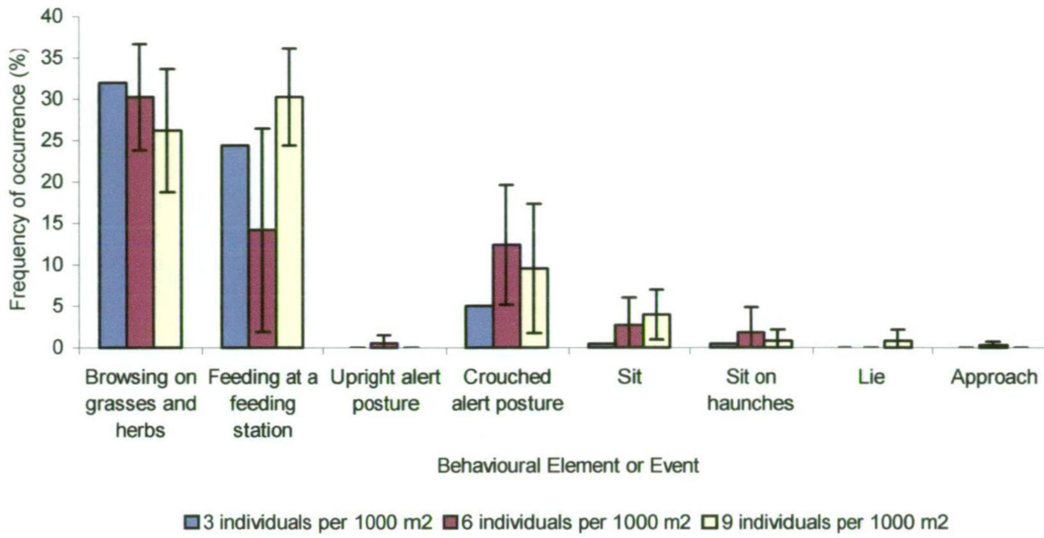


Figure 6.15: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing the key elements of behaviour. N=1 for Trial 1 and 3 for Trials 2 and 3.

Males were rarely observed directing grooming actions towards themselves. The most frequently recorded grooming actions were directed towards wallabies' sides.

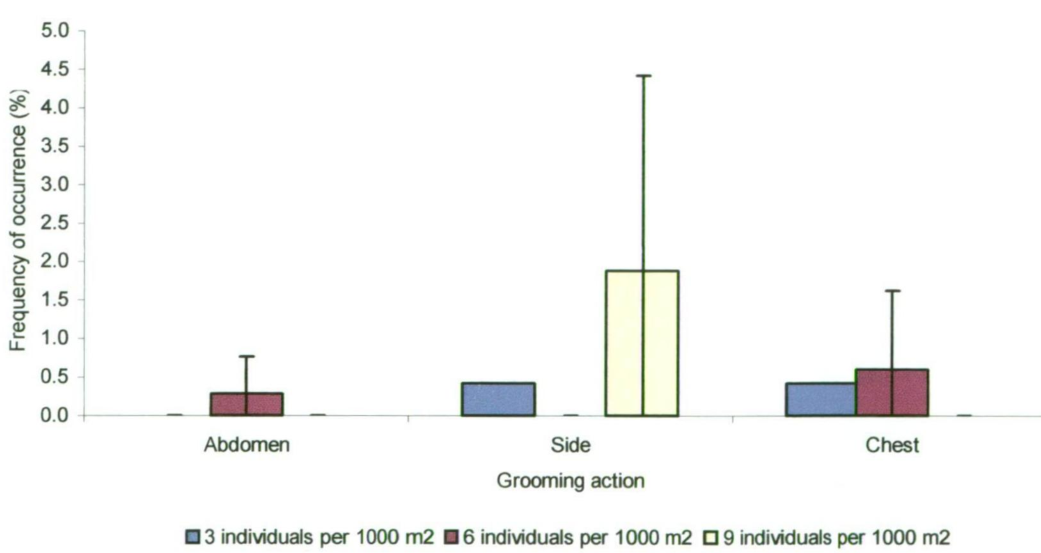


Figure 6.16: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing grooming actions. N=1 for Trial 1and 3 for Trials 2 and 3.

6.3.3 (iii) Frequencies of Observing Members of Each Age Class Performing Each of the Elements of Behaviour

The frequencies with which members of each performed specific behavioural elements are displayed in Figures 6.17 – 6.20.

Adults

Adults sat, lay and adopted crouched alert postures more frequently in the medium density group. These animals both browsed about the enclosure and attended feeders less frequently at the medium stocking rate compared to the other two.

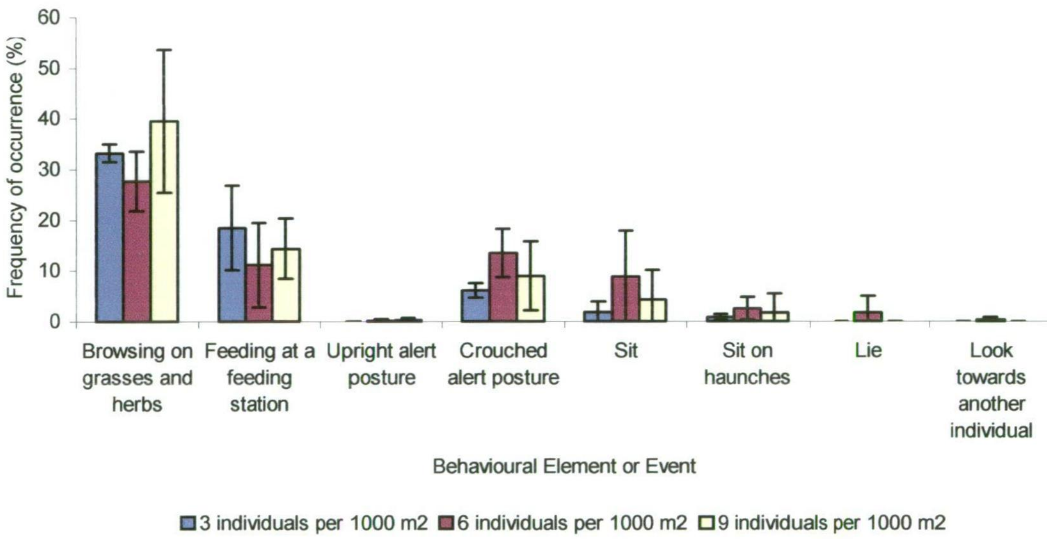


Figure 6.17: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing the key elements of behaviour. N=2 for Trial 1 and 5 for Trials 2 and 3.

Grooming actions were again more common during Trial 2, with the exception of grooming the hind limbs, which occurred more often at the highest stocking rate.

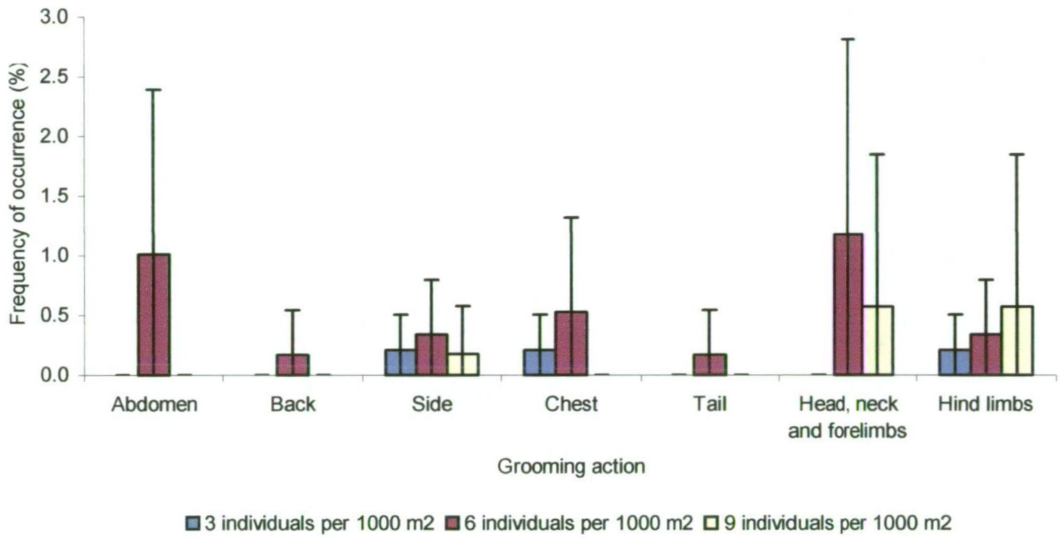


Figure 6.18: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing grooming actions. N=2 for Trial 1 and 5 for Trials 2 and 3.

Subadults and juveniles

Subadults browsed about the enclosure more frequently during Trial 1 and fed less from feeders at that time. There was little differentiation in the frequencies of other activities occurring in each trial.

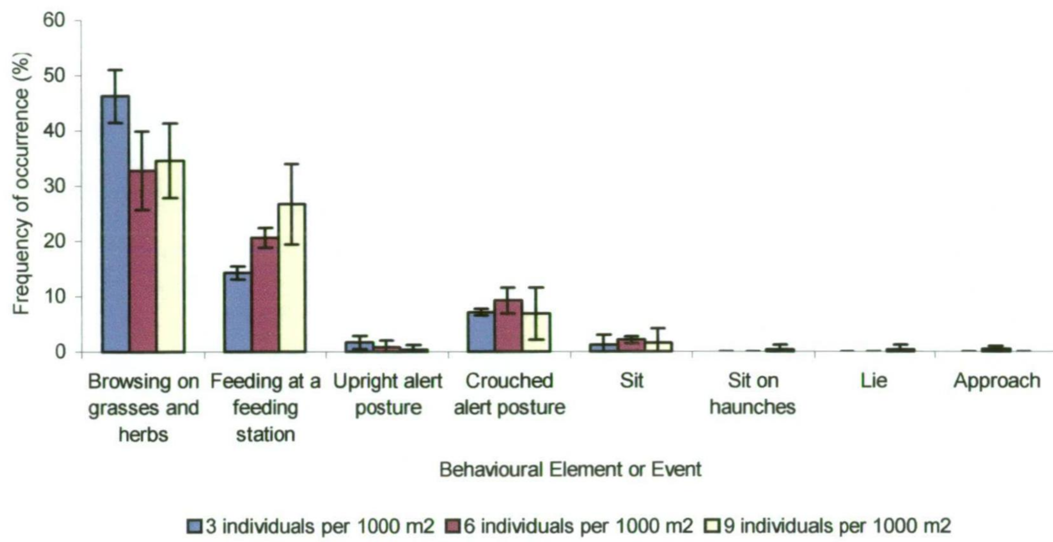


Figure 6.19: The mean percentages (± standard deviations) of overall sightings in which subadults and juveniles were recorded performing the key elements of behaviour. N=2 for Trials 1 and 2 and 7 for Trial 3.

Subadults directed grooming actions towards their sides relatively commonly during Trial 3, while other types of grooming actions were rare at that time.

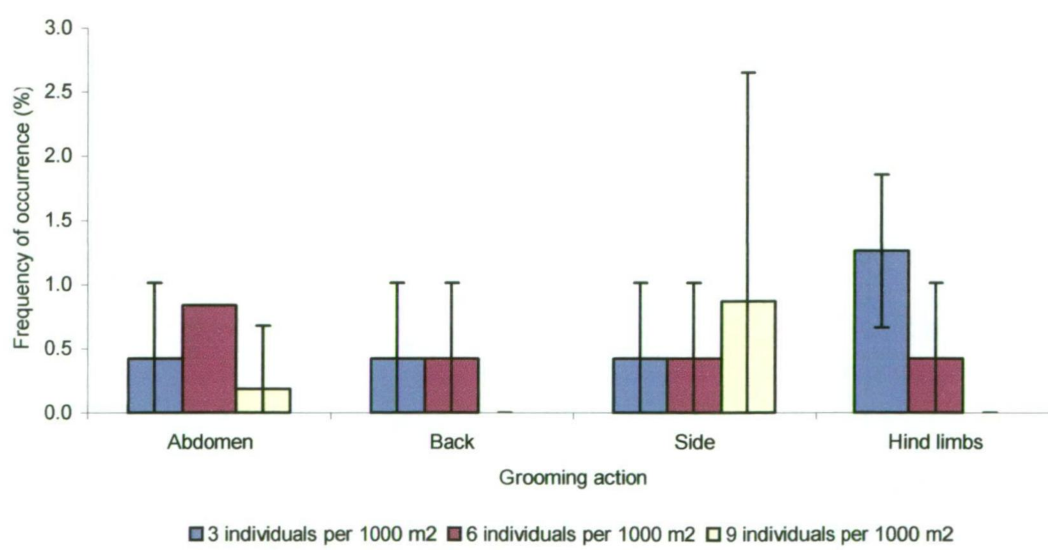


Figure 6.20: The mean percentages (± standard deviations) of overall sightings in which subadults and juveniles were recorded performing grooming actions. N=2 for Trials 1 and 2 and 7 for Trial 3.

6.3.4 Duration of Behavioural Elements and Events

6.3.4 (i) Group Durations of Behavioural Elements and Events

The mean durations of individual behavioural acts were also calculated and these are presented in Table 6.4. The durations of periods when focal animals were recorded as not in sight were greatest at the lowest stocking rate (Trial 1) and least at the medium stocking rate (Trial 2). Wallabies in Trial 2 browsed on grasses and herbs, fed at feeding stations and drank for shorter periods than in either of the other groups.

Crouched alert postures were maintained for significantly briefer periods in the medium density group, while upright alert postures were very prolonged at the highest stocking level.

Wallabies lay for lengthy periods at the medium stocking rate (Trial 2) and were subsequently recorded starting up from this position. Wallabies sat back on their haunches for similarly extended periods in the highest density group and sat for shorter periods at the two lower stocking levels.

The greatest variety of social acts was recorded at the medium stocking rate, but in general these behavioural elements lasted for similarly brief periods. Wrestling occurred for relatively longer periods in the medium density group, while focal individuals looked at other group members for the longest duration of any social act in the highest stocking rate (Trial 3).

Periods of grooming lasted for similar durations in Trial 1 and 3, while these were briefer during Trial 2. Individuals groomed their tails for relatively longer periods during Trial 2 and their chests longer during Trial 1.

Statistical analyses were performed in order to compare the duration of the various behavioural elements and events and determine whether any of these differed significantly under the three trial conditions. When comparing the lowest and medium stocking rates, focal animals adopted alert postures, sat and browsed on grasses and herbs for longer periods when stocking levels were reduced. However, they looked at one another and groomed their heads, necks and forelimbs for more extended periods at the medium stocking rate (Trial 2). Wallabies also groomed their heads necks and forelimbs for longer periods during Trial 2, when compared to Trial 3. At the highest stocking rate, individuals adopted alert postures and browsed for periods of greater duration, when compared to the medium stocking rate.

Table 6.4: The mean durations in seconds (± standard deviations) of elements of behaviour recorded during all sampling periods during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 4 for Trial 1, 7 for Trial 2 and 12 for Trial 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1	Trial 2	Trial 3
Browsing on grasses and herbs	347 ± 165 (4)	101 ± 45 (7)	306± 66 (12)
Feeding at a feeding station	485 ± 103 (4)	303 ± 92 (6)	543± 24 (12)
Browsing on trees and shrubs		230 ± 382 (6)	
Drinking from a water receptacle	112 ± 69 (2)	101 ± 59 (7)	152± 18 (11)
Merycism	3 (1)	4 ± 2 (3)	4± 1 (2)
Upright alert posture	36 ± 7 (4)	30 ± 28 (7)	93± 57 (5)
Crouched alert posture	47 ± 15 (4)	22 ± 5 (7)	49± 23 (12)
Start up		18 ± 1 (2)	
Sit	185 ± 216 (2)	195 ± 162 (6)	345± 469 (8)
Lie		442 ± 508 (2)	36± 21 (2)
Sit on haunches	464 ± 588 (2)	264 ± 379 (5)	596± 1 (2)
Look at another individual	6 ± 3 (4)	6 ± 2 (7)	8± 6 (6)
Nose	3 (1)	3 (5)	3 (7)
Sinusoidal tail movements	3 (1)	3 (2)	3 (1)
Kick		3 (2)	3 (2)
Scratch		3 (4)	3 (3)
Wrestle		6 ± 7 (6)	3 (1)
Approach	3 (1)	3 (4)	3 (7)
Retreat	3 (1)	3 (6)	3 (4)
Bite		3 (1)	
Inspect abdominal area		3 (2)	
Follow	3 (1)	3 (3)	3 (2)
Move away	3 (1)	3 (2)	3 (1)
Crouch		5 ± 2 (2)	3 (1)
Groom abdominal area	4 ± 1 (4)	7 ± 5 (6)	9± 14 (1)
Groom pouch	33 ± 26 (2)	10 ± 10 (2)	9± 12 (4)
Groom back	6 ± 5 (4)	6 ± 8 (6)	4± 2 (3)

Behavioural element or event	Trial 1	Trial 2	Trial 3
Groom sides	6 ± 4 (4)	4 ± 2 (6)	3± 1 (9)
Groom chest	14 ± 12 (4)	4 ± 1 (7)	3 (5)
Groom tail	3 (1)	11 ± 11 (2)	5 (1)
Groom head, neck and forelimbs	4 ± 1 (4)	5 ± 2 (7)	3± 1 (9)
Groom hind limbs	4 ± 2 (4)	4 ± 2 (7)	5± 5 (6)
Groom sessions	16 ± 6 (4)	10 ± 5 (7)	17± 14 (1)
Inspect trap		9 ± 8 (3)	51 (1)
Feed young at foot		102 ± 133 (3)	
Allogroom		3 (2)	232 (1)
Stand for pouch young to enter the pouch		3 (2)	
Not sighted	546 ± 46 (4)	439 ± 78 (7)	499± 147 (11)

Table 6.5: Results of a Kruskal-Wallis one way analysis of variance comparing the durations of elements of behaviour performed by focal individuals during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. P values less than 0.05 were considered significant. N = 4 for Trial 1, 7 for Trial 2 and 12 for Trial 3.

Behavioural element or event	F value	Trial 1 vs. Trial 2 P value	Trial 2 vs. Trial 3 P value	Trial 1 vs. Trial 3 P value
Browsing on grasses and herbs	16.17	0.001	0.001	-
Crouched alert posture	5.25	0.015	0.015	
Upright alert posture	8.06		0.005	0.005
Groom chest	4.96	0.025	-	0.025
Groom head, neck and forelimbs	4.19	0.033	0.033	-

6.3.4 (ii) The Durations of Behavioural Elements and Events Performed by Members of Each Sex

Females

The durations of behavioural elements performed by females are presented in Tables 6.6 and 6.7.

When comparing the duration of alert postures, females held upright and crouched postures for longer periods at the lowest and highest stocking rates (Trials 1 and 3), and also browsed on grasses and herbs for longer at these times. Females also fed from feeding stations for longer periods during Trials 1 and 3 than during Trial 2. These animals looked directly towards others for slightly shorter periods at the medium stocking rate. Grooming sessions were shorter during Trial 2, although females groomed their tails for longer periods at that time.

Males

Males maintained crouched alert postures for briefer periods at the lowest (Trial 1) and medium (Trial 2) stocking rates when comparing each of these to the highest rate. Upright alert postures were sustained for relatively brief periods at the medium stocking rate. Males, similarly to females, browsed on grasses and herbs for longer during Trials 1 and 3 than during Trial 2.

Table 6.6: The mean durations in seconds (± standard deviations) of elements of behaviour performed by females recorded during all sampling periods during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 3 for Trial 1, 4 for Trial 2 and 9 for Trial 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	378 ±188	(3)	120 ±47	(4)	317 ±73	(9)
Feeding at a feeding station	505 ±117	(3)	279 ±99	(4)	519 ±275	(9)
Upright alert posture	40 ±3	(3)	18 ±10	(4)	112 ±46	(4)
Crouched alert posture	50 ±18	(3)	23 ±4	(4)	47 ±23	(9)
Sit	338	(1)	152 ±110	(4)	312 ±537	(5)
Lie			442 ±508	(2)	51	(1)
Sit back on haunches	880	(1)	101 ±125	(4)	667	(1)
Look towards another individual	7 ±3	(3)	5 ±2	(4)	6 ±4	(3)
Approach			3	(1)	3	(4)
Groom abdominal area	4 ±1	(3)	8 ±6	(4)	11 ± 17	(7)
Groom back	6 ±6	(3)	8 ±10	(4)	5 ±3	(2)
Groom side	6 ±4	(3)	5 ±2	(4)	3 ± 1	(6)
Groom chest	17 ±12	(3)	4 ±1	(4)	3	(2)
Groom tail			11 ±11	(2)	5	(1)
Groom head neck and forelimbs	3 ±1	(3)	6 ±2	(4)	3 ± 1	(6)
Groom hind limbs	4 ±2	(3)	5 ±2	(4)	3 ± 1	(3)
Grooming session	17 ±7	(3)	12 ±4	(4)	20 ± 15	(7)
Stand for pouch young			3	(2)		
Not sighted	548 ±57	(3)	451 ±86	(4)	512 ± 142	(8)

Table 6.7: The mean durations in seconds (± standard deviations) of elements of behaviour performed by males recorded during all sampling periods during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 1 for Trial 1 and 3 for Trials 2 and 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	**Trial 1**		**Trial 2**		**Trial 3**	
Browsing on grasses and herbs	254	(1)	75 ±30	(3)	272 ± 24	(3)
Feeding at a feeding station	427	(1)	352 ±74	(2)	616 ± 60	(3)
Upright alert posture	26	(1)	45 ±40	(3)	19	(1)
Crouched alert posture	39	(1)	21 ±6	(3)	57 ± 23	(3)
Sit	33	(1)	281 ±270	(2)	399 ± 430	(3)
Lie					21	(1)
Sit back on haunches	48	(1)	914	(1)	525	(1)
Look towards another individual	3	(1)	7 ±3	(3)	10 ± 7	(3)
Approach	3	(1)	3	(3)	3	(3)
Groom abdominal area	3	(1)	5 ±3	(2)	3	(3)
Groom back	3	(1)	3	(2)	3	(1)
Groom side	3	(1)	4 ± 1	(2)	3	(3)
Groom chest	3	(1)	3	(3)	3	(3)
Groom tail	3	(1)				
Groom head neck and forelimbs	5	(1)	5 ±3	(3)	3	(3)
Groom hind limbs	3	(1)	4 ± 1	(3)	8 ± 8	(3)
Grooming session	13	(1)	7 ±4	(3)	11 ± 7	(3)
Not sighted	539	(1)	423 ±79	(3)	462 ± 189	(3)

6.3.4 (iii) The Durations of Behavioural Elements and Events Performed by Members of Each Age Class

The results of an examination of data collected from observations of the two nominated age groups are presented in Tables 6.8 and 6.9.

Adults

Adults browsed about the enclosure, fed at feeding stations and adopted alert postures for periods of lesser duration at the medium stocking rate (Trial 2). However, the opposite is true of grooming activities. Periods for which adults were recorded as out of sight were also briefer in the medium stocking rate when compared to the other two trial conditions. Adults looked for longer periods at other group members during Trials 2 and 3 when compared to those in Trial 1, with the longest bouts of looking occurring during Trial 3.

Subadults and Juveniles

Subadults, similarly to adults, browsed about the enclosure, fed at feeding stations and adopted alert postures for periods of lesser duration during Trial 2. Subadults groomed their backs for longer periods during Trial 1 compared to bouts of back grooming occurring at other times. However, grooming of the head, neck and forelimbs was sustained for longer periods during Trial 2 than either of the other trials.

Table 6.8: The mean durations in seconds (± standard deviations) of elements of behaviour performed by adults recorded during all sampling periods during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 2 for Trial 1 and 5 for Trials 2 and 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	248 ±9	(2)	105 ±54	(5)	356 ± 63	(5)
Feeding at a feeding station	480 ±76	(2)	267 ±91	(4)	549 ± 347	(5)
Upright alert posture	32 ±8	(2)	33 ±33	(5)	94 ± 64	(3)
Crouched alert posture	52 ±18	(2)	24 ±4	(5)	61 ± 31	(5)
Sit	185 ±216	(2)	248 ±181	(4)	497 ± 673	(3)
Lie			442 ±508	(2)	51	(1)
Sit back on haunches	464 ±588	(2)	317 ±416	(4)	667	(1)
Look towards another individual	3 ±1	(2)	6 ±3	(5)	10 ±7	(3)
Approach	3	(1)	3	(3)	3	(2)
Groom abdomen	4 ±1	(2)	7 ±7	(4)	3	(5)
Groom back	3	(2)	8 ±10	(4)	7	(1)
Groom side	7 ±6	(2)	5 ±2	(4)	4 ± 1	(4)
Groom chest	3	(2)	4 ±1	(5)	3	(3)
Groom tail	3	(1)	18	(1)	5	(1)
Groom head, neck and forelimbs	4 ±1	(2)	5 ±2	(5)	4 ± 1	(4)
Groom hind limbs	3	(2)	4 ±2	(5)	3 ± 1	(3)
Grooming session	11 ±3	(2)	9 ±5	(5)	14 ± 16	(5)
Not sighted	576 ±53	(2)	413 ±78	(5)	621 ± 73	(4)

Table 6.9: The mean durations in seconds (± standard deviations) of elements of behaviour performed by subadults and juveniles recorded during all sampling periods during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. N = 2 for Trials 1 and 2 and 7 for Trial 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1	Trial 2	Trial 3
Browsing on grasses and herbs	446 ±206 (2)	89 ±17 (2)	264 ± 57 (3)
Feeding at a feeding station	490 ± 161 (2)	375 ±40 (2)	593 ± 166 (3)
Upright alert posture	41 ±3 (2)	21 ±14 (2)	143 (1)
Crouched alert posture	42 ±16 (2)	18 ±5 (2)	47 ± 5 (3)
Sit		90 ± 1 (2)	476 ± 593 (2)
Lie			21 (1)
Sit back on haunches		50 (1)	
Look towards another individual	9 ±2 (2)	4 ± 1 (2)	11 (1)
Approach		3 (1)	3 (3)
Groom abdomen	4 ± 1 (2)	6 ± 1 (2)	3 (2)
Groom back	8 ±7 (2)	3 (2)	3 (2)
Groom side	4 ± 1 (2)	4 ± 1 (2)	3 (2)
Groom chest	24 ±3 (2)	3 ± 1 (2)	3 (1)
Groom tail		3 (1)	
Groom head, neck and forelimbs	4 ± 1 (2)	6 ±4 (2)	3 (2)
Groom hind limbs	5 ±2 (2)	4 ± 1 (2)	3 (2)
Grooming session	21 ± 1 (2)	12 ± 1 (2)	19 ± 16 (2)
Not sighted	516 ±4 (2)	503 ±5 (2)	47 ± 181 (3)

6.4 Discussion

The stocking regimes to which captive individuals are subjected can affect their behaviour in several important ways. If wallabies are too intensively stocked, fighting and injuries may occur (Murböck, 1977). Overstocking may also be a stressor that affects the health of captive individuals (Carlstead, 1996). Both time budgets and spatial patterns can be affected by stocking rates, influencing the number and type of interactions engaged in, how active individuals are and where they spend their time (Murböck, 1977; Crebbin, 1982). Thus stocking rates can play a role, not only in animal welfare, but also in determining the attractiveness of an exhibit to zoo or park visitors.

Zoo visitors prefer exhibits with young and active animals and will spend more time viewing these (Croke, 1997). Bennett's wallabies stocked at the medium level could be viewed most frequently. Occupation of the more exposed sectors nearer the observer's post increased at the medium and high densities. Focal animals were also sighted at greater frequencies in the more heavily-vegetated areas at the medium stocking rate. Subadults occupied sectors 11 and 12 more frequently at the medium and high stocking rates than when only three wallabies were present in the enclosure. In this instance, subadults appeared to queue in nearby areas while waiting their turn at feeders. With regard to the attractiveness of an exhibit to a zoo or park visitor, the captive group stocked at this medium density had a relatively high appeal resulting from several factors. Wallabies were, in general, more visible, all individuals spending more time in the section of the enclosure where they were easiest to observe. In particular, younger individuals increased their occupation of that same open section of the enclosure where they were easy to view whilst queuing for periods of time.

Ensuring that, at higher stocking rates, all animals are still able to access feeding stations is an important issue that must be addressed in enclosure design in order to prevent serious health issues (Finnie, 1982). As well as a number of feeding stations, provision must be made to maintain an adequate amount of browsing material that is not contaminated with faecal matter. In this study, when stocking rates were increased to nine animals per 1000 m^2, wallabies frequented all feeding stations. In the two lower density groups, males utilised the feeder at sector seven, which was better concealed and further from the observer's post, to a greater extent than for the high density group. When stocking rates were increased, males attended alternative feeding stations as well

Chapter 7 The Effects of Varying Group Structure

7.1 Introduction

A number of issues were identified from the survey reported in Chapter 3 as key considerations for current managers of captive macropods. These included the provision of supplemental feed, an issue considered in Chapter 5, and the maintenance of appropriate stocking rates, examined in Chapter 6. Nine of the 25 respondents to the questionnaire also nominated managing aspects of the age and sex ratios of members of captive groups as a key concern and this will be considered in the current chapter.

A great variety of species, including marsupials, primates, rodents, cervids, bovids, carnivores, chiropterans and cetaceans, produce offspring in captivity such that the sex ratio is skewed towards one sex (Glatston, 1997). The sex ratio of these offspring may be influenced by factors such as the nutritional and general condition of individuals, stress, population density, social status, the age of the mother and the timing of pregnancies. The presence of members of either sex in disproportionate numbers may be an issue required to be addressed with appropriate strategies. Male Bennett's wallabies may engage in frequent, ritualised agonistic interactions in enclosure environments and interact more frequently and with greater intensity in the presence of oestrus females (Murböck, 1977). Although aggressive interactions that include female macropods are rare for larger species, female aggression is more common among smaller macropods and may be related to the captive environment. Adult female brush tailed rock wallabies (*Petrogale penicillata*) in a captive breeding colony engaged in aggressive female-female interactions that were probably related to resource protection or other aspects of the enclosure environment (Bulinski *et al.,* 1997). Female Goodfellow's tree-kangaroos, *Dendrolagus goodfellowii,* attacked and killed several males maintained in captivity at London Zoo, despite the use of the largest available cages to minimise these types of interactions. Similarly, female aggression among captive Matschie's tree-kangaroos, *D. matschiei,* negatively impacted the survivorship of offspring. Survivorship was improved by isolating mothers with pouch young (Hutchins *et al.,* 1991). Understanding the effects of the presence of members of each sex within captive groups is clearly of importance in order to minimise potentially harmful interactions.

Appropriate social groupings should also be ascertained with reference to the age class and related behaviour of individuals (Baker, 2000). Although fights resulting in injuries are undesirable, agonistic interactions are an important part of the behavioural repertoire of Bennett's wallabies. Males exhibit an ontogeny of these elements of behaviour that begins when they are young at foot, play fighting with their mothers. The training and experience males gain in fighting with their mother, and later with other males from the same or older age classes, may be critical in order for these animals to have the opportunity to father their own offspring (Murböck, 1977).

Members of different age or sex classes may each exhibit behaviour, apart from agonistic behaviour, that is distinct to that class. Both sex and age differences in habitat use and spatial patterns can result in variations in foraging and other behaviours (Conradt, 1998). These differences may arise as a result of variations in sensitivity to predation, foraging energetics or shelter requirements. Age and hierarchical rank are related in captive Dama gazelles, *Gazella dama mhorr,* so that younger animals hold lower ranks and perform more submissive behaviours (Cassinello and Pieters, 2000). Captive chimpanzees (*Pan troglodytes*) in two age groups (old = 30-44 years, young = 11-22 years) differed with regard to a number of behaviours (Baker, 2000). Older chimpanzees were less aggressive and less mobile. Older females exhibited more submissive behaviours than young females, although the frequencies of affiliative behaviours did not differ significantly from their younger counterparts. Older females also manipulated enrichment devices less. Höhn *et al.* (2000) noted that, in captivity, eastern grey kangaroos differed from their wild counterparts with regard to their time budgets and the social interactions they engaged in. The amount of time devoted to feeding, vigilance and locomotory activities, as well as resting, all varied according to sex, age class and between wild and captive animals. Large and medium sized males were most active and adult females least. Large males engaged in the greatest numbers of social interactions. These are the factors that determine the appeal of enclosures to zoo visitors and thus may determine the success of the collection (Croke, 1997).

Thus, managing the age and sex ratio of captive groups ensures that agonistic interactions can be regulated and still provide an appropriately enriched environment (Höhn *et al.,* 2000). This practice also permits consideration to be given to creating a collection that is appealing to zoo visitors with regard to both the general levels of activity and the types of activities engaged in (Croke, 1997).

This chapter describes the effect of manipulating a third aspect of the enclosure environment of Bennett's wallabies at the university: the age and sex ratio of group members. The numbers of individuals from each age and sex class in the 1000 m^2 of the enclosure were varied to investigate whether this would significantly alter the frequencies of focal individuals:

1. occupying each of the sectors of the enclosure;
2. performing any element from each category of behaviour and
3. performing individual behavioural elements.

7.2 Materials and Methods

7.2.1 Age structure

7.2.1.1 Experimental Methods

Captive subjects were once again observed in the enclosure at the University of Tasmania's Hobart campus under three trial conditions. In each of these trials, wallabies were maintained at a stocking rate of eight/1000 m^2. The group structure was manipulated by changing the ratio of adults, subadults and juveniles in each group. It was intended to select treatment types based on the information provided by current macropod managers in response to the questionnaire reported on in Chapter 3. However, as was noted in Section 3.3.2.7, no clear trend was seen from these data. Stocking rates were once again determined using responses to the questionnaire to provide guidelines. Trial groups were as follows:

- Trial 1 - Four adults, two subadults and two juveniles;
- Trial 2 - Two adults, four subadults and two juveniles and
- Trial 3 - Two adults, two subadults and four juveniles.

These trials represented three possible groupings. In each of these trials, the number of males and females remained the same; three of the wallabies in each trial were male and one of these each was adult, subadult and juvenile.

Observations were conducted between 15:00 and 23:00 h. The group containing four adults was observed between March and June 1999. The second group, with more subadults, was observed between January and February in 2000. Finally, the group containing four juveniles was observed between March and April 2000. Observations were collected in the manner described previously. During each of these trial conditions, three wallabies were again substituted once half of the observations had been collected.

During the sample period, all activities that the focal animal engaged in were recorded. Any interactions with other wallabies were recorded, including acts performed by all participants from instigation to cessation. A record was also made every 5 min, starting at 0 min, of the sector of the enclosure occupied by the focal animal. Finally, the duration of each behavioural element or event performed by the focal individual was recorded, with the exception of those acts that lasted less than 3 s; these were recorded as lasting for 3 s.

7.2.1.2 Data Treatment

Data collected from focal animal observations were used to produce descriptive statistics. Data collected on the patterns of enclosure occupation and the frequency of the occurrence of behavioural elements or events and categories of behaviour were compiled into percentages in the manner previously described in section 6.2.2. Average scores per animal were calculated for all data types. The data collected from all focal animals were examined together and then further consideration was given to whether differences may occur between the trial conditions when considering each sex by itself, as well as each age class.

7.2.1.3 Statistical analyses

A Kruskal-Wallis one-way analysis of variance was utilised to identify any significant differences between the three trial conditions in:

1. the frequency of the occupation of each sector of the enclosure;
2. the frequency of the performance of acts and events belonging to each behavioural category;
3. the frequency of the performance of specific behavioural events; and
4. the duration of performing individual behavioural elements.

Data for all focal individuals were analysed and, where a significant difference was identified, a Mann-Whitney U test was then performed on pairs of trials to identify which trials gave rise to this difference. P values less than 0.05 were considered significant in each instance.

A one-way analysis of variance was utilised to test whether the duration of individual behavioural acts varied significantly between the three trial conditions.

7.2 2 Sex structure

7.2.2.1 Experimental Methods

Respondents to the questionnaire typically held captive groups of macropods, including Bennett's wallabies, that contained more females than males (35%) or an even number of males and females (36%). While only a small proportion of collections had more males than females, managing aggressive interactions between males was noted to be a major concern facing these macropod managers.

It was intended to again observe captive subjects in the enclosure at the University of Tasmania's Hobart campus under three trial conditions. In each of these trials, wallabies were to be maintained at a stocking rate of eight/1000 m^2, while the group structure was manipulated by changing the ratio of males and females in each group. For the first trial, the group was composed of five females and three males. The second group comprised four males and four females. The final group was to have held five males and three females. In each of these trials, the number individuals from each age class was to be the same.

Observations were conducted between 16:00 and 00:00 h. The group containing five females and three males was observed between March and June 1999, during which time 75 hours worth of focal animal observations were recorded. The second group, comprising four males and four females, was observed between July and September 1999. This trial was terminated after 56 h of observations had been collected following the sudden death of one of the two adult males in the group. An autopsy revealed that this animal had died from pneumonia after sustaining a cut in his mouth that abscessed. Individuals had all been weighed before observations commenced and were trapped and weighed again following the death of the male. Weight gains were the lowest of any recorded during all enclosure experiments. Some individuals had lost weight, the only time this was seen. Faecal pellets were collected from two individuals in order to perform faecal flotations. These revealed levels of coccidea and other gastro-intestinal parasites that were subsequently treated by worming with an oral dose formulation. After worming, the remaining seven individuals were trapped and weighed again, at which time it was discovered that all were gaining weight at a typical rate of approximately 1 kg per week. The decision was then made to discontinue these trials permanently, due to concern that the group composition was related to the decline in health of group members resulting in the risk that more wallabies might become seriously ill or die.

Observations were recorded in the same fashion as previously described.

7.2.2.2 Data Treatment

As an incomplete data set was collected from these trials, no statistical analyses were performed. However, data collected from focal animal observations were used to produce descriptive statistics regarding:

1. the frequency of the occupation of each sector of the enclosure;
2. the frequency of the performance of acts and events belonging to each behavioural category; and
3. the performance of individual behavioural elements.

All data were pooled for these analyses as an incomplete data set was available for the trial in which an even number of males and females were present in the enclosure.

7.3 Results

7.3.1 Age Structure of Groups

7.3.1.1 Spatial Patterns

7.3.1.1 (i) Group Spatial Patterns

The mean percentages of time individuals were recorded in each of the sectors of the enclosure were calculated and are presented in Figure 7.1.

General trends in sector occupation can be seen from this data. The occupation of the more heavily-vegetated sectors of the enclosure were similar in each trial, as was the occupation of open areas with browse matter. Individuals were in sight more often during Trial 2, when a greater number of subadults were present, and least during Trial 1, when more adults were included in the group. The use of sectors one and two, containing feeders, also showed some variation between trials; when more juveniles were present, members of the captive group were recorded in sector one less frequently and sector two far more so. The occupation of sector two during Trial 2 was similarly high when compared to Trial 1.

Statistical analyses performed on the data revealed almost no significant differences in the use of the various areas in the three trial conditions, as can be seen in Table 7.1. When comparing Trial 1 to both Trials 2 and 3, focal animals in the latter of these trial conditions occupied sector three, with a feeding station and a relatively high degree of cover, significantly more frequently.

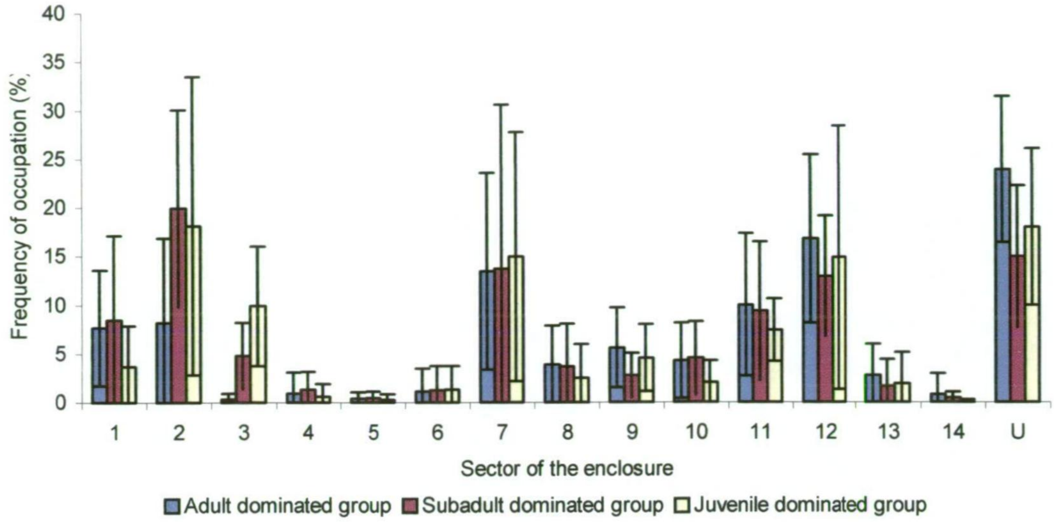


Figure 7.1: The mean percentages (± standard deviations) of overall sightings in which focal individuals were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=11 in Trials 1 and 3 and 10 in Trial 2.

Table 7.1: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of sector occupation had been identified. Differences were considered significant if $p<0.05$. . Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N=11 in Trials 1 and 3 and 10 in Trial 2. .

Sector		Trial 1 vs. Trial 2	Trial 2 vs. Trial 3	Trial 1 vs. Trial 3
	H value	P value	P value	P value
3	19.92	0.001	-	0.001

7.3.1.1 (ii) Spatial Patterns of Members of Each Sex

The results of analyses of data from each sex can be seen in Figures 7.2 and 7.3.

Females

The rates of occupation of each sector by females during the three trials did not vary greatly. Females occupied sectors two and three more frequently, and sector one less frequently, during Trial 3, when juveniles were present in increased numbers. When more adults were present, females occupied sector one relatively frequently but wee rarely seen in sector three.

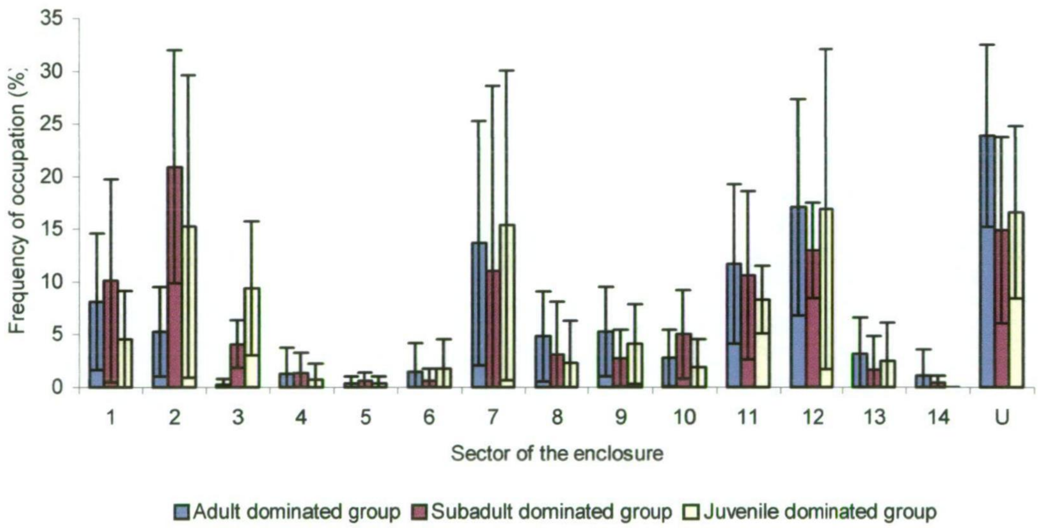


Figure 7.2: The mean percentages (± standard deviations) of overall sightings in which females were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. Sector 15 represents those occasions when a focal animal was not in sight at the time a recording fell due. N= 8 in each Trial.

Males

Males were more frequently recorded in sector 1 and were hidden from sight more often during Trial 1, compared to other trials. When more juveniles were included in the group, the frequency of occupying sector 1 decreased compared to that of females, while the occupation of sectors 2 and 3 was comparably high.

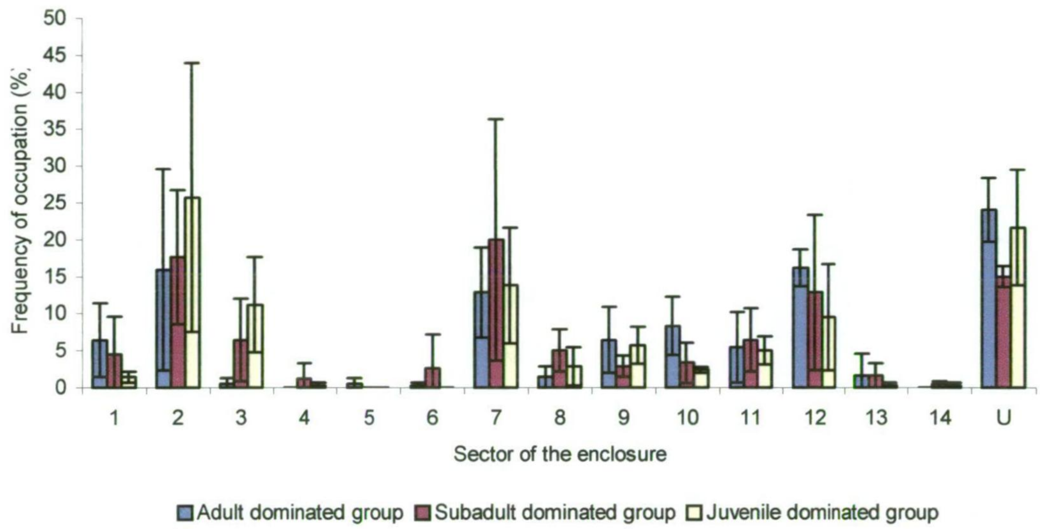


Figure 7.3: The mean percentages (± standard deviations) of overall sightings in which males were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. Sector 15 represents those occasions when a focal animal was not in sight at the time a recording fell due. N=3 in each Trial.

7.3.1.1 (iii) Spatial Patterns of Members of Each Age Class

The results of an examination of data collected from members of each age class are presented in Figures 7.4, 7.5 and 7.6.

Adults

Adult members of each experimental group occupied the more heavily vegetated sectors and the open sectors with browse matter as similar frequencies in each trial. When more subadults were present, the rates of occupation of sectors one and seven by adults increased compared to those seen for the whole group. Adults were most visible when the number of subadults included in the group was highest and occupied sector seven at relatively high rates in each trial, particularly Trial 2.

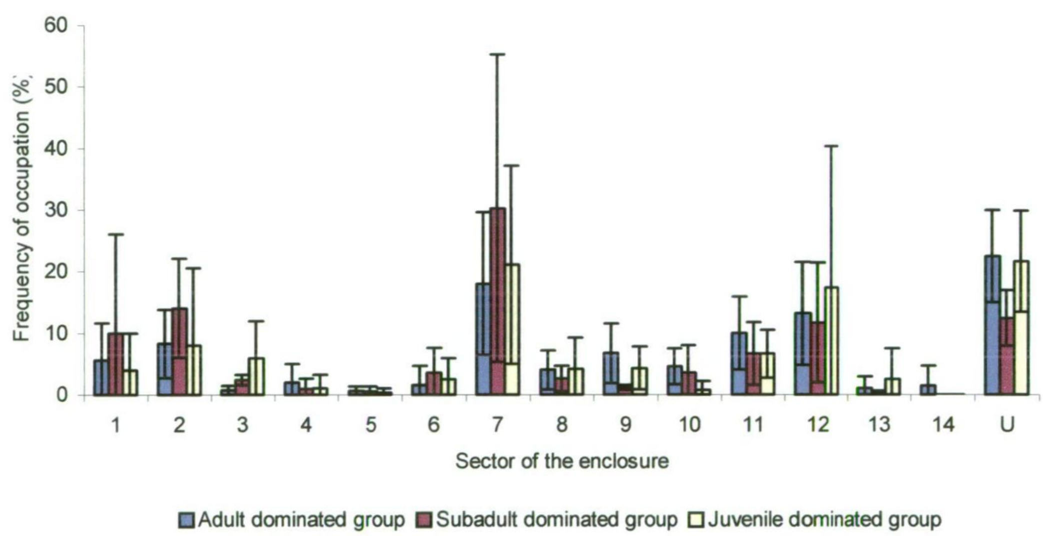


Figure 7.4: The mean percentages (± standard deviations) of overall sightings in which adults were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=5 for Trial 1, 3 for Trial 2 and 4 for Trial 3.

Subadults

Subadults occupied sector three, with a well-concealed feeding station, less frequently during Trial 1 when compared to either of the other trials. By comparison, they occupied sectors two and eleven more frequently when they formed the largest segment of the group. Subadults were also present in sectors 12 and 13 at greater frequencies during Trial 3 than at other times. These individuals remained hidden from sight least often when they themselves formed the largest segment of the captive group (Trial 2).

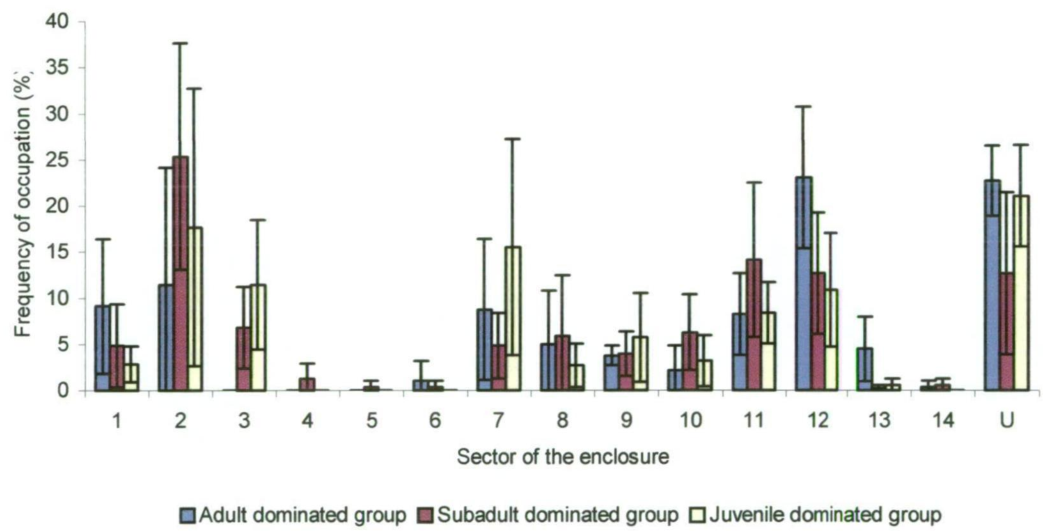


Figure 7.5: The mean percentages (± standard deviations) of overall sightings in which subadults were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. Sector 15 represents those occasions when a focal animal was not in sight at the time a recording fell due. N=4 for each Trial.

Juveniles

Juveniles occupied sector two considerably less frequently during Trial 1 compared to either of the other trials, particularly Trial 2. A similar pattern is seen for the occupation of sector three by juveniles: these animals were rarely seen here during Trial 1. Juveniles were hidden from sight most frequently when more adults were present than in either Trials 2 or 3.

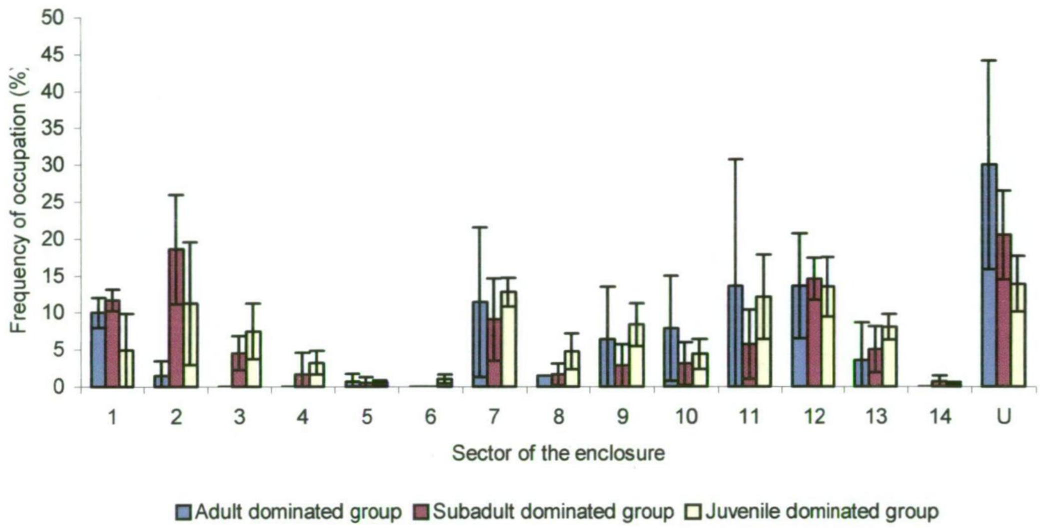


Figure 7.6: The mean percentages (± standard deviations) of overall sightings in which juveniles were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.11. Sector 15 represents those occasions when a focal animal was not in sight at the time a recording fell due. N=2 for Trial 1 and 3 for Trials 2 and 3.

7.3.1.2 Frequency of Behavioural Categories

7.3.1.2 (i) The Frequencies of Group Members Performing Any of the Acts from Each Category of Behaviour

The percentages of time devoted to activities from each of the behavioural categories in each of the three trial conditions are presented in Figure 7.7 and the results of the statistical testing of these data in Table 7.2.

The total amount of time devoted to eating and drinking was greatest when juveniles dominated the group and decreased as the age of individuals in the group increased. When adults dominated the group, individuals adopted alert postures relatively frequently, but this was not reflected in either of the other two trial conditions. When subadults were present in greater numbers, focal animals rested in sight more frequently and moved about the enclosure less. When more adults were present, individuals rested far less frequently where they could be seen and were unsighted more often and spent more time grooming. When members of the youngest age class dominated the group, individuals interacted most frequently, fed more often and rested for relatively long periods.

When statistical analyses were performed on the data from groups containing more adults or more subadults, the former proved to remain out of sight more frequently. Members of the former group rested significantly less often where they could be viewed compared to both Trials 2 and 3. Members of the group containing more juveniles were significantly less frequently recorded grooming than the adult-dominated group. Alert postures were adopted significantly more frequently in Trial 1, when more adults were present, than in either Trial 2 or Trial 3.

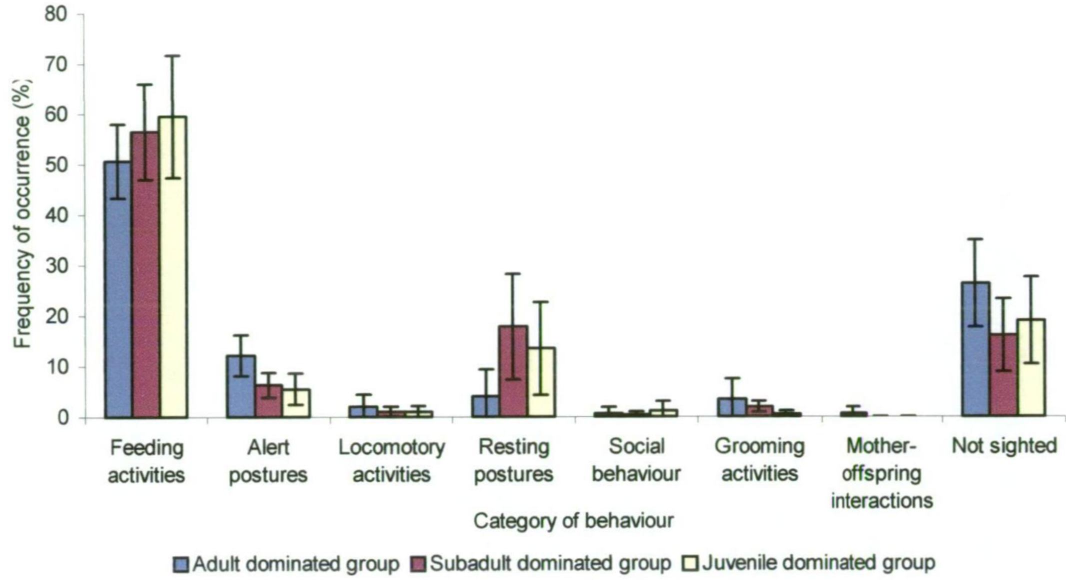


Figure 7.7: The mean percentages (± standard deviations) of overall sightings in which focal individuals were recorded performing any of the acts from categories of behaviour. N=11 for Trials 1 and 3 and 10 for Trial 2.

Table 7.2: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing any of the acts from each category of behaviour. Differences were considered significant if $p<0.05$. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N=11 for Trials 1 and 3 and 10 for Trial 2. H values provided are from the Kruskal-Wallis one-way analysis of variance.

Category of behaviour		Trial 1 vs. Trial 2	Trial 2 vs. Trial 3	Trial 1 vs. Trial 3
	H value	P value	P value	P value
Alert postures	15.51	0.001	0.001	0.001
Resting postures	13.48	0.001	-	0.001
Grooming activities	10.80	-	-	0.003
Not sighted	7.738	0.021	-	-

7.3.1.2 (ii) The Frequencies of Members of Each Sex Performing Any of the Acts from Each Category of Behaviour

The mean frequencies of members of each sex performing behavioural acts from each category of behaviour were calculated as percentages of the total observed time and are presented in Figures 7.8 and 7.9.

Females

The patterns of spatial distribution seen for females closely mirrors that described for the group as a whole. Females were hidden from view more frequently when more adults were present (Trial 1) than either of the other trial conditions. Females in Trial 3, with the youngest mean age of group members, devoted less time to grooming activities than their counterparts in the other trials, while feeding and resting more often than females in Trial 1.

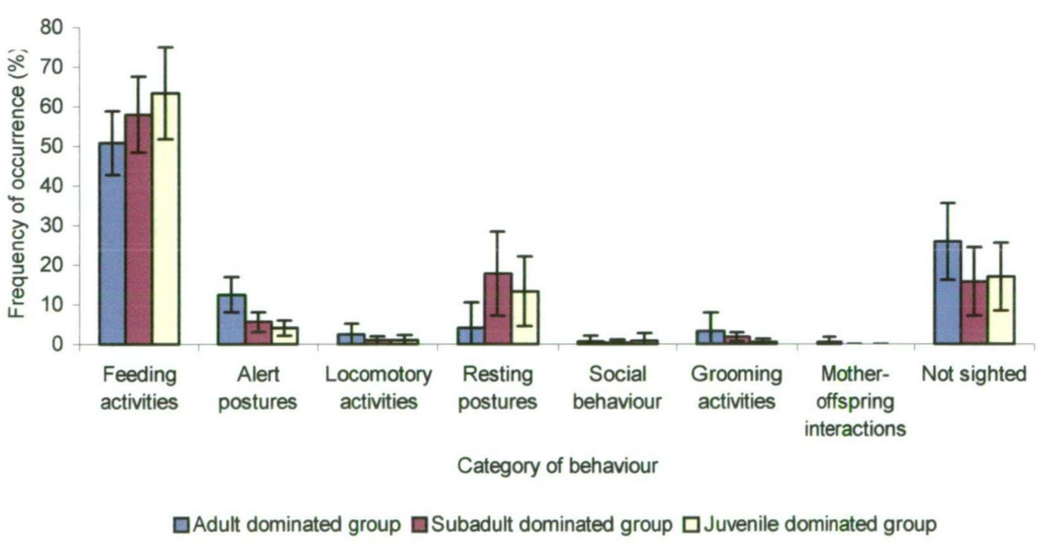


Figure 7.8: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing any of the acts from categories of behaviour. N = 8 for each Trial.

Males

Males generally apportioned time between the categories of activities similarly in the three trials. They were more often out of sight during Trial 2, when more subadults were included in the group and rested in view relatively infrequently in Trial 1 compared to the other trials. Males also groomed for less time during Trial 3, where the captive group had the youngest average age.

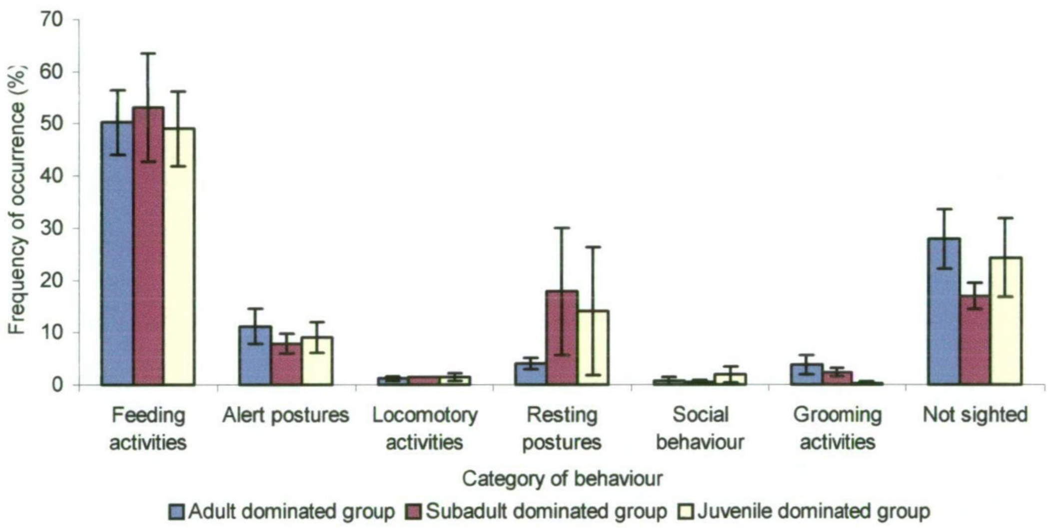


Figure 7.9: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing any of the acts from categories of behaviour. N=3 for each Trial.

7.3.1.2 (iii) The Frequencies of Members of Each Age Class Performing Any of the Acts from Each Category of Behaviour

The mean frequencies with which members of each age group performed acts belonging to the various categories of behaviour are presented in Figures 7.10, 7.11 and 7.12.

Adults

Adults did not differ greatly in the apportioning of time to different categories of activities. In each trial, adults devoted around half of the observed time to activities related to eating and drinking. Adults were recorded in resting postures least frequently in Trial 1, at which time they formed half of the group members. These animals engaged in fewer social interactions when more subadults were present in the group (Trial 2) compared to their counterparts in Trial 3.

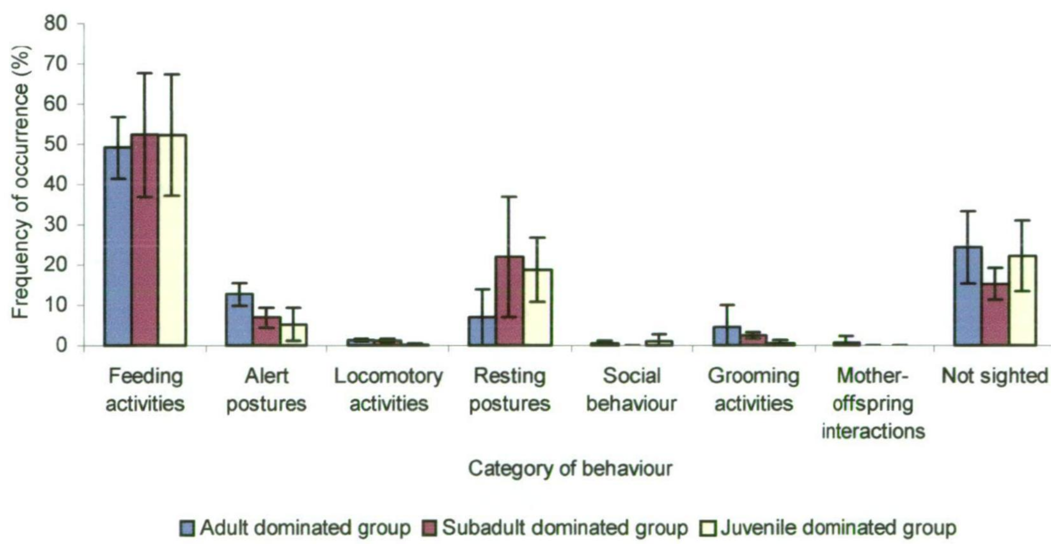


Figure 7.10: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing any of the acts from categories of behaviour. N = 5 for Trial 1, 3 for Trial 2 and 4 for Trial 3.

Subadults

Subadults also devoted similar amounts of time to acts from each category of behaviour in the three trials. They devoted even greater amounts of time to feeding activities in each trial than adults. Subadults rested more frequently in Trial 2 than in either of the other trials and were generally more visible at this time than in the other trials.

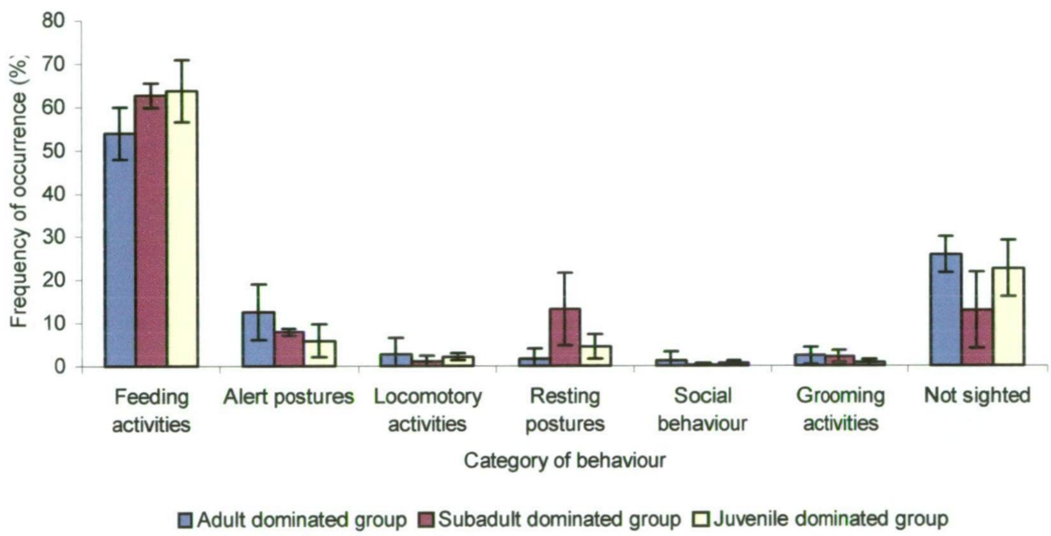


Figure 7.11: The mean percentages (± standard deviations) of overall sightings in which subadults were recorded performing any of the acts from categories of behaviour. N=4 for each Trial.

Juveniles

Again, juveniles devoted similar amounts of time to performing acts from each category of behaviour in each trial. Mother-offspring interactions were most frequently recorded during Trial 1, when a greater number of adults were present, but the frequencies of recording other types of social interactions did not differ significantly between trials. Juveniles adopted cryptic positions most frequently when they formed the smallest segment of the captive group, during Trial 1, and were more visible when present in increased numbers. They rarely rested in view when adults were present in comparatively high numbers.

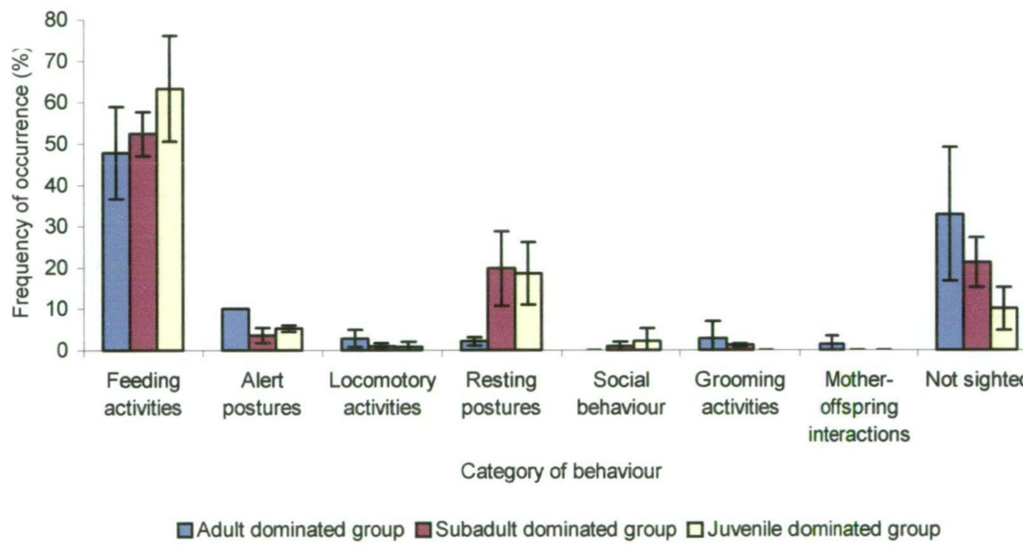


Figure 7.12: The mean percentages (± standard deviations) of overall sightings in which juveniles were recorded performing any of the acts from categories of behaviour. N = 2 for Trial 1 and 3 for Trials 2 and 3.

7.3.1.3 Frequency of Behavioural Elements and Events

7.3.1.3 (i) Frequencies of Group Members Performing Each of the Elements of Behaviour

The frequencies with which focal animals performed specific elements of behaviour are presented in Figures 7.13 and 7.14. Wallabies browsed on grasses and herbs for a significantly smaller portion of the day when more adults were present in the captive group (Trial 1). In this same trial, both crouched and upright alert postures occurred significantly more frequently than in either of the other trials.

When more subadults were present (Trial 2), individuals were seen lying or sitting back on their haunches more frequently. During Trial 3, focal wallabies were sighted sitting more commonly.

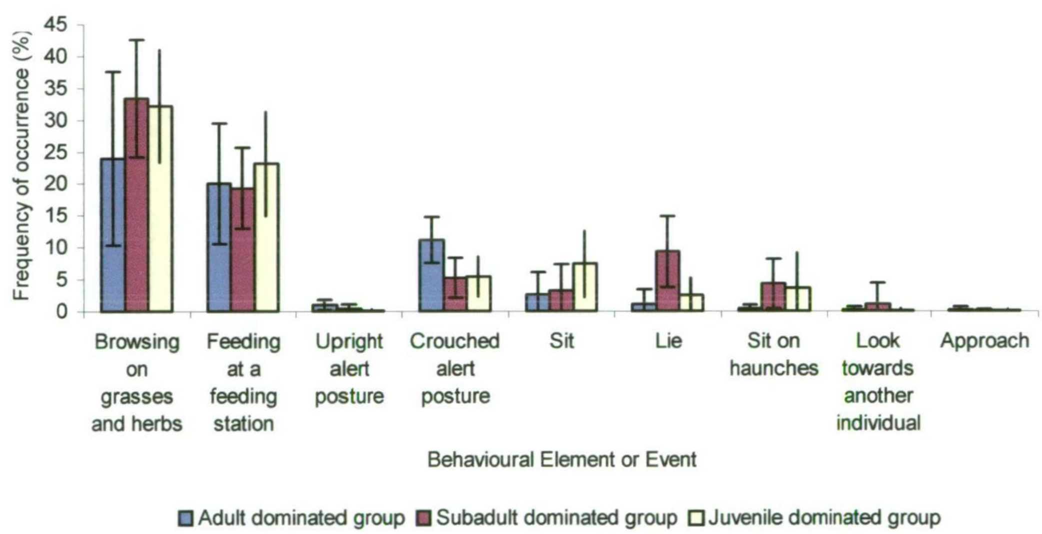


Figure 7.13: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing the key elements of behaviour. N=11 for Trials 1 and 3 and 10 for Trial 2.

Most grooming actions were generally performed when more adults were present (Trial 1), declining in frequency as the average age of group members decreased.

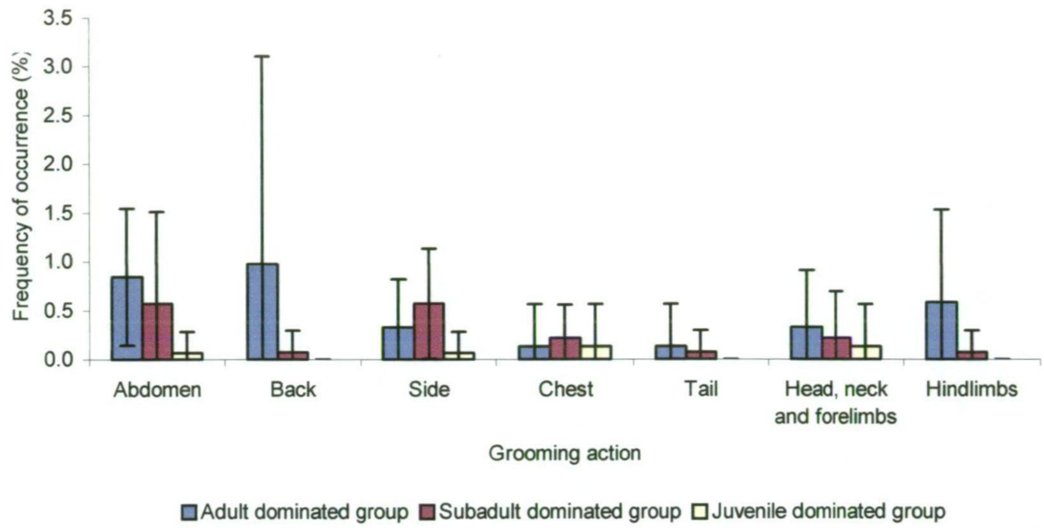


Figure 7.14: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing grooming actions. N=11 for Trials 1 and 3 and 10 for Trial 2.

Table 7.3: Results of post-hoc Mann-Whitney U tests performed on data from pairs of trial conditions where a significant difference in the frequencies of recording focal individuals performing elements of behaviour. Differences were considered significant if $p<0.05$. . Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 11 for Trials 1 and 3 and 10 for Trial 2. H values provide are from the Kruskal-Wallis one-way analysis of variance.

Behavioural element or event	H value	Trial 1 vs. Trial 2 P value	Trial 2 vs. Trial 3 P value	Trial 1 vs. Trial 3 P value
Browsing on grasses and herbs	7.531	0.023	-	0.023
Crouched alert posture	14.06	0.001	-	0.001
Upright alert posture	11.49	0.048	-	0.003
Sit	6.891	-	0.029	0.029
Lie	15.16	0.001	0.001	-
Sit back on haunches	6.322	0.029	-	-
Groom abdominal area	5.710	-	-	0.022
Groom hind limbs	2.398	0.050	-	0.050
Groom side	4.296	-	0.047	-

7.3.1.3 (ii) Frequencies of Members of Each Sex Performing Each of the Elements of Behaviour

The results of examinations of data from observations of female Bennett's wallabies are presented in Figures 7.15 and 7.16 and that of males in Figures 7.17 and 7.18.

Females

Female wallabies browsed more frequently during Trials 2 and 3, when more juveniles were present, and less so during Trial 1, when a greater number of adults were included in the group. By contrast, these animals adopted both crouched and upright alert postures more frequently during Trial 1.

Females were observed to adopt sitting postures relatively more frequently during Trial 3, but lay in sight relatively frequently during Trial 2.

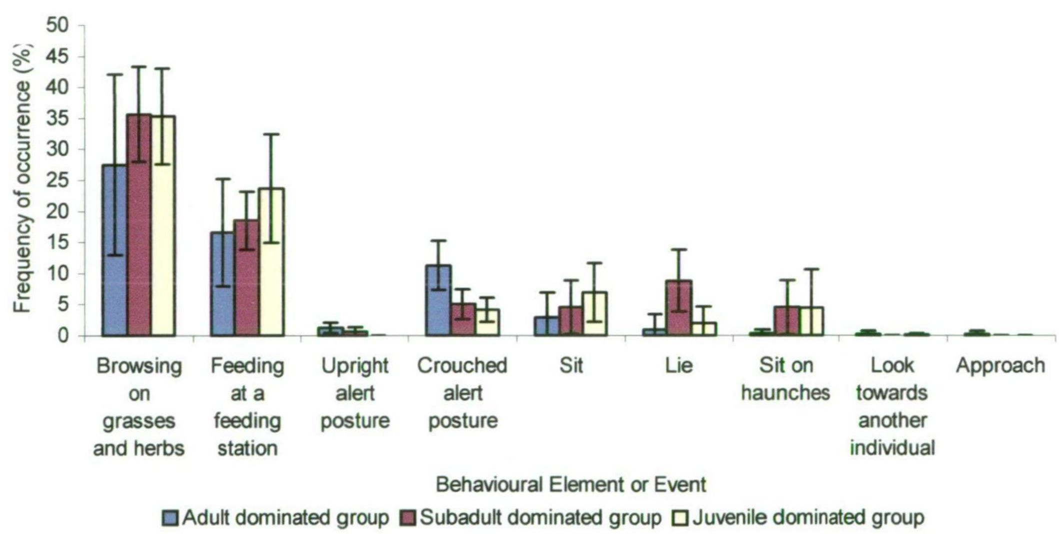


Figure 7.15: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing the key elements of behaviour. N=8 for each Trial.

Females groomed their hind limbs, abdomens and backs more often in the adult dominated group (Trial 1) and less as the average age of group members declined. By contrast, wallabies groomed their sides more often during Trial 2 and their chests during Trial 3.

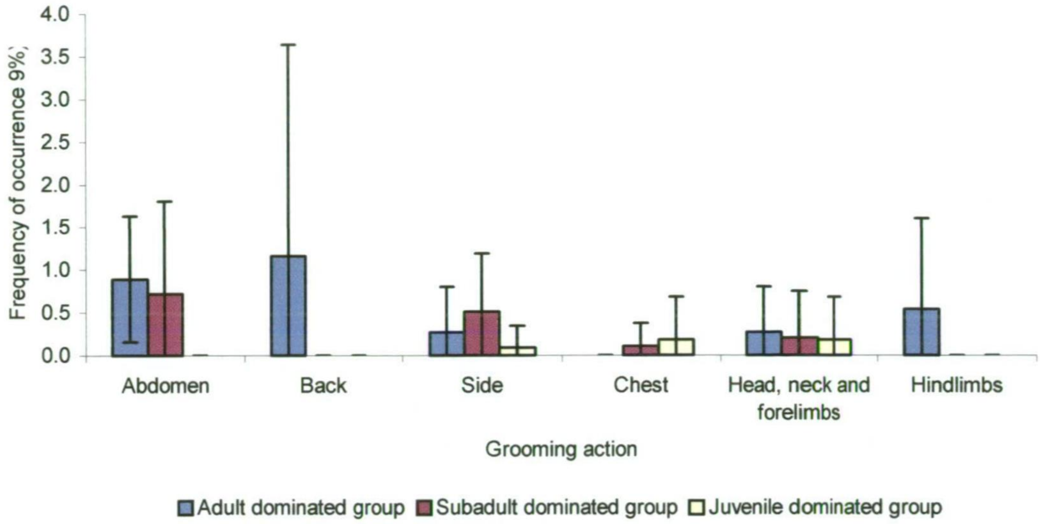


Figure 7.16: The mean percentages (± standard deviations) of overall sightings in which females were recorded performing grooming actions. N=8 for each Trial.

Males

The amount of time males devoted to browsing and attending feeding stations was similar to that of females, although the differences between the three trial conditions was more pronounced. Males adopted alert postures at similar frequencies in the three trials, with the lowest frequencies of both upright and laert postures being seen when proportionally more subadults were present.

Males adopted sitting postures relatively more frequently during Trial 3 and lay and sat back on their haunches more frequently in positions where they were visible to the observer during Trial 2. Males approached other wallabies in the enclosure at similar frequencies in each trial. By contrast, males looked directly at other wallabies more frequently during Trial 2.

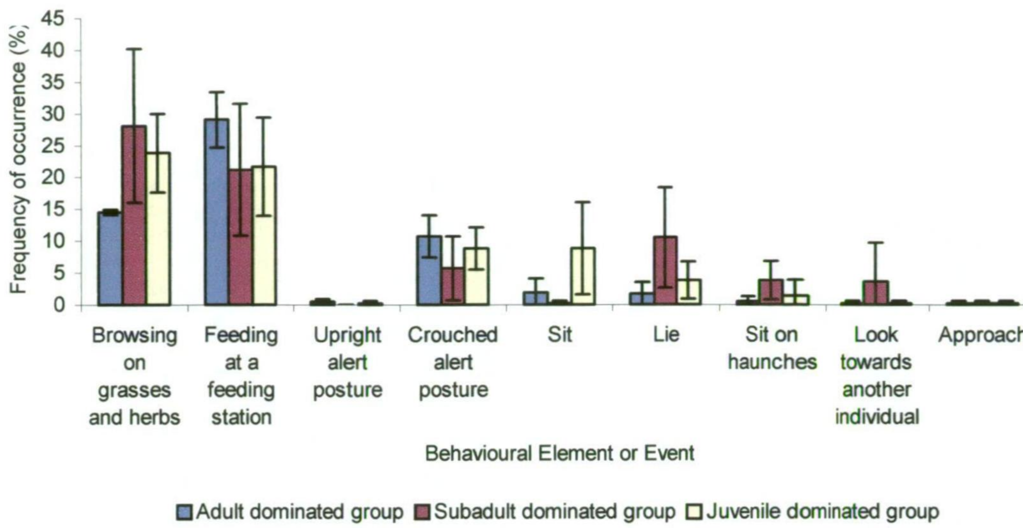


Figure 7.17: The mean percentages (± standard deviations) of overall sightings in which males were recorded performing the key elements of behaviour. N=3 for each Trial.

Males performed grooming actions most frequently during Trial 1. By contrast, grooming actions were rarely recorded during Trial 3.

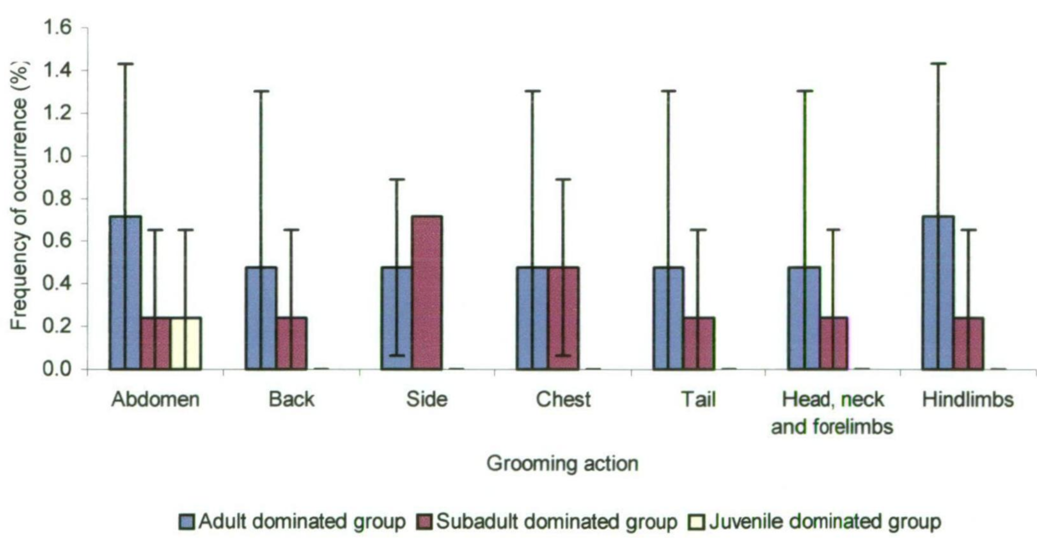


Figure 7.18: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing grooming actions. N=3 for each Trial.

7.3.1.3 (iii) Frequencies of Members of Each Age Class Performing Each of the Elements of Behaviour

The mean frequencies with which acts were performed are presented for each age class in Figures 7.19 - 7.24.

Adults

Adults devoted similar amounts of time to browsing on grasses and herbs and feeding at feeding stations in each trial, but adopted crouched and upright alert postures more frequently during Trial 1 than in the other trials.

Adults lay in positions in view more frequently when more subadults were included in the group and sat in either position with increasing frequency as the mean age f the group decreased.

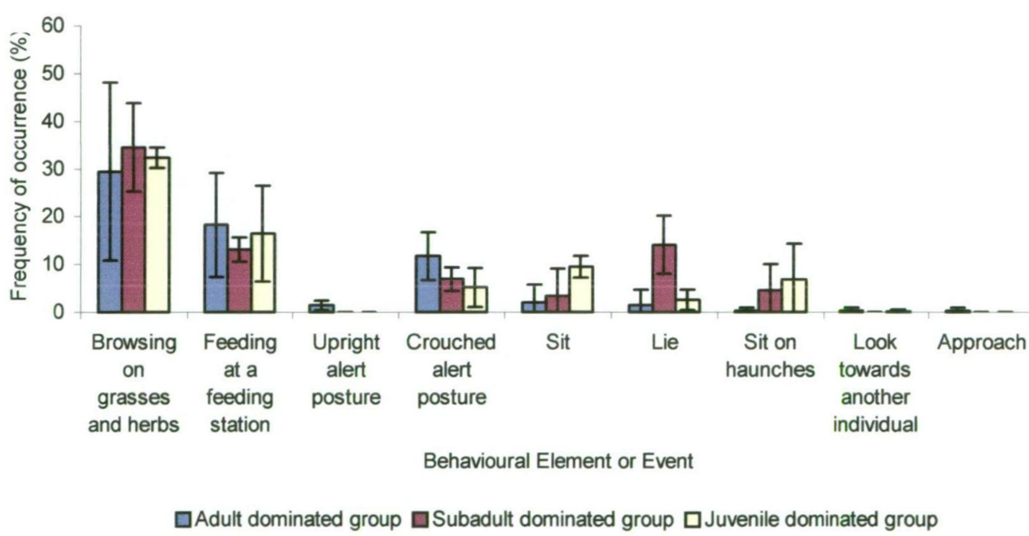


Figure 7.19: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing the key elements of behaviour. N=5 for Trial 1, 3 for Trial 2 and 4 for Trial 3.

Adult wallabies groomed their hind limbs and backs more frequently during Trial 1, while grooming actions were directed towards their abdomens more commonly during Trial 2 and towards their chests during Trial 3.

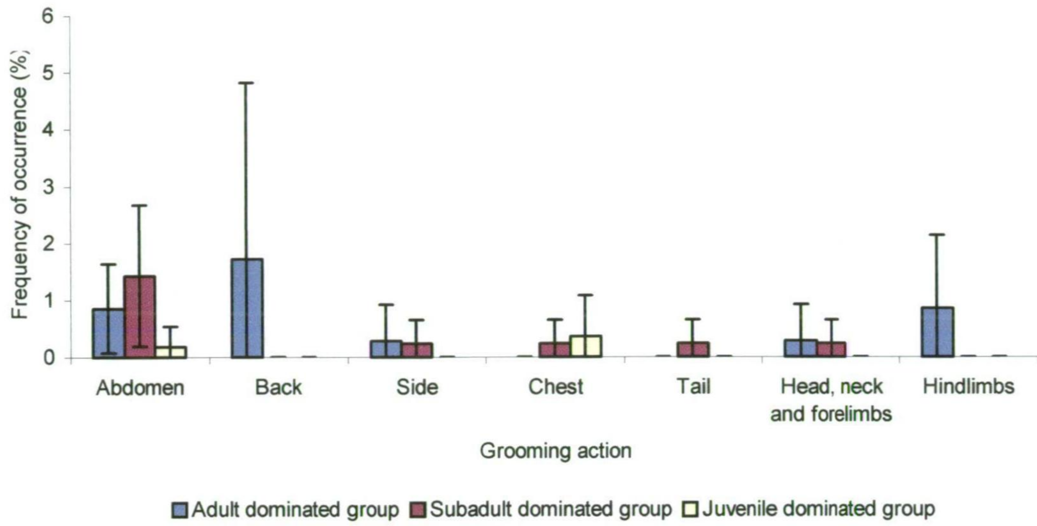


Figure 7.20: The mean percentages (± standard deviations) of overall sightings in which adults were recorded performing grooming actions. N=5 for Trial 1, 3 for Trial 2 and 4 for Trial 3.

Subadults

Subadults browsed on grasses and herbs less frequently during Trial 1 compared to the other trials. In this trial, subadults also adopted relatively higher numbers of upright alert postures. Subadults in Trial 3 almost never adopted crouched alert postures. These individuals adopted resting postures in view more frequently in Trial 2 than either of the other trials, when their own numbers were reduced.

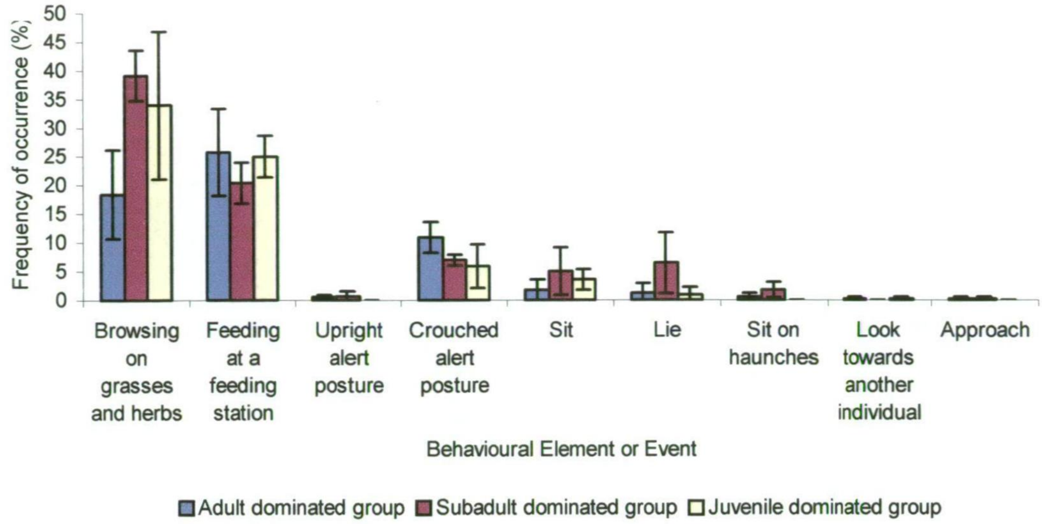


Figure 7.21: The mean percentages (± standard deviations) of overall sightings in which subadults were recorded performing the key elements of behaviour. N=4 for each Trial.

Subadults were more easily viewed performing grooming actions during Trial 1, when adults were present,, while grooming activity was rarely recorded during Trial 3, when more juveniles were present.

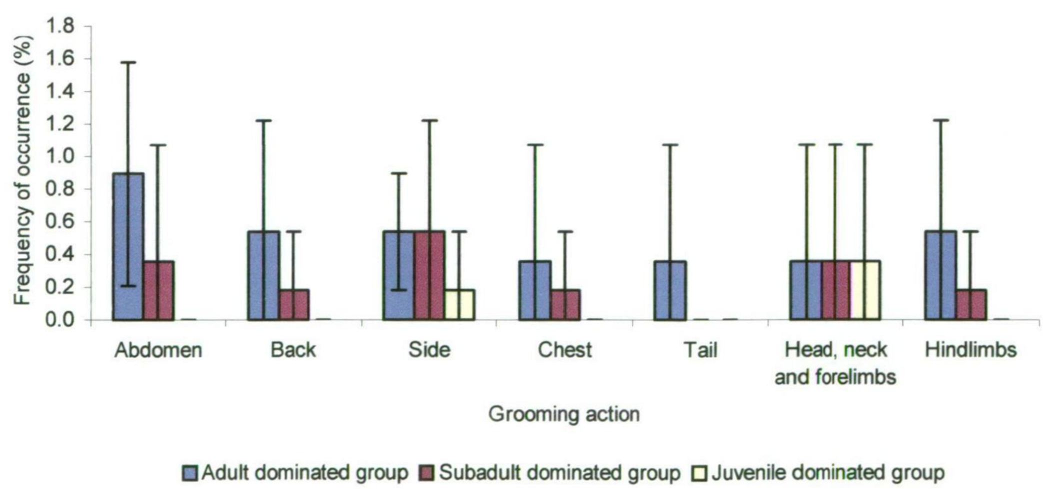


Figure 7.22: The mean percentages (± standard deviations) of overall sightings in which subadults were recorded performing grooming actions. N=4 for each Trial.

Juveniles

Juveniles browsed around the enclosure at similar frequencies during the three trials, but fed at feeding stations least often when more adults were present and most frequently when they themselves formed a larger portion of the group. They adopted crouched alert postures most frequently during Trial 1 and least frequently during Trial 2. Juveniles lay or sat back on their haunches more frequently during Trials 2 and 3 but sat in the more upright position less frequently when more subadults were present.

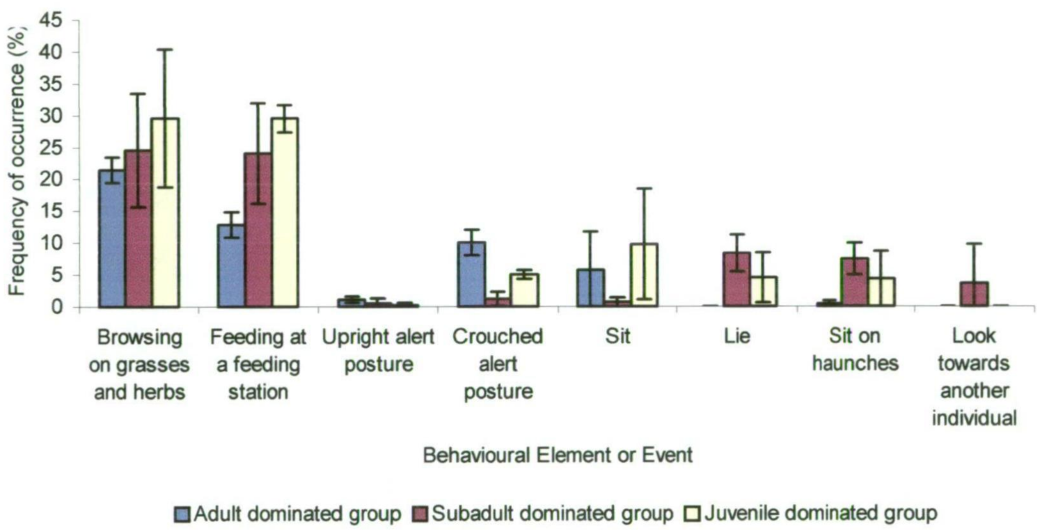


Figure 7.23: The mean percentages (± standard deviations) of overall sightings in which juveniles were recorded performing the key elements of behaviour. N=2 for Trial 1 and 3 for Trials 2 and 3.

Juveniles were rarely seen grooming in any of the three trials. Grooming actions were occasionally directed towards the abdomen, tail, head, neck and forelimbs during Trial 1 and towards the sides and chests during Trial 2.

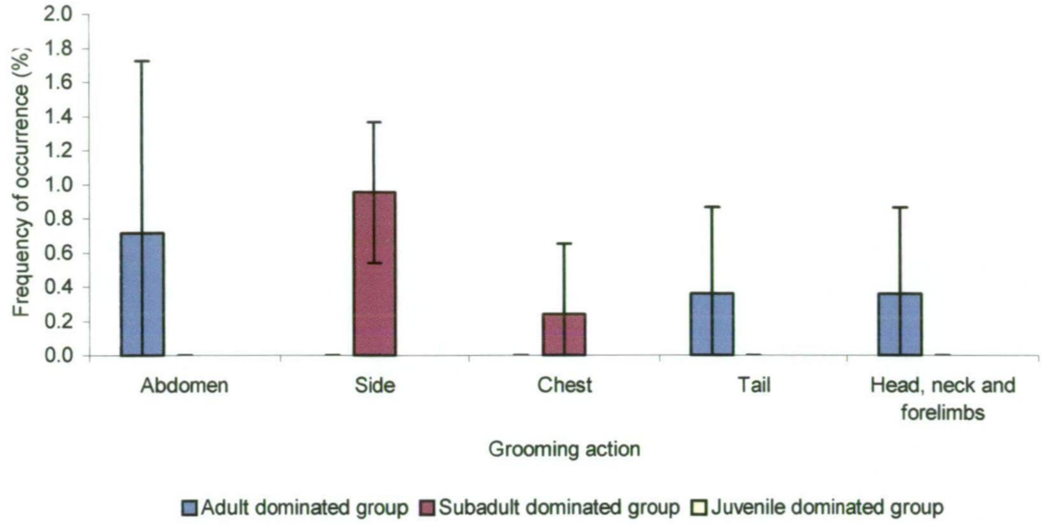


Figure 7.24: The mean percentages (± standard deviations) of overall sightings in which juveniles were recorded performing grooming actions. N=2 for Trial 1 and 3 for Trials 2 and 3.

7.3.1.4 Duration of Behavioural Elements and Events

7.3.1.4 (i) Durations of Behavioural Elements and Events Performed by Group Members

Previously, the frequencies with which individual elements of behaviour were performed were examined. The durations of behavioural elements in each of the three trial conditions were also compared and the results of these analyses are presented in Tables 7.4 and 7.5.

Feeding activities and the adoption of alert postures lasted for shorter periods when more adults were included in the captive group (Trial 1): periods of browsing and attending feeding stations were significantly briefer at this time. By contrast, some social interactions, such as wrestling and sinusoidal tail movements, lasted for longer periods.

Upright alert postures were sustained for the briefest periods when adults formed a larger portion of the group and longest when more subadults were present. Crouched alert postures were also sustained for longer periods when subadults predominated, but lasted for periods of similar duration in the other trial conditions.

Wallabies sat up for the longest periods during Trial 1 and groomed their tails for significantly longer periods at that time. Periods of lying down and sitting back on the haunches were more prolonged during Trial 2. The latter posture occurred for significantly briefer periods when more adults were present when compared to either of the other trials.

Table 7.4: The mean durations in seconds (± standard deviations) of elements of behaviour recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 11 for Trials 1 and 3 and 10 for Trial 2. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	**Trial 1**		**Trial 2**		**Trial 3**	
Browsing on grasses and herbs	153± 63	(11)	313± 78	(10)	245± 137	(10)
Feeding at a feeding station	330± 135	(11)	491± 91	(10)	455± 230	(10)
Browsing on trees and shrubs	132± 31	(8)	69± 49	(3)		
Drinking from a water receptacle	183± 103	(11)	195± 65	(10)	268± 200	(9)
Merycism	3	(1)	7± 5	(2)	27± 33	(2)
Upright alert posture	29± 9	(9)	45± 38	(9)	37± 54	(6)
Crouched alert posture	36± 10	(11)	45± 19	(10)	36± 15	(10)
Start up	6± 5	(3)	24± 18	(4)	158	(1)
Sit	193± 179	(9)	178± 118	(9)	151± 102	(9)
Lie	343± 317	(3)	714± 489	(10)	219± 151	(3)
Sit on haunches	175± 105	(6)	854± 595	(8)	805± 566	(4)
Look at another individual	6± 5	(11)	5± 2	(10)	4± 1	(8)
Touch nose to another individual	3	(7)	3	(7)	2± 1	(6)
Sinusoidal tail movements	19± 27	(3)	3	(2)	3	(1)
Kick	3	(1)			3	(2)
Scratch	3	(4)	3	(2)	2± 1	(3)
Wrestle	17± 13	(3)	3	(1)		(1)
Approach	3	(7)	3	(7)	2± 1	(8)
Retreat	3	(8)	3	(6)	2± 1	(8)
Chase	3	(1)				
Arc	3	(2)			2± 2	(2)
Inspect abdominal region	3	(2)	3	(2)	1	(1)
Inspect anogenital region			3	(1)		(1)
Move away	3	(3)	3	(3)	3	(1)
Scratch head			3	(1)		
Sternal rub			3	(1)		(1)
Follow	3	(5)	3	(3)	1	(2)
Crouch	3	(1)	3	(4)	23± 34	(3)
Copulate	3	(1)			2	(1)
Groom abdominal region	8± 6	(11)	5± 3	(10)	4± 6	(10)
Groom pouch	7± 6	(2)	12± 10	(3)	35± 45	(2)
Groom back	3± 1	(9)	3	(6)	2± 2	(3)
Groom sides	3± 1	(10)	8± 14	(9)	2± 1	(5)
Groom chest	3	(9)	4± 2	(8)	2± 1	(5)
Groom tail	30± 54	(4)	4± 3	(8)	2± 1	(5)

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Groom head, neck and forelimbs	4± 2	(11)	6± 9	(10)	2± 1	(9)
Groom hind limbs	5± 3	(10)	4± 2	(10)	2± 1	(10)
Grooming sessions	11± 8	(11)	14± 10	(10)	8± 8	(10)
Fence running	3	(1)				
Cough	3	(1)				
Feed young at foot	3	(1)				
Feed from mother			299±	(1)		
Allogroom	278	(1)	18±	(1)		
Play	409	(1)				
Not sighted	423± 76	(11)	497± 158	(9)	381± 196	(10)

Table 7.5: Results of a Kruskal-Wallis one way analysis of variance comparing the durations of elements of behaviour performed by focal individuals during the three trials. Trial 1 = 3 animals/1000 m^2. Trial 2 = 6 animals/1000 m^2. Trial 3 = 9 animals/1000 m^2. P values less than 0.05 were considered significant. N=11 in Trials 1 and 3 and 10 in Trial 2, degrees of freedom = 2.

Behavioural element or event	F value	Trial 1 vs. Trial 2 P value	Trial 2 vs. Trial 3 P value	Trial 1 vs. Trial 3 P value
Browsing on grasses and herbs	7.57	0.002	-	0.002
Feeding at a feeding station	7.63	0.002	-	0.002
Sit on haunches	7.74	0.004	-	0.004
Groom tail	4.27	0.034		0.034

7.3.1.4 (ii) Durations of Behavioural Elements and Events Performed by Members of Each Sex

The mean durations of behaviour elements for each sex are presented in Tables 7.6 and 7.7.

Females

Females browsed on grasses and herbs growing within the enclosure for relatively brief periods during Trial 1, when more adults were included in the captive group, but for periods of similar duration in the other two trials. In contrast, the duration of attendance at feeders increased in Trial 3, when more juveniles were present and declined as the average age of group members decreased.

Females were recorded sitting back on their haunches for shorter periods during Trials 1 than either Trial 2 or 3. These individuals also slightly increased the average length of time spent grooming their tails, heads, forelimbs and hind limbs during Trial 1, although the duration of grooming sessions were similar in each trial.

Table 7.6: The mean durations in seconds (± standard deviations) of elements of behaviour performed by females recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 8 in each Trial. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	164 ±71	(8)	302 ±66	(7)	305 ± 119	(7)
Feeding at a feeding station	292 ±136	(8)	491 ±75	(7)	571 ± 160	(7)
Upright alert posture	27	(1)	16 ±4	(3)	12	(1)
Crouched alert posture	31 ±9	(2)	35 ±29	(3)	26 ± 16	(2)
Sit	11	(1)	203 ±105	(2)	154 ± 73	(2)
Lie	126	(1)	1001 ±693	(3)	46	(1)
Sit back on haunches	123 ±88	(4)	1063 ±673	(5)	1023± 443	(3)
Look towards another individual	3 ±1	(2)	5 ±3	(3)	3 ± 1	(2)
Approach	3	(1)	3	(2)	2 2	(2)
Groom back	3	(1)	3	(1)		
Groom side	3	(2)	17 ±23	(3)		
Groom chest	3	(2)	4 ±1	(2)	3	(1)
Groom tail	39 ±62	(3)	5 ±4	(5)	3	(4)
Groom head, neck and forelimbs	6 ±5	(2)	3 ±	(3)	3 ±	(1)
Groom hind limbs	7 ±5	(2)	5 ±4	(3)	2 ± 2	(2)
Grooming sessions	12 ±6	(2)	18 ±16	(3)	4 ± 1	(2)
Not unsighted	416 ±81	(8)	525 ± 185	(6)	457 ± 186	(7)

Males

Male Bennett's wallabies both browsed about the enclosure and attended feeders for longer periods during Trial 2, when more subadults were present. Both alert and resting postures were maintained for briefer durations when more juveniles were present. Similarly, grooming actions were sustained for shorter periods during Trial 3 and males were out of sight less at this time. As previously described for their female counterparts, the length of time for which males sustained alert postures did not vary significantly between any of the three captive groups.

The duration of intervals during which both male and female focal individuals were out of sight were similar in each instance; no significant variation was found in any instance.

Table 7.7: The mean durations in seconds (± standard deviations) of elements of behaviour recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 3 for each Trial. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	122 ±2	(3)	338 ±116	(3)	105± 19	(3)
Feeding at a feeding station	432 ±66	(3)	489 ±141	(3)	185± 58	(3)
Upright alert posture	25 ±5	(3)	28 ±9	(3)	7 ± 5	(3)
Crouched alert posture	34 ±6	(3)	49 ±16	(3)	19 ± 7	(3)
Sit	368 ±317	(2)	162 ± 100	(3)	56 ± 47	(3)
Lie	161 ±50	(2)	432 ±156	(3)	46 ±	(1)
Sit back on haunches	279 ± 1	(2)	505±200	(3)	151 ±	(1)
Look towards another individual	5 ±2	(3)	4 ±1	(3)	4 ± 2	(2)
Approach	3	(3)	3	(3)	1 ± 1	(3)
Groom abdominal region	9 ±5	(3)	7 ±3	(3)	1 ± 1	(3)
Groom back	3	(2)	3	(3)	1	(1)
Groom side	3	(3)	3	(3)	1	(1)
Groom chest	3	(3)	5 ±2	(3)	1	(2)
Groom tail	3	(1)	3	(3)	1	(1)
Groom head, neck and forelimbs	6 ±3	(3)	13 ±16	(3)	1 ± 1	(3)
Groom hind limbs	6 ±4	(3)	5 ±4	(3)	1 ± 1	(3)
Grooming sessions	11 ±5	(3)	18 ±10	(3)	2 ± 2	(3)
Not sighted	443 ±69	(3)	443 ±89	(3)	203 ± 34	(3)

7.3.1.4 (iii) Durations of Behavioural Elements and Events Performed by Members of Each Age Group

The mean duration that members of each age class performed individual elements of behaviour are presented in Tables 7.8, 7.9 and 7.10.

Adults

Adults browsed for periods of shorter duration during Trial 1 than at other times. However, the length of episodes of attendance at feeding stations did not vary greatly. Adults both sat back on their haunches and started up for periods of the longest duration when fewest members of this age group were present. The opposite is true of grooming the tail: this activity was sustained the longest when the most adults were present.

Table 7.8: The mean durations in seconds (± standard deviations) of elements of behaviour performed by adults, recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 5 for Trial 1, 3 for Trial 2 and 4 for Trial 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1	Trial 2	Trial 3
Browsing on grasses and herbs	181±76 (5)	298±76 (3)	253± 161 (4)
Feeding at a feeding station	379±163 (5)	401±80 (3)	389±253 (4)
Upright alert posture	26 ±8 (4)	36 ±3 (2)	75 ± 98 (2)
Crouched alert posture	43 ± 10 (5)	41 ±7 (3)	40 ± 15 (4)
Sit	306 ± 196 (4)	163 ±205 (3)	161 ± 101 (3)
Lie	706 (1)	861 ±428 (3)	306 ± 21 (2)
Sit back on haunches	185 ±89 (4)	656±54 (2)	1242± 322 (2)
Look towards another individual	4 ± 1 (5)	5 ±2 (3)	4 ± 1 (2)
Approach	3 (3)	3 (2)	2 ± 2 (2)
Groom abdominal region	9 ±6 (5)	4 ±2 (3)	2 ± 1 (4)
Groom back	3 ± 1 (5)	3 (3)	3 (1)
Groom side	3 ± 1 (5)	3 ± 1 (3)	2 ± 2 (2)
Groom chest	3 ± 1 (4)	3 (3)	2 ± 2 (2)
Groom tail	57±76 (2)	6±5 (3)	3 ± (3)
Groom head, neck and forelimbs	3 ± 1 (5)	12 ± 16 (3)	2 ± 1 (4)
Groom hind limbs	5 ±4 (4)	3 (3)	2 ± 1 (4)
Grooming sessions	13 ± 11 (5)	17 ± 12 (3)	9 ± 9 (4)
Not sighted	430 ± 52 (5)	417 ±210 (3)	374 ± 206 (4)

Subadults

Subadults browsed around the enclosure, fed at feeding stations and sat on their haunches for relatively brief periods during Trial 1 and at similar levels in the other two trials. Grooming of the tail lasted for similarly brief periods in each trial, while grooming of the chest lasted relatively longer and the abdomen relatively shorter when more subadults were present.

Table 7.9: The mean durations in seconds (± standard deviations) of elements of behaviour performed by subadults recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 4 for each Trial. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	122 ±49	(4)	268±67	(4)	287± 140	(4)
Feeding at a feeding station	265 ±75	(4)	525±63	(4)	515± 210	(4)
Upright alert posture	33 ±10	(4)	72 ±44	(4)	19 17	(3)
Crouched alert posture	31 ±7	(4)	55 ±14	(4)	37 16	(4)
Sit	125 ±114	(4)	177 ±71	(4)	141 138	(4)
Lie	196 ±	(1)	389 ±174	(4)		
Sit back on haunches	31	(1)	465±147	(3)	585	(1)
Look towards another individual	11 ±6	(4)	6 ±3	(4)	5 ± 1	(4)
Approach	3	(3)	3 ±	(3)	2 ± 1	(4)
Groom abdominal region	7 ±8	(4)	4 ±2	(4)	8 ± 8	(4)
Groom back	3	(3)	3	(2)	2 ± 2	(2)
Groom side	3	(3)	3	(3)	3	(3)
Groom chest	3	(3)	5 ±3	(3)	2 ± 2	(2)
Groom tail	3	(1)	3	(3)	3	(1)
Groom head, neck and forelimbs	3 ±1	(4)	3 ±1	(4)	3 ± 2	(4)
Groom hind limbs	3	(4)	3 ±1	(4)	2 ± 1	(4)
Grooming sessions	7 ±4	(4)	10 ±4	(4)	10 ± 8	(4)
Not sighted	416 ±106	(4)	605 ±143	(3)	470 ±207	(4)

Juveniles

Juveniles browsed about the enclosure, fed at feeders and sat back on their haunches for periods of the longest duration when greater numbers of subadults were present. Crouched alert postures lasted for similar periods in each trial, while upright alert postures were sustained for longer periods when more adults were present. Grooming sessions were most prolonged during Trial 2, and least when more juveniles were included in the group.

Table 7.10: The mean durations in seconds (± standard deviations) of elements of behaviour performed by juveniles, recorded during all sampling periods during the three trials. Trial 1 = 4 adults, 2 subadults and 2 juveniles. Trial 2 = 2 adults, 4 subadults and 2 juveniles. Trial 3 = 2 adults, 2 subadults and 4 juveniles. N = 2 for Trial 1 and 3 for Trials 2 and 3. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	Trial 1		Trial 2		Trial 3	
Browsing on grasses and herbs	144 ±34	(2)	388 ±47	(3)	146 ± 78	(2)
Feeding at a feeding station	337 ±171	(2)	534 ±86	(3)	470 ± 346	(2)
Upright alert posture	27	(1)	16 ±4	(3)	12	(1)
Crouched alert posture	31 ±9	(2)	35 ±29	(3)	26 ± 16	(2)
Sit	11	(1)	203 ±105	2	154 ± 73	(2)
Lie	126	(1)	1001 ±693	(3)	46	(1)
Sit back on haunches	278	(1)	1375 ±735	(3)	151	(1)
Look towards another individual	3 ±1	(2)	5 ±3	(3)	3 ± 1	(2)
Approach	3	(1)	3	(2)	2 ± 2	(2)
Groom back	3	(1)	3	(1)		
Groom side	3	(2)	17 ±23	(3)		
Groom chest	3	(2)	4 ±1	(2)	3	(1)
Groom tail	3	(1)	3	(2)	1	(1)
Groom head, neck and forelimbs	6 ±5	(2)	3	(3)	3	(1)
Groom hind limbs	7 ±5	(2)	5 ±4	(3)	2 ± 2	(2)
Grooming sessions	12 ±6	(2)	18 ±16	(3)	4 ± 1	(2)
Not sighted	421 ±112	(2)	470 ±85	(3)	217 ± 62	(2)

7.3.2 Sex Structure

7.3.2.1 Spatial Patterns

The frequency with which focal individuals were sighted in each of the trial conditions can be seen in Figure 7.25.

The frequencies of the occupation of the more heavily vegetated areas of the enclosure were similar in both trials, as were those areas open areas with browsing matter. When the numbers of males and females within the group were even, the occupation rates of sectors one, two and 12, containing feeding stations or a water receptacle, increased compared to the other trial condition.

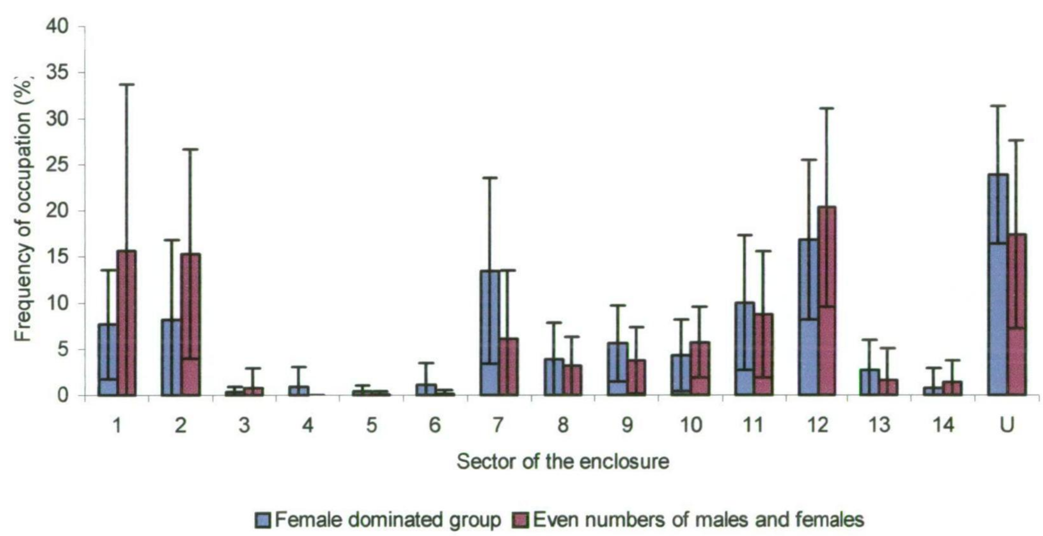


Figure 7.25: The mean percentages (± standard deviations) of overall sightings in which focal individuals were present in each section of the university enclosure. The sectors here refer to those described in Figure 2.1. U represents those occasions when a focal animal was not in sight at the time a recording fell due. N=11 for each Trial.

7.3.2.2 Frequency of Behavioural Categories

The mean percentages of time devoted by focal individuals to each of the categories of behaviour under the two trial conditions can be seen in Figure 7.26.

The frequencies at which individuals in each of the two trials apportioned their time between the various categories of activities were similar. When more females were included in the group, individuals remained in refuges out of sight for a slightly larger proportion of the time and devoted more time to grooming activities. Individuals also adopted alert postures slightly more often when more females were present than males. Feeding activities were recorded at a greater frequency when males and females were included in even numbers.

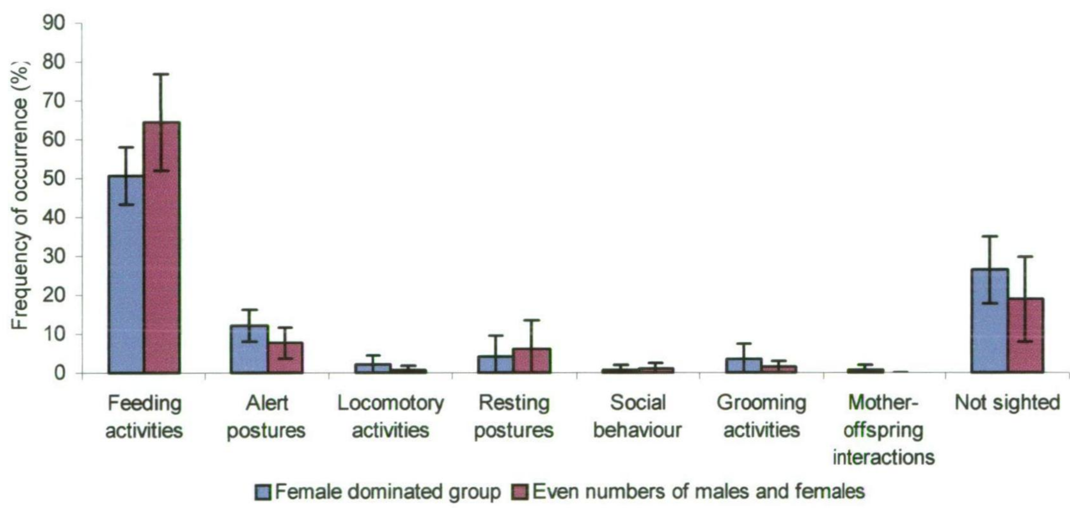


Figure 7.26: The mean percentages (± standard deviations) of overall sightings in which focal individuals were recorded performing any of the acts from categories of behaviour. N=11 for each Trial

7.3.2.3 Frequency of Behavioural Elements and Events

The percentages of time apportioned to specific individual behavioural elements and events were calculated and are presented in Figures 7.27 and 7.28. Wallabies browsed on grasses and herbs and fed at feeding stations more frequently when the number of males and females in the group were even (Trial 2). Both upright and crouched alert postures were seen more frequently when females were present in greater numbers (Trial 1).

During Trial 2, individuals adopted both of the sitting postures, resting back on their haunches or sitting upright more frequently, while lying was slightly more common in Trial 1.

Focal animals looked directly at and approached others at similarly low frequencies in both trials, although the former was slightly more common when males and females were present in equal numbers.

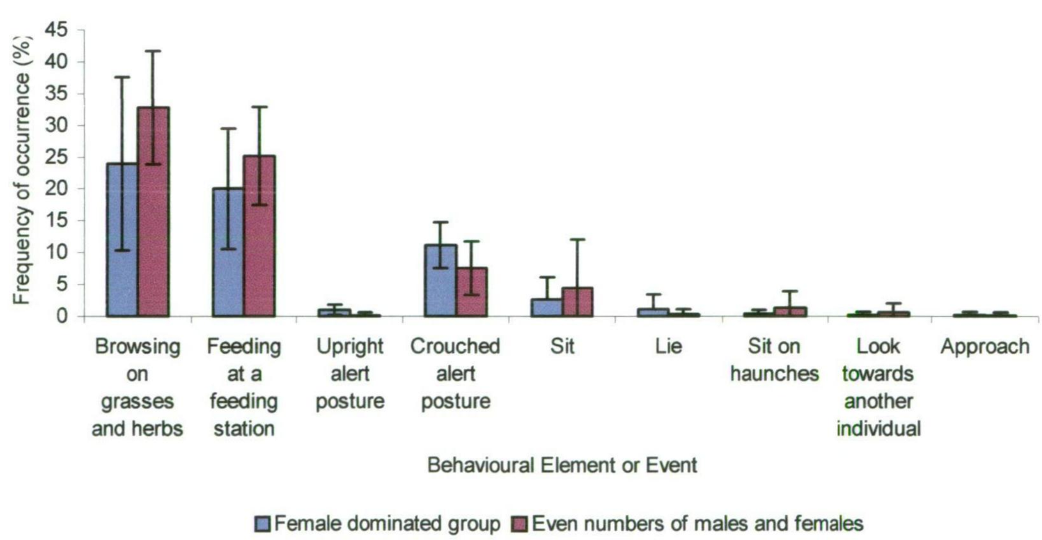


Figure 7.27: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing the key elements of behaviour. N=11 for each Trial.

Wallabies groomed both their backs, hind limbs and abdominal regions in Trial 1, but performed other grooming actions at similar frequencies in both trials.

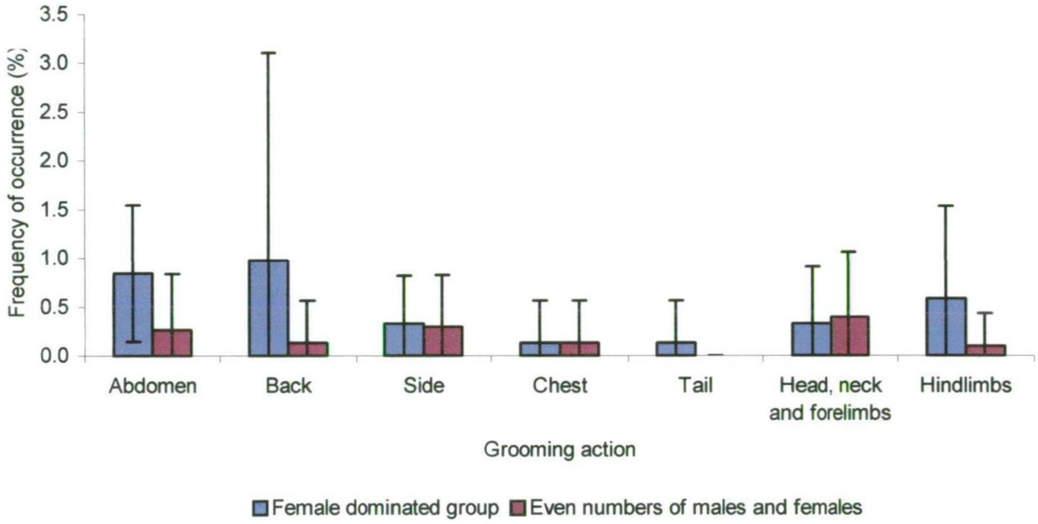


Figure 7.28: The mean percentages (± standard deviations) of overall sightings in which focal animals were recorded performing grooming actions. N=11 for each Trial.

7.3.2.4 Duration of Behavioural Elements and Events

The mean durations of the acts performed by focal individuals in the two trial conditions can be seen in Table 7.11. The durations of periods in which focal animals were recorded as out of sight were similar in the two trials. Both upright and crouched alert postures were sustained for similar periods in both trials.

The duration of browsing and attending feeding stations was greater during Trial 2; the opposite is true of drinking from the water receptacle.

All resting postures were maintained for longer periods when the group contained equal numbers of males and females. The durations of social acts were generally similar with the exceptions of looking at another individual (greater in Trial 2) and wrestling (greater in Trial 2). Although the total length of grooming sessions lasted for similar periods, grooming actions aimed at the abdomen or chest were sustained for longer periods during Trial 2.

Table 7.11: The mean durations in seconds (± standard deviations) of elements of behaviour recorded during all sampling periods during the three trials. Trial 1 = 5 females and 3 males. Trial 2 = 4 males and 4 females. N = 11 for each Trial. Average scores were calculated for each focal animal using every instance that a behavioural element was observed. Not every element of behaviour was recorded with the same frequencies, so the number in brackets (n) is the number of focal animals that performed that particular element of behaviour during the total of all observations.

Behavioural element or event	**Trial 1**		**Trial 2**	
Browsing on grasses and herbs	153± 63	(11)	284± 145	(13)
Feeding at a feeding station	330± 135	(11)	422± 153	(13)
Browsing on trees and shrubs	132± 31	(8)	205± 165	(2)
Drinking from a feeding station	183± 103	(11)	165± 82	(11)
Merycism	3	(1)	3	(2)
Upright alert posture	29± 9	(9)	29± 28	(6)
Crouched alert posture	36± 10	(11)	33± 13	(13)
Start up	6± 5	(3)		
Sit	193± 179	(9)	334± 425	(7)
Lie	343± 317	(3)	600±	(1)
Sit on haunches	175± 105	(7)	261± 154	(3)
Look at another individual	6± 5	(11)	11± 12	(11)
Touch nose to another individual	3	(7)	3± 1	(10)
Sinusoidal tail movements	19± 27	(3)	17± 20	(2)
Kick	3	(1)	3	(2)
Scratch	3	(4)	3± 1	(3)
Wrestle	17± 13	(3)	3	(2)
Approach	3	(7)	3± 1	(10)
Retreat	3	(8)	3± 1	(10)
Chase	3	(1)		
Arc	3	(2)		
Inspect abdominal area	3	(2)	3	(1)
Move away	3	(3)	3	(3)
Follow	3	(5)	3	(2)
Crouch	3	(1)	3	(1)
Copulate	3	(1)		
Groom abdominal region	8± 6	(11)	11± 18	(7)
Groom pouch	7± 6	(2)	15± 21	(2)
Groom back	3± 1	(9)	4± 3	(7)
Groom sides	3± 1	(10)	3	(9)
Groom chest	3	(9)	10± 15	(4)
Groom tail	30± 54	(4)	3	(1)
Groom head, neck and forelimbs	4± 2	(11)	3± 1	(9)
Groom hind limbs	5± 3	(10)	7± 10	(8)
Grooming session	11± 8	(11)	10± 8	(9)
Inspect trap			107	(1)
Escape			3	(1)
Flee			2	(1)

Behavioural element or event	**Trial 1**		**Trial 2**	
Feed young at foot	3	(1)		
Allogroom	278	(1)		
Playfight	409	(1)		
Not sighted	423± 76	(11)	420± 166	(10)

7.4 Discussion

LaFollette (1971) asserted that captive Bennett's wallabies, although engaging in overt agonistic bouts, did not assert dominance over food. This contrasts with previous findings for eastern grey kangaroos (Grant, 1973); dominant members of that species maintained preferential positions at feeding stations and excluded subordinates. In the present study, when the age structure of the group was altered, the use of those areas of the enclosure where feeders were positioned varied in response to these alterations. Females, utilised the feeding stations that had better concealment less frequently when more adults were included in the captive group. However, when fewer adults were present, these individuals appeared to exclude subadults from the better-concealed feeder in sector three. Males utilised the feeder in sector two, which had better cover, at similar, relatively high, levels and sector one, with less cover, at low levels in each trial. Thus, adult males appeared to utilise those feeders with the best cover, displacing adult females to less preferred feeders. When fewer adults were present, adult females were able to utilise more optimal feeders so that subadults were displaced to less preferred feeders or queued in sector 12, a relatively open area with browse available. Juvenile Bennett's wallabies were also displaced from preferred feeders when more adults were present but gained greater access when the numbers of adults were reduced. Thus, in contrast to LaFollette's (1971) findings, Bennett's wallabies in this study appeared to assert dominance over food so that dominant individuals gained preferential positions at feeders, as described for eastern grey kangaroos by Grant (1973).

Utilisation of available space may be related to age or sex specific needs. The patterns of habitat occupation seen in coastal populations of huemul *Hippocamelus bisulcus* in Chile have been related to both the age and sex of deer (Frid, 1994). Members of each age class and sex primarily utilised the same herb as a food source, but adult males and juveniles primarily occupied periglacial grassland while adult females occupied bluffs. Newborn fawns were only recorded on bluffs. These differences were related to anti-predator strategies and the related trade off of food resource quality and energetics for mothers with recent offspring. Female Bennett's wallabies with young at foot are more sedentary than males or other females and may stay closer to vegetative refuges while increasing both browsing time and bite rate (Catt, 1977, Clarke and Loudon, 1985). However, they will alter patterns of habitat use in response to variations in the value of food resources, for example during periods of poor weather that effects the availability of browsing matter (Catt, 1978). In this study, group members devoted the largest portion of the observed time to activities associated with eating and drinking. However, the frequency and duration of feeding activities varied for members of each sex and age class as the group structure was altered. Similarly to Frid's (1994) finding, Bennett's wallabies from each age and sex class in this study appeared to alter the amount of time devoted to feeding and vigilance activities as part of a trade off between the anti-predator behaviour and the availability of preferred food resources. For example, female Bennett's wallabies fed for periods longer in duration when more juveniles were included in the group, at which time the females' lactational demands would have been relatively high. Adult Bennett's wallabies browsed on grasses and herbs for similar periods when they predominated in each group, while subadults browsed on grasses and herbs significantly less frequently and for briefer periods when more adults were present. Males also attended feeding stations more frequently when more adults were present. These findings may again have been a result of dominant individuals suppressing the feeding activities of subordinates. Juveniles browsed for longer periods when more subadults were present than at other times, perhaps because they suffered less interference from dominant individuals at that time. Similarly, they both browsed and attended feeding stations more frequently when they formed the largest part of the group. The greatest numbers of both crouched and upright alert postures were recorded when the numbers of adults present were greatest. Both adults and juveniles adopted more alert postures at this time. Red-necked wallabies with young at foot in the wild tend to remain close to the forest edge when foraging (Johnson, 1989). Banks (2001) previously suggested that young at foot may provide lactating mothers with a vigilant partner. These observations appear to support this idea.

Bennett's wallabies in the wild rest in refuges within vegetative cover (Merchant and Calaby, 1981). In captivity, resting behaviour should be easier to view than for wild conspecifics. Medium sized eastern grey males in captivity have been reported to rest more frequently than males from other age/size classes and to be seen sitting, a behaviour rarely seen among wild counterparts (Höhn *et al.*, 2000). In this study, wallabies from different age classes and sexes adopted the various resting postures at different frequencies in each trial. When more adults were present focal individuals were out of sight more often and individuals lay for significantly briefer periods.

This may have been due to the adoption of the lying posture once in refuges within vegetative cover inside the enclosure.

Endangered bridled nailtailed wallabies, *Onychogalea fraenata,* were translocated to the edge of their former habitat as part of a breeding program (Pople *et al.*, 2001). Groups released at different sites produced different success rates in terms of survivorship, reproductive output and gains in condition. One of the main factors contributing to the lower rates of success at some sites was the poor predator avoidance behaviour of wallabies bred in captivity. Yoerg and Shier (1997) reported that wild caught and captive bred kangaroo rats *Dipodomys heermanni arenae* exposed to a snake exhibited different responses. Wild caught rats were less active and more vigilant than captive bred juvenile rats that were snake-naïve. Captive bred adults did alter their behaviour in line with wild caught rats. Pups presented with the snake in the presence of a sibling or alone did not alter their behaviour, but those in the presence of their mother and a snake faced the snake less, followed their mother more and remained closer to her. Thus, both experience with the predator and maternal influence appeared to play a role in the development of anti-predator behaviour. Captive bred tammar wallabies, *M. eugenii,* were trained to recognise a predator (a fox) and after training altered their behaviour to respond more cautiously to this predator than they previously had (Griffin *et al.,* 2001). Tammars reduced foraging, grooming and sitting and increased vigilance and locomotion in response to the presentation of the fox stimulus. Tammar wallabies also generalised their response to the fox stimulus to a cat stimulus, of which they were previously naïve. In this study, wallabies, and in particular subadults, in the group comprising more subadults than members of other age classes were significantly more visible than those in other trials. Subadults were most visible when they themselves formed the largest portion of the captive group. These animals lay for longer periods where they could be viewed, rather than in cryptic positions, at this time. Subadults also adopted sitting postures more frequently when they were present in the largest numbers. This failure to adopt cryptic resting positions may reflect a level of naivety related to their upbringing within the enclosure environment where predators were excluded and is likely to also have been influenced by the reduced presence of adults.

Wallabies in the university enclosure devoted more time to grooming activities when more adults were present, grooming their abdomens, backs and hind limbs significantly more often. Grooming of the tail lasted for significantly longer periods at that time. As wallabies have their heads lowered when performing this action, this activity places wallabies in a position from which it is difficult to detect predators and so appears to indicate a more relaxed state. However, both males and females, as well as adults groomed their hind limbs for longer periods at this time. These actions suggest that wallabies in this trial exhibited less vigilance towards potential threats of predation but more towards other group members.

Females that have a number of possible mates available and males that have the opportunity to interact with conspecifics from different age classes will have a more enriched and naturalistic environment that will improve their welfare (Gansloßer, 1995). However, aggressive interactions between male Bennett's wallabies that at times are intense and exceedingly violent have previously been reported (LaFollette, 1971). Adequate management strategies must balance these two concerns to maximise the welfare of captive Bennett's wallabies. In this study, the spatial patterns of members of the two captive groups utilised to examine the effect of varying the sex ratio of group members were very similar. Although statistical tests were not applied to these data, it seems unlikely many significant differences would have been found. Slightly more differentiation is seen in the apportioning of time between the categories of behaviour. When the captive group comprised even numbers of males and females, wallabies were recorded engaging in feeding activities more frequently and were hidden from sight less frequently. These individuals also adopted fewer upright alert postures. However, care needs to be taken when considering this. Males were often out of sight for long periods and tended to emerge primarily to attend feeding stations or browse. Females adopted less cryptic resting positions were they were more easily viewed both resting and grooming. Wallabies groomed slightly more frequently when more females were present and this was attributable to a greater amount of time being devoted to grooming the abdominal region, the back and the hind limbs. However, grooming actions were generally sustained for longer periods when the numbers of males and females were equal. The frequencies with which Bennett's wallabies in this study engaged in social interactions were similar in the two trials. Most elements of social behaviour were also sustained for periods of similar duration with two notable exceptions. Wrestling lasted for longer periods when more females were present. By contrast, individuals sustained direct looks at other group members for periods lasting twice as long when four males were present than when three were included in the captive group. Extended periods of back and hind limb grooming may have occurred as part of monitoring of cohorts and this, together with extended bouts of looking behaviour may indicate a more stressful environment for males. In order to record observations of males when they formed half of the captive group, longer periods were required than during the other trial. Those very frequent occasions when males emerged for only a few minutes before returning to cover were excluded from consideration, skewing these results. Thus, males in the trial where the numbers of animals of each sex were even were actually more cryptic and exhibited more vigilance and alert behaviour than counterparts in the other trial. As this experiment was terminated before completion, following the death of one of the subjects, and as the affect of that individual's ill–health on its own and other group member's behaviour is not known, it is difficult to make any assertions, except that other studies should be undertaken to assist in clarifying this critical issue of the effect of sex ratios on the behaviour of captive Bennett's wallabies.

The ratio of members of each age class and sex within captive groups is an issue that needs to be addressed as part of a management plan and addressed as early as possible. By managing the sex ratio within captive groups, macropod managers can reduce levels of aggressive and injurious interactions. One management strategy is to maintain only single-sex groups. This is advantageous in terms of reducing the cost of fertility management (ACT Advisory Committee, 1996). A review of the behaviour of members of different age/sex classes of the Macropodoidea revealed that those elements of agonistic behaviour most likely to result in injuries were performed less than would be expected in bouts between adult and subadult males (Gansloßer, 1995). Subadults engage in more agonistic behaviour than adult males. "Type C" species, where the presence of females is unpredictable and males roam in search of females, are readily adaptable to the formation of all male groups in captivity because they are predisposed to form stable hierarchies. Murböck (1977) noted an ontogeny of agonistic behaviour in male Bennett's wallabies, with male young at foot engaging in these interactions with their mothers in the form of play fights, with the mother remaining passive. After weaning, males gain a position within the hierarchy of adult males from where they may eventually achieve matings and sire offspring. Red kangaroos, *M. rufus,* can be divided in six age/sex classes based on behavioural differences (Croft, 1980). Adult males were the most likely of these groups to engage in non-agonistic social interactions. These may assist in the sexual and/or individual recognition. However, animals in single-sex enclosures have limited opportunity to engage in the full range of behaviours that they otherwise would. Agonistic interactions are part of the ontogeny of social behaviour for macropodoids and restricting these interactions may have detrimental affects on the welfare of these animals. The advantages of maintaining a number of males together must be weighed against the requirements of managing their interactions. Although overt agonistic interactions did not increase in frequency in this study when the age and sex ratio of members of the captive group was manipulated, subordinate animals appeared to be displaced into less-preferred sectors. Increasing the numbers of males present generally reduced the visibility of these animals and increased alert and vigilance behaviour. Thus, this is an important issue to address and highlights the need for the adequate provision of feeders and refuges.

In this study, members of each age class and sex varied their behaviour and patterns of enclosure utilisation in response to manipulations of the group structure. Again, these findings suggest that consideration be given to the provision of adequate food and shelter resources within the enclosure for all group members. Finally, by managing these ratios, exhibited collections of Bennett's wallabies can be managed as a popular and attractive exhibit.

Chapter 8 General Discussion

A collection of Bennett's wallabies was established within an enclosure at the University of Tasmania so that research could examine the effects of varying specific components of the captivity environment, to determine ways to optimise conditions of captivity to improve the welfare of the captive animals. Components of the captivity environment were determined and these were prioritised utilising the knowledge of current managers of captive macropodoids, reported in Chapter 3. A behavioural inventory was compiled so that it could be employed as a tool of measurement in comparative studies of behaviour under the various experimental conditions (Chapter 4). Finally, comparative studies were undertaken that permitted an assessment of the components of the captive environment as they impacted the Bennett's wallabies subject to them (Chapter 5, 6 and 7).

When considering information collected from current managers of captive macropods, together with the results reported in this case study, a number of recommendations can be made regarding the successful management of these captive Bennett's wallabies as a successful public exhibit. Future studies should aim to confirm these findings in order to support these recommendations for more general application to zoos and wildlife parks holding collections of captive Bennett's wallabies.

1) Maintain stocking rates at approximately six individuals per 1000 m^2. Stocking rates either higher or lower than this appeared to result in a more stressful environment. They also affected the use of the available space and the type and amount of activities engaged in a way that would have degraded the value of this enclosure as an exhibit.
2) Provide a number of alternative feeding stations that are spaced apart from one another. These can be positioned in that part of the exhibit that is nearer onlookers, providing sufficient feeders are present. Dominant individuals may preferentially utilise feeders that are better concealed and further from visitor disturbance, but the resultant displacement of subordinate individuals should result in the positioning of young and active animals in areas where they are highly visible, enhancing the attractiveness of the exhibit.

3) Limit the number of adult males included in captive groups. No more than one adult male should be included in groups of six or fewer animals. Two adult males in larger groups may be sustainable if sufficient refuges are provided and appropriate checks are put in place.

4) Include members from each age class in the group. Zoo visitors prefer exhibits with young, active animals (Croke, 1997). The presence of adults will slightly increase the amount of time in which wallabies will adopt cryptic positions. However, it also stimulates activity at other times, including the alternation of browsing and feeding with the adoption of alert postures, increased locomotory activity, more grooming and a greater number of social interactions. It will also increase the probability that members of younger age classes will queue in visible positions while waiting a turn at feeding stations.

5) Include wild-caught adults if possible, if it is intended to release some wallabies from the collection into the wild. Subadult and juvenile individuals in this study adopted fewer alert postures and were slower to respond to potential threats if experienced adults were not present. However, when adult Bennett's wallabies who had been wild for at least part of their life were included in the group, subadults responded to the vigilant and alarmed behaviour of their older counterparts by mirroring their behaviour.

Using the results reported here and the recommendations arising from them, the implications of these for recommending best practice in captive management will now be considered.

Bennett's wallabies have been popularly exhibited for almost two centuries. Members of this subspecies are maintained in great numbers in wildlife parks and zoos within Australia as well as Britain and Europe. However, the management of these animals in captivity is beset with challenges. The Bennett's wallaby is a solitary macropod with large, individual home ranges. Although sizeable feeding aggregations can form, very little social behaviour has been reported for this subspecies. Play fighting between mothers and their offspring has been described (Murböck, 1977). Males opportunistically inspect females to ascertain their reproductive status, but these encounters are generally brief (Fleming *et al.*, 1983). However, the breeding season is characterised by overt and often intense agonistic interactions between males escorting a female in oestrus (LaFollette, 1971). Copulation can also lead to intense bouts between males, which may violently kick and scratch the male engaged in copulation (Fleming *et al.*, 1983). This type of interaction can be intensified by captive conditions, where a subordinate individual may not have the opportunity to terminate a bout or retreat from sight (Murböck, 1977).

Hanover Zoo reported designing an enclosure for the public display of Bennett's wallabies, together with red kangaroos and western grey kangaroos, which was fenceless but surrounded by a moat (Dittrich, 1971). In order to satisfy visitor expectations, a 40 cm long strip of drainage gravel was laid along the moat wall so that animals could not position themselves here, out of sight. In the first few days of residence in the new enclosure, individuals of all three species repeatedly escaped by jumping out onto the visitors' footpath. Most animals ceased this practice after a short period. One male Bennett's wallaby continued to escape over the first six weeks. This animal frequently engaged in agonistic bouts with another male, but ceased escaping once a hierarchical order was established within the new environment.

Macropodoid species, including the Bennett's wallaby, are known to be susceptible to a number of diseases, especially "lumpy jaw" (Calaby and Poole, 1971; Bergin, 1978), a disease that is difficult to treat, often fatal and poses a serious threat to the success of captive breeding programs. Crowding, trauma and stress can lead to an increased rate of necrobacillosis in captive macropodoids and diet can be used to control it (Bergin, 1978; Spielman, 2000). Similarly, the occurrence of salmonellosis has been linked to overcrowding, stress and poor hygiene (Spielman, 2000).

Capture myopathy can severely affect many macropods. Death may follow rapidly after capture, or affected individuals may die after a day or two in captivity (Williams, in Hand, 1995). This illness is thought to occur when a psychological stressor is applied over a period of time. Nervous or excitable species are more likely to be affected (Shepherd, in Hand, 1995). Bennett's wallabies are highly susceptible to capture myopathy and death from cardiac arrest can occur within minutes of release into the captive environment (Statham, pers. comm.). Bennett's wallabies have also been noted to be especially susceptible to secondary infections in traumatic injuries from capture and handling, leading at times to severe pneumonia with multiple abscessation (Presidente, 1978).

It can clearly be seen that developing management strategies for captive Bennett's wallabies requires these serious matters to be addressed. However, it must be borne in mind that any problems that result from the strategies employed may not be immediately apparent. Bennett's wallabies in this study rarely engaged in overt interactions of any kind. By contrast, covert interactions commonly occurred and played an important role in determining the time budgets and spatial patterns of wallabies in an enclosure environment. Many elements of behaviour observed would not ordinarily fall under the umbrella of social behaviour, but appeared nonetheless to result from interactions with other members of the captive group. For example, the number, type and duration of alert postures, often related to anti-predator behaviour, appeared to have a role in interactions between wallabies. Similarly, some evidence has been provided to suggest that wallabies directing grooming actions towards their backs may have been covertly watching others. Periods of browsing by subadult wallabies were often extended in response to the occupation of feeders by more dominant individuals. These observations thus reinforce the concept that a thorough understanding of the behaviour of members of this subspecies is vital to good management practices.

The seasonal breeding patterns of this subspecies may also impact on their behaviour. Agonistic interactions increase in both number and intensity during the breeding season (Murböck, 1979). Individual time budgets may alter to permit increases in reproductive or maternal interactions at a cost to other activities. Due to time and financial constraints, possible effects of season on the behaviour of Bennett's wallabies were not investigated. Each trial for a particular experiment was timed to occur within the same period (breeding or non-breeding season) as other trials for that experiment. Additional studies examining whether seasonal changes in social behaviour occur and their importance to management strategies would be highly recommended.

Seasons also affect the amount and type of browse matter available. In addition, the amount of vegetative matter available is influenced by browsing pressure. In this study, available browse varied in response to the number of wallabies present and the amount of time wallabies spent in the enclosure. In order to control for this, a variety of types of additional browse were collected, including acacia, eucalypt and casuarina branches, apples, carrots and lettuce. These were distributed evenly throughout the enclosure.

Approximately 10, 000 zoos exist worldwide, of which around 150 are privately-funded institutions in Australia. Wildlife parks and zoos encompass an enormous variety of captive conditions (Weigel, 1992), as can clearly be seen from the responses to questionnaires detailed in Chapter 3. The number of species maintained, the conditions in which they are held, the reasons for keeping them and methods and principles employed varied from institution to institution. Bennett's wallabies are commonly maintained in multi-species enclosure, although this is not always the case. They breed successfully in captivity, at times giving rise to concerns over stocking rates and the management of excess stock. They may be maintained in groups that vary with regard to the genders and ages of members. Visitors may enter some enclosures and interact with exhibited animals, but are excluded from others.

Despite the degree of variation in the types of institutions that responded to the questionnaire, many zoos and parks identified common challenges facing them. These included employing appropriate strategies to manage diets, housing, stocking rates and group composition. When considering the range of conditions of captivity for macropodoids, it is immediately apparent that a single set of rules cannot be applied. However, principles of good management can be devised that will have general and useful application; this has been the key concern of this study.

Many studies of animal behaviour have compared the behaviour of wild individuals with their captive counterparts with the aim of implementing conditions of captivity that result in what is considered more natural behaviour. While this idea has some merit, it cannot be assumed that reproducing the condition of wild conspecifics will necessarily provide the most benefit to animal welfare. Studies of animals in the wild can provide some information that is vital to the proper care of captive individuals. However, studies of individuals in a variety of captive conditions can be critical to the successful formulation of management strategies (Veasey *et al.*, 1996).

The first step in formulating management strategies for captive macropodoids is to develop a comprehensive behavioural inventory (Crockett, 1996). Previous studies had provided some understanding of the behaviour of both captive and wild Bennett's wallabies (LaFollette, 1971; Murböck, 1975, 1977, 1979; Catt, 1978; Tighe *et al.*, 1981; Merchant and Calaby, 1981; Fleming *et al.,* 1983; Clarke and Loudon, 1985). This study builds upon that groundwork by utilising observations of both captive and wild wallabies to provide a comprehensive inventory of behaviour. Behavioural elements that are identified in this way, together with an understanding of the type and intensity of interactions that occur, can provide a yardstick by which to judge the impact of specific conditions of captivity and to determine the success of strategies employed (Coulson, 1989).

In this study, varying specific conditions of captivity resulted in variations in the way that Bennett's wallabies utilised the space available to them, the frequency with which they engaged in a variety of activities and periods for which they sustained these activities. These results can be related to several important issues for managers of captive animals, including the visibility of animals, the degree to which they were active, the impact of captive conditions on their welfare and ways in which enclosures could be managed to provide economic benefits.

The methods used in of this study can be generalised in principles that, if applied, will yield a system of best practice for managing captive macropodoids. These are detailed here.

1) Specify the purpose of maintaining a collection.

Determining the purpose for maintaining a collection of macropodoids is critical before any attempt to devise management strategies can commence. The purpose of keeping captive macropodoids may fall into one of the following categories.

i. **Conservation.** Conservation is the primary aim of most modern zoos (de Courcy, 1999). This will typically refer to a captive breeding colony that may be in a zoo enclosure or a sanctuary. A number of endangered or rare macropodoids are bred in captivity in Australia.

ii. **Education**. Public education plays an important role in garnering the support that is required for the success of conservation programmes (Butler, 1992; Giles and Kelly, 1992; Weigel, 1992; Bradley *et al.*, 1999). The Taxon Advisory Groups operating under the auspices of the Australasian Species Management Program (ASMP) manage the relevant species' and subspecies' needs according to a set of priorities that give weight to a number of factors including the ability of a species in captivity to garner public support for the protection of others, to serve an educational role (Jakob-Hoff, 1992), or to serve as a surrogate in the development of captive breeding or husbandry skills that may benefit others (Jakob-Hoff, 1992; Bradley *et al.*, 1999).

iii. **Research.** A collection may be maintained in order to conduct research and share information about the general biology, husbandry and veterinary care of captive species. A by-product of this activity is the creation of a resource of skilled workers with valuable knowledge in these fields (Mumaw, 1992; Denney, 1996). The specific purposes for maintaining animals involved in research programs should be relatively easy to formulate: they are fundamental to the research itself. One of these purposes may simply be to breed individuals so that they are available to researchers. The needs of the researcher will determine the specific purpose. For example, in order to investigate prenatal growth, female macropodoids must be maintained in conditions conducive to conceiving and maintaining pregnancies.

iv. **Recreation.** Zoo and park exhibits may be maintained in order to provide a source of recreation for visitors.

It should be acknowledged that a collection may be formed for two or more purposes. In this instance it is highly recommended that consideration be given to prioritising these aims. This will assist in prioritising the implementation of strategies that address these purposes. For example, a species may be kept in captivity as part of a captive breeding and re-release program. The individuals may also be exhibited to the public in order educate zoo visitors about related conservation issues. Priority should be given to either of these aims so that conflicts in practices can be resolved. Breeding programs may require enclosures that provide good refuge, low densities of stock, or appropriate social structures. The results may be an exhibit where the primary aim is satisfied, but animals are difficult to see and rarely active. Alternatively, and particularly if participating in a larger breeding program, creating concern about the need for conservation of the species as a whole may be of greater importance. A lower number of successful rearings may than be traded off for a more attractive exhibit.

2) Set standards that will determine whether you are meeting the purpose of maintaining a collection.

The success of collections should be measurable. Standards can be set with reference to the purposes you have now specified and prioritised. For example, the success of a collection of rock wallabies established with a principle aim of breeding offspring that can be released into the wild can be measured in the number of successful rearings each year.

A secondary priority may be to educate park visitors about the conservation status of these individuals. A standard can be set to measure how successfully this aim has been accomplished by, for example, counting the number of enquiries received from members of the public or by setting fundraising goals. Alternatively, the number of people who stop and read educational material provided at the site of an exhibit, and the time spent in this activity, can be measured.

Collections that are constructed for recreational purposes should also be able to meet standards of success. For example, a target can be set for the total number of people who stop at the exhibit for a period of at least 30 seconds, or the number of people who report having interacted with exhibited animals.

3) Consider issues of animal welfare as an overriding concern

Zoos and wildlife parks within every state and territory in Australia are licensed by number of government agencies to keep macropodoids in captivity. Licence agreements may cover the numbers of animals or the types of species maintained and generally contain conditions such as the maintenance of studbooks and regular returns. Annual inspections of the conditions in which animals are maintained are generally required. Even universities that maintain wallabies and kangaroos in collections for research purposes are subject to approval processes by ethics committees, which consider both the value of the research and the welfare needs of subjects before approving research programs.

Regardless of the purpose for which you determine to keep captive animals, once you are the manager of a collection, the welfare of these animals is your responsibility. At all times this must be held as an overriding priority when making management decisions. Their basic needs with regard to housing, nutrition, veterinary care and husbandry must be met. These needs must be assessed in the context of a detailed knowledge of the species biology and behaviour.

4) Determine what are the conditions of captivity to which your animals will be subject.

These will include the size and shape of the enclosure, the number of species included in it, stocking rates, the age and sex of individuals, the provision of food and shelter from both the weather and other animals, whether members of the public can interact with animals on exhibit, whether animals are aware of others in neighbouring exhibits, climate and numerous other factors. Once the conditions of captivity have been identified, their effect on the captive individuals can be considered. An understanding of animal welfare issues is crucial at this stage, as is an understanding of the biology and behaviour of your species.

5) Utilise studies to assess and modify the captive environment in order to both meet welfare considerations and your purposes for having the collection.

Comparative behavioural studies should be employed by macropod managers as a means of determining the impact of each condition of captivity and making decisions about how to manage these. Quantifying aspects of the behaviour of captive individuals assists in the implementation of standards of best practice. In this study, comparative studies were utilised to consider how the number and position of feeders available, stocking rates and group composition affected captive Bennett's wallabies at the university enclosure. From these examinations, appropriate stocking rates, provision of feeding stations and group structures can be recommended.

By considering how variations in the conditions of captivity will impact captive animals, priorities can again be assigned to addressing each. You should have reference to your purpose in maintaining a collection at this point. For example, if you wish to breed members of an endangered species, the delivery of adequate nutrition is likely to be extremely important.

Other types of studies can provide extremely useful information for managers of captive macropodoids. In particular, studies of stress physiology can be undertaken in conjunction with behavioural studies and provide further useful information. Genetic studies can also be employed to determine the effect of some captive conditions. These are of obvious use in conservation programs but can also assist in avoiding problems associated with a limited gene pools. These types of studies are outside the scope of this thesis, except to say that it is recommended that these be conducted in conjunction with, rather than instead of, comparative studies of behaviour.

By implementing management practices that utilise the principles outlined here, standards of best practice can be set and met. Your collection will aim to serve a specific purpose and your success in this endeavour can be measured. Factors that influence the degree of success achieved can be identified, as can their relative importance. These can then be "fine tuned" using comparative behavioural studies to increase the successful outcomes of your collection.

This thesis has provided a model for the use of scientific studies of the behaviour of captive animals in recommending guidelines for captive management.

References

A. C. T. Kangaroo Advisory Committee (1996). Kangaroos in Captivity, vol. 2002: Department of Urban Services.

Altman, J. (1996). Observational study of behaviour: sampling methods. In "Foundations of Animal Behaviour" (ed. Houck, L. D. & Drickamer, L. C.), pp. 177-217. Chicago: The University of Chicago Press.

Baker, K. C. (2000). Advanced age influences chimpanzee behaviour in small social groups. *Zoo Biology*, 19, 111-119.

Banks, P. B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour*, 61, 1013-1021.

Batchelor, T. A. (1980). *The social organisition of the brush-tailed rock-wallaby (Petrogale penicilatta penicillata) on Motutaou island.* M.Sc. Thesis Thesis, University of Auckland.

Baudinette, R. V. (1994). Locomotion in macropodoid marsupials: gaits, energetics and heat balance. *Australian Journal of Zoology*, 42, 103-123.

Bergin, T. J. (1978). Husbandry of monotremes and marsupials. In "Course for Veterinarians (The J D Stewart Course for 1978)", vol. 36, pp. 46-47. Taronga Zoo: Post Graduate Committee University of Sydney.

Blumstein, D. T., Daniel, J. C. & Evans, C. S. (2001). Yellow-footed rock-wallaby group size effects reflect a trafe-off. *Ethology*, 107, 655-664.

Blumstein, D. T., Daniel, J. C. & McClean, I. G. (2001). Group size effects in quokkas. *Australian Journal of Zoology*, 49, 641-649.

Blumstein, D. T., Evans, C. S. & Daniel, J. C. (1999). An experimental study of behaviour group size effects in tammar wallabies, *Macropus eugenii*. *Animal Behaviour*, 58, 351-360.

Bradley, M. P., Lambert, C., Poewr, V., Mills, H., Gaikhorst, G. & Lawrence, C. (1999). Reproduction and captive breeding as a tool for mammal conservation: the role of modern zoos. *Australian Mammalogy*, 21, 47-54.

Brinklow, B. R. & Loudon, A. S. I. (1993). Evidence for a circannual rhythm of reproduction and prolactin secretion on a seasonally breeding macropod marsupial, the Bennett's wallaby (*Macropus rufogriseus rufogriseus*). *Journal of Reproduction and Fertility*, 98, 625-630.

Bulinski, J., Goldney, D. & Bauer, J. (1997). The habitat utilisation and social behaviour of captive rock-wallabies:implications for management. *Australian Mammalogy*, 19, 191-198.

Butler, D. J. (1992). The role of zoos in the captive breeding of New Zealand's threatened fauna. *International Zoo Yearbook*, 31, 4-9.

Calaby, J. (1989). Foreward. In "Kangaroos, Wallabies & Rat-Kangaroos", vol. 1 (ed. Griggs, G., Jarman, P and Hume, I), pp. xv-xvi. Sydney: Surrey Beatty & Sons Pty Limited.

Calaby, J. H. (1983). Red-necked Wallaby. In "The Australian Museum Complete Book of Australian Mammals" (ed. Calaby, J. H.). Sydney: Angus & Robertson Publishers.

Calaby, J. H. (1998). Red-necked wallaby *Macropus rufogriseus* (Desmarest, 1817). In "The Mammals of Australia" (ed. Strahan, R.), pp. 350-352. Australia: New Holland Publishers.

Calaby, J. H. & Poole, W. E. (1971). Keeping kangaroos in captivity. *International Zoo Yearbook*, 11, 5-12.

Carlstead, K. (1996). Effects of captivity on the behaviour of wild mammals. In "Wild Mammals in Captivity Principles and Techniques" (ed. Dleeman, D.G.) pp. 317-329. Chicago: The University of Chicago Press.

Cassinello, J. & Pieters, I. (2000). Multi-male captive groups of endangered dama gazelle: social rank, aggression and enclosure effects. *Zoo Biology*, 19, 121-129.

Catt, D. C. (1978). The breeding biology of Bennett's wallaby (*Macropus rufogriseus fruiticus*) in South Canterbury, New Zealand. *New Zealand Journal of Zoology*, 4, 401-411.

Catt, D. C. (1979). Age determination in Bennett's wallaby, *Macropus rufogriseus fruticus* (Marsupialia), in South Canterbury, New Zealand. *Australian Wildlife Research*, 6, 13-18.

Catt, D. C. (1981). Growth and condition of Bennett's wallaby (*Macropus rufogriseus fruticus*) in South Canterbury, New Zealand. *New Zealand Journal of Zoology*, 8, 295-300.

Clancy, T. F. (1982). *Aspects of the Behaviour of the Red-bellied Pademelon Thylogale* *billardierii (Desmarest 1822) in Captivity*. Honours Thesis, University of Tasmania.

Clarke, J. & Loudon, A. S. I. (1985). The effect of differences in herbage height on the grazing behaviour of lactating Bennett's wallabies (*Macropus rufogriseus rufogriseus*). *journal of zoology*, 207, 537-544.

Colagross, A. M. L. & Cockburn, A. (1993). Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus*. *Australian Journal of Zoology*, 41, 325-334.

Conradt, L. (1998). Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology*, 67, 217-226.

Coulson, G. (1989) Repertoires of social behaviour in the Macropodoidea. In "Kangaroos, Wallabies and Rat-kangaroos" (ed. Griig, G., Jarman, P and Hume, I), pp. 457-473. Sydney: Surrey Beatty & Sons Pty Limited.

Coulson, G. (1999). Monospecific and heterospecific grouping and feeding behaviour in grey kangaroos and red-necked wallabies. *Journal of Mammalogy*, 80, 270-282.

Coulson, G. M. (1980). A preliminary appraisal of electric fencing for wallaby control in Tasmania: Centre for Environmental Studies, University of Tasmania.

Crebbin, A. (1982). *Social Organisation and Behaviour of the Swamp Wallaby, Wallabia biclor (Desmarest) (Marsupialia: Macropodidae) in Captivity*. Honours Thesis, University of New South Wales.

Crockett, C. M. (1996). Data collection in the zoo setting, emphasizing behaviour. In "Wild Mammals in Captivity Principles and Techniques" (ed. Dleeman, D. G.), pp. 545-562. Chicago: The University of Chicago Press.

Croft, D. B. (1980). Behaviour of red kangaroos, *Macropus rufus* (Desmarest, 1822) in northwestern New South Wales, Australia. *Australian Mammalogy*, 4, 5-58.

Croft, D. B. (1989). Social organisation of the Macropodoidea. In "Kangraoos, Wallabies and Rat-Kangaroos", vol. 2 (ed. Griggs, G. J., P and Hume, I D), pp. 505-525. Sydney: Surrey Beatty and Sons Pty Limited.

Croke, V. (1997). *The Modern Ark*, pp. 11-254. New York: Scribner Publishers.

Cronin, I. (1991). *Key Guide to Australian Mammals* (1st edition), pp. 74-103. New South Wales: Reed Books Pty Limited.

Curlewis, J. D. (1989). The breeding season of Bennett's wallaby (*Macropus rufogriseus rufogriseus*) in Tasmania. *Journal of Zoology, London*, 218, 337-339.

Curlewis, J. D. (1991). Seasonal changes in the reproductive organs and plasma and pituitary hormone content of the male Bennett's wallaby (*Macropus rufogriseus rufogriseus*). *Journal of Zoology, London*, 223, 223-231.

Curlewis, J. D. & Loudon, A. S. I. (1989). The role of refractoriness to long daylength in the annual reproductive cycle of the female Bennett's wallaby (*Macropus rufogriseus rufogriseus*). *Journal of Experimental Zoology*, 252, 200-206.

Davies, S. (1996). Stressed out. *New Scientist*, 2050, 38-41.

Dawson, T. J. (1989). Diets of Marsupials: General patterns and environmental influences. In "Kangaroos, Wallabies & Rat-Kangaroos", vol. 1 (ed. Griig, G., Jarman, P and Hume, I), pp. 129-142. Sydney: Surrey Beatty & Sons, Pty Limited.

de Courcy, C. (1999). The origin and growth of zoos. *Sanctuary*, 1, 16-19.

Denney, I. (1996). Australian and New Zealand zoos - captive breeding, husbandry and species management. *ANZCCART News*, 9, 2-3.

Dittrich, L. (1971). New fenceless enclosures for kangaroos. *International Zoo Yearbook*, 11, 62-63.

Eisenberg, J. F. & Kleiman, D. G. (1977). The usefulness of behaviour studies in developing captive breeding programmes for mammals. *International Zoo Yearbook*, 17, 81-89.

Finnie, E. P. (1982). Husbandry of large macropods at Taronga Zoo, Sydney. In "The management of captive mammals in captivity" (ed. Evans, D. D.), pp. 100-101. Melbourne: The Zoological Board of Victoria.

Fisher, D. O. (2000). Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. *Journal of Applied Ecology*, 37, 660-671.

Fisher, D. O. & Owens, I. P. F. (2000). Female home range size and the evolution of social organisation in macropod marsupials. *Journal of Animal Ecology*, 69, 1083-1098.

Flannery, T. F. (1989). Phylogeny of the Macropodoidea; a study in convergence. In "Kangaroos, Wallabies and Rat-kangaroos", vol. 1 (ed. Griig, G., Jarman, P and Hume, I), pp. 1-46. Sydney: Surrey Beatty and Sons Pty Limited.

Fleming, D., Cinderey, R. N. & Hearn, J. P. (1983). The reproductive biology of Bennett's wallaby (*Macropus rufogriseus rufogriseus*) ranging free and Whipsnade Park. *Journal of Zoological Proceedings, London*, 201, 283-291.

Fraser, D., Weary, D. M., Pajor, E. A. & Milligan, B. N. (1997). A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare*, 6, 187-205.

Frid, A. (1994). Observations on habitat use and social organization of a huemal *Hippocamelus bisulcus* coastal population in Chile. *Biological Conservation*, 67, 13-19.

Ganslosser, U. (1989). Agonistic behaviour in Macropodoids-a review. In "Kangaroos, Wallabies and Rat-Kangaroos", vol. 2 (ed. Griig, G., Jarman, P and Hume, I), pp. 475-503. Sydney: Surrey Beatty & Sons Pty Limited.

Ganslosser, U. (1992). Behavioural data support the currently proposed phylogeny of the Macropodoidea (Marsupialia). *Australian Mammalogy*, 15, 89-104.

Ganslosser, U. (1995). The importance of age/sex class relationships for captive-breeding - a review of Macropodoidea (kangaroos, wallabies and rat-kangaroos) as a case study. *Animal Welfare*, 4, 239-249.

George, G. G. (1990). Monotreme and marsupial breeding programs in Australian zoos. *Australian Journal of Zoology*, 37, 181-205.

Giles, J. R. & Kelly, J. D. (1992). Conservation and research programme: proposals by the Zoological Parks Board of New South Wales. *International Zoo Yearbook*, 31, 1-4.

Glatson, A. R. (1997). Sex ratio research in zoos and its implications for captive management. *Applied Animal Behaviour Science*, 51, 209-216.

Glickman, S. E. & Sroges, R. W. (1965). Curiosity in zoo animals. *Behaviour*, 26, 151-188.

Grant, T. R. (1973). Dominance and association among members of a captive and a free-ranging group of grey kangaroos (*Macropus giganteus*). *Animal Behaviour*, 21, 449-456.

Hand, S. J. (1995). *Care and Handling of Australian Native Animals: Emergency Care and Captive Management*, pp. 210 (2 edn). Sydney: Surrey Beatty & Sons Pty Limited.

Heathcote, C. F. (1989). Social behaviour of the Black-striped wallaby *Macropus dorsalis*, in captivity. In "Kangaroos, Wallabies and Rat-Kangaroos", vol. 2 (ed. Grigg, G., Jarman, P and Hume, I D), pp. 625-628. Sydney: Surrey Beattie and Sons Pty Limited.

Higginbottom, K. & Johnson, C. N. (2000). Partial seasonality of breeding in red-necked wallabies (*Macropus rufogriseus banksianus*). *Journal of Zoology, London*, 251, 71-77.

Hohn, M., Kronschnabi, M. & Ganslosser, U. (2000). Similarities and differences in activities and agonistic behaviour of male eastern grey kangaroos (*Macropus giganteus*) in captivity and the wild. *Zoo Biology*, 19, 529-539.

Hopkins, C. (1992). Zoo education: into the 1990's. *International Zoo Yearbook*, 31, 99-103.

Hosey, G. R. (1997). Behavioural research in zoos: academic perspectives. *Applied Animal Behaviour Science*, 51, 199-207.

Hurst, J. L., Barnard, C. J., Tolladay, U., Nevison, C. M. & West, C. D. (1999). Housing and welfare in laboratory rats: effects of cage stocking density and behavioural predictors of welfare. *Animal Behaviour*, 58, 563-586.

Hutchins, M., Smith, G. M., Mead, D. C., Elbin, S. & Steenberg, J. (1991). Social behaviour of matschie's tree kangaroo (*Dendrolagus matschiei*) and its implications for captive management. *Zoo Biology*, 10, 147-164.

Jakob-Hoff, R. M. (1992). Recent developments in the Australasian Species Management Program. *International Zoo Yearbook*, 31, 12-19.

Jarman, P. J. (1991). Social behaviour and organistation in the Macropodoidea. *Advances in the Study of Behaviour*, 20, 1-50.

Johnson, C. N. (1989). Grouping and the structure of association in the Red-necked wallaby. *Journal of Mammalogy*, 70, 18-26.

Johnson, C. N. (1989). social interactions and reproductive tactics in Red-necked wallabies (*Macropus rufogriseus banksianus*). *Journal of Zoology*, 217, 267-280.

Johnson, K. A. (1971). Methods for the census of wallaby and possum in Tasmania: National Parks and Wildlife Service.

Johnston, P. G. & Sharman, G. B. (1979). Electrophoretic, chromosomal and morphometric studies on the red-necked wallaby, *Macropus rufogriseus* (Desmarest). *Australian Journal of Zoology*, 27, 433-441.

LaFollette, R. M. (1971). Agonistic behaviour and dominance in confined wallabies, *Wallabia rufogriseus frutica*. *Animal Behaviour*, 19, 93-101.

Lentle, R. G., Potter, M. A., Springett, B. P. & Stafford, K. J. (1997). A trapping and immobilisation technique for small macropods. *Wildlife Research*, 24, 373-377.

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect.

Animal Behaviour, 49, 11-20.

Lowry, P. S., Eldridge, M. D. B. & Johnston, P. G. (1995). Genetic analysis of a female Macropodid hybrid (*Macropus agilis* x *M. rufogriseus*) and her backcross offspring. *Australian Mammalogy*, 18, 79-82.

Merchant, J. C. & Calaby, J. H. (1981). Reproductive biology of the Red-necked wallaby (*Macropus rufogriseus banksianus*) and Bennett's wallaby (*M. r. rufogriseus*) in captivity. *Journal of Zoology, London*, 194, 203-217.

Morris, D. (1964). The response of animals to a restricted environment. *Symposia of the Zoological Society of London*, 13, 99-118.

Mumaw, L. M. (1992). ARAZPA: developing the Australasian zoo industry as a conservation resource. *International Zoo Yearbook*, 31, 9-12.

Murböck, T. (1975). Zum Kampfverhalten des Bennettwallabis, *Protemnodon rufogrisea frutica* (Ogilby, 1838). *Saugetierk. Mitt.*, 23, 79-80.

Murböck, T. (1977). Komment- und Beschadigungskampf beim Bennettwallaby, *Macropus rufogriseus fruticus. Verhandlungen der Deutschen Zoologischen Gesellschaft*, 70, 337.

Murböck, V. A. (1979). Welchen Einfluss haben Gehegegrosse und Tierdichte auf das Verhalten des Bennettwallabis, *Macropus rufogriseus fruticus* Ogilby, 1938? *Saugetierk Mitt*, 27, 216-240.

Murray, A. J., Waran, N. K. & Young, R. J. (1998). Environmental enrichment for Australian mammals. *Animal Welfare*, 7, 415-425.

Murray, A. J., Waran, N. K. & Young, R. J. (1998). Environmentally enriched enclosures. 25, 101-103.

Peacock, W. J., Dennis, E. S., Elizur, A. & Calaby, J. H. (1981). Repeated DNA sequences and kangaroo phylogeny. *Australian Journal of Biological Science*, 34, 325-340.

Poole, W. E. (1982). Management of captive Macropodidae. In "The Management of Australian Mammals in Captivity" (ed. Evans, D. D.), pp. 91-97. Melbourne: The Zoological Board of Victoria.

Pople, A. R., Lowry, J., Lundie-Jenkins, G., Clancy, T. C., McCallum, H. I., Sigg, D., Hoolihan, D. & Hamilton, S. (2001). Demography of bridled nailtail wallabies translocated to the edge of their former range from captive and wild stock. *Biological Conservation*, 102, 285-299.

Presidente, P. J. A. (1978). Diseases seen in free-ranging marsupials and those held in captivity. In "Course for Veterinarians (The J D Stewart Course for 1978)", vol. 36, pp. 457-471. Taronga Zoo: Post Graduate Committee University of Sydney.

Ride, W. D. L. (1970). *A Guide to the Native Mammals of Australia*, pp. 39-47. Melbourne: Oxford University Press.

Robinson, M. H. (1998). Enriching the lives of zoo animals and their welfare; where research can be fundamental. *Animal Welfare*, 7, 151-175.

Russell, E. M. (1989). Maternal behaviour in the Macropodoidea. In "Kangaroos, wallabies and rat-kangaroos", vol. 2 (ed. Griggs, G., Jarman, P and Hume, I D), pp. 549-569. Sydney: Surrey Beattie and Sons Pty Limited.

Sharman, G. B. (1989). A chromosome phylogeny of kangaroos. In "Kangaroos, wallabies and rat-kangaroos", vol. 1 (ed. Grigg, G., Jarman, P and Hume, I D), pp. v-vii. Sydney: Surrey Beatty and Sons.

Short, J. (1987). Factors affecting food intake of rangeland herbivores. In "Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia" (ed. Caughley, G. S., Neil and Short, Jeff), pp. 84-99. Cambridge, Melbourne: Cambridge University Press.

Spielman, D. (2000). Veterinary Care of Australian Native Mammals. In "Urban Wildlife". Sydney: Post Graduate Committee in Veterinary Science University of Sydney.

Statham, M. (1994). Electric fencing for the control of wallaby movement. *Wildlife Research*, 21, 697-707.

Stirrat, S. C. & Fuller, M. (1998). The repertoire of social behaviour of Agile wallabies, *Macropus agilis*. *Australian Mammalogy*, 20, 71-78.

Tasmanian National Parks and Wildlife Service (1984). The status and management of Bennetts wallaby (*Macropus rufogriseus*) and rufous wallaby (*Thylogale billardierii*) in Tasmania. In "Kangaroo Management Programs of the Australian States", pp. 61-79. Canberra.

Tighe, P. J., Davies, R. J. & Coulson, G. M. (1981). Exploitation and management of wallabies. In "Exploited and Endangered Wildlife" (ed. Jones, R.), pp. 1-36. Hobart: Board of Environmental Studies, University of Tasmania.

Tyndale-Biscoe, C. H., Hearn, J. P. & Renfree, M. B. (1974). Control of reproduction in macropodid marsupials. *Journal of Endocrinology*, 63, 589-614.

Veasey, J. S., Waran, N. K. & Young, R. J. (1996). On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare*, 5, 139-153.

Wahungu, G. M., Catterall, C. P. & Olsen, M. F. (2001). Predator avoidance, feeding and habitat use in the red-necked pademelon, *Thylogale thetis*, at rainforest edges. *Australian Journal of Zoology*, 49, 45-58.

Walker, M. T. (1977). *Prenatal Growth in Bennett's Wallaby Macropus rufogriseus fruticus*. Bachelor of Science (Honours) Thesis, University of Tasmania.

Wallberg, L. (1999). The ooga-booga boy comes home. *Sanctuary*, 1, 40-45.

Yoerg, S. I. & Shier, D. M. (1997). Maternal presence and rearing condition affect resopnses to a live predator in kangaroo rats (*Dipodomys heermanni arenae*). *Journal of Comparative Psychology*, 111, 362-369.

Appendix 1 The Questionnaire

1.) What kangaroo and wallaby species do you have?

Sp 1 -- **Sp 2** --
Sp 3 -- **Sp 4** --
Sp 5 -- **Sp 6** --
Sp 7 -- **Sp 8** --
Sp 9 -- **Sp 10** --

2.) Do you hold each species in a separate enclosure?

Yes ------------------------ No ------------------------

3.) If not, which species do you keep together?

____
____
____

4.) How many of each species do you have?

Sp 1 -- **Sp 2** --
Sp 3 -- **Sp 4** --
Sp 5 -- **Sp 6** --
Sp 7 -- **Sp 8** --
Sp 9 -- **Sp 10** --

5.) How many of the adult animals are male and how many female?

Sp 1 -- **Sp 2** --
Sp 3 -- **Sp 4** --
Sp 5 -- **Sp 6** --
Sp 7 -- **Sp 8** --
Sp 9 -- **Sp 10** --

6.) Are your animals breeding (Please circle)?

Sp 1	Yes	No	**Sp 2**	Yes	No
Sp 3	Yes	No	**Sp 4**	Yes	No
Sp 5	Yes	No	**Sp 6**	Yes	No
Sp 7	Yes	No	**Sp 8**	Yes	No
Sp 9	Yes	No	**Sp 10**	Yes	No

7.) Approximately how many of your animals are adults, how many weaned but not fully grown, how many young-at-foot and how many pouch young?

Sp 1	Adults	Subadults	**Sp 2**	Adults	Subadults
	YAF	Pouch Young		YAF	Pouch Young
Sp 3	Adults	Subadults	**Sp 4**	Adults	Subadults
	YAF	Pouch Young		YAF	Pouch Young
Sp 5	Adults	Subadults	**Sp 6**	Adults	Subadults
	YAF	Pouch Young		YAF	Pouch Young
Sp 7	Adults	Subadults	**Sp 8**	Adults	Subadults
	YAF	Pouch Young		YAF	Pouch Young
Sp 9	Adults	Subadults	**Sp 10**	Adults	Subadults
	YAF	Pouch Young		YAF	Pouch Young

8.) From where do you acquire your animals? How do you deal with excess animals?

____
____
____
____
____

9.) How big are the enclosures? Approximately what shape are they?

____
____
____
____

10.) Are the enclosures of the look-in (where visitors are excluded from the enclosure) or the walk though (where visitors can enter the enclosure) type?

Enclosure 1 Look in ________ Walk-through ________________
Enclosure 2 Look in ________ Walk-through ________________
Enclosure 3 Look in ________ Walk-through ________________
Enclosure 4 Look in ________ Walk-through ________________
Enclosure 5 Look in ________ Walk-through ________________
Enclosure 6 Look in ________ Walk-through ________________

11.) Can visitors feed the animals?

Yes ______________ No________________

12.) What do the animals eat?

Enclosure vegetation ________________
Feed provided______________________
Other (please specify) ________________

13.) If fed by you, what are your animals fed, how frequently and what time of day are they fed?

____
____
____
____
____
____
____

14.) Are animals added or removed from the enclosures (e.g. separate males during breeding)?

____
____
____
____
____

15.) During what times of the day and the year do you get the most visitors?

____
____
____
____

16.) What time of day do you notice that the animals are most active?

17.) What do you consider to be the important issues in managing your kangaroos and wallabies (e.g. stocking rates, type of feed, etc)?

Appendix 2 Respondents to the Questionnaire

Table A.1: Zoos and wildlife parks that responded to the questionnaire

Respondents	State
Bonorong Wildlife Park	Tasmania
Talune Wildlife Park	Tasmania
Trowunna Wildlife Park	Tasmania
Zoo Doo	Tasmania
Ballarat Wildlife and Reptile Park	Victoria
Currawong Bush Park	Victoria
Gumbuya Leisure Park	Victoria
Healesville Sanctuary	Victoria
Melbourne Zoo	Victoria
Werribee Zoo	Victoria
Birdland Animal Park	NSW
Coffs Harbour Zoo	NSW
Mogo Zoo	NSW
Taronga Zoo	NSW
Western Plains Zoo	NSW
Currumbin Sanctuary	Queensland
Fleays Wildlife Park	Queensland
Lone Pine Koala Sanctuary	Queensland
Qld Reptile and Fauna Park	Queensland
South Bank Parklands	Queensland
Territory Wildlife Park	Northern Territory
Bannamah Wildlife Park	Western Australia
Caversham Wildlife Park and Zoo	Western Australia
Greenough Wildlife and Bird Park	Western Australia
Perth Zoo	Western Australia
Adelaide Zoo	South Australia
Cleland Wildlife Park	South Australia
Dundee's Wildlife Park	South Australia
Monarto Zoo	South Australia
Urimbirra Wildlife Park	South Australia
Auckland Zoological Park	New Zealand
Wellington Zoological Park	New Zealand

Appendix 3 Species Held by Wildlife Parks and Zoos

Table A.3: Species held by respondents to the Questionnaire

	M. parma	*M. eugenii*	*M. parryi*	*M. dorsalis*	*M. r. banksianus*	*M. r. rufogriseus*	*M. agilis*	*M. giganteus*	*M. fuliginosus*	*M. robustus*	*M. antilopinus*	*M. bernardus*	*M. rufus*	*P. tridactylus*	*B. penicillata*	*B. gaimardi*	*B. lesueur*
Urimbirra Wildlife Park	✓✓✓	✓			✓✓			✓✓	✓				✓				
Monarto Zoological Park																	
Dundee's Wildlife Park	✓												✓				
Cleland Wildlife Park		✓							✓	✓			✓				
Adelaide Zoo		✓					✓		✓	✓			✓		✓		✓
Perth Zoological Gardens									✓	✓	✓		✓				✓
Greenough Wildlife & Bird Park									✓	✓			✓				
Caversham Wildlife Park and	✓	✓				✓	✓		✓	✓			✓				
Bannamah Wildlife Park									✓	✓			✓		✓		
Territory Wildlife Park							✓			✓	✓	✓	✓				
South Bank Parklands	✓		✓	✓	✓			✓									
Qld Reptile and Fauna Park			✓	✓	✓			✓					✓				
Lone Pine Koala Sanctuary					✓			✓					✓				
Fleays Wildlife Park			✓	✓	✓		✓	✓					✓				
Currumbin Sanctuary			✓	✓	✓		✓	✓		✓			✓	✓			
Western Plains Zoo			✓		✓			✓	✓	✓			✓				
Taronga Zoo					✓			✓	✓				✓	✓	✓		
Mogo Zoo								✓									
Coffs Harbour Zoo	✓	✓			✓			✓		✓			✓				
Birdland Animal Park					✓			✓					✓				
Werribee Zoo						✓		✓					✓				
Melbourne Zoo	✓		✓	✓		✓		✓	✓	✓	✓		✓	✓			
Healesville Sanctuary	✓					✓		✓	✓	✓			✓				
Gumbuya Leisure Park		✓				✓		✓	✓				✓				
Currawong Bush Park		✓						✓									
Ballarat Wildlife and Reptile									✓				✓				
Zoo Doo						✓											
Trowunna Wildlife Park						✓		✓								✓	
Talune Wildlife Park						✓		✓						✓			
Bonorong Wildlife Park						✓		✓						✓		✓	

	Bonorong Wildlife Park	Talune Wildlife Park	Trowunna Wildlife Park	Zoo Doo	Ballarat Wildlife and Reptile	Currawong Bush Park	Gumbuya Leisure Park	Healesville Sanctuary	Melbourne Zoo	Werribee Zoo	Birdland Animal Park	Coffs Harbour Zoo	Mogo Zoo	Taronga Zoo	Western Plains Zoo	Currumbin Sanctuary	Fleays Wildlife Park	Lone Pine Koala Sanctuary	Qld Reptile and Fauna Park	South Bank Parklands	Territory Wildlife Park	Bannamah Wildlife Park	Caversham Wildlife Park and	Greenough Wildlife & Bird Park	Perth Zoological Gardens	Adelaide Zoo	Cleland Wildlife Park	Dundee's Wildlife Park	Monarto Zoological Park	Urimbirra Wildlife Park
A. rufescens												Y				Y						Y								
L. conspicillatus																					Y									
L. hirsutus															Y														Y	
O. unguifera																					Y		Y							
O. fraenata																	Y													
P. lateralis																									Y					
P. pencillata								Y																						
P. xanthopus									Y					Y	Y										Y	Y	Y		Y	
P. brachyotis																					Y									
P. concinna																					Y									
T. stigmatica									Y							Y	Y			Y										
T. billardierii	Y	Y	Y	Y				Y															Y							Y
T. thetis														Y			Y			Y			Y							Y
S. brachyurus					Y				Y					Y								Y			Y					
W. bicolour						Y	Y	Y	Y		Y	Y			Y		Y	Y		Y		Y	Y				Y	Y		Y
D. goodfellowi									Y					Y		Y														
D. matschiei																									Y	Y				
D. luctuosa									Y							Y									Y	Y				

Appendix 4 Single and Multiple Species Enclosures Maintained by Respondents to the Questionnaire

Table A.4: Species held in either single- or multi-species enclosures

Zoo or Park	Single-Species Enclosures	Multi-species enclosures
Bonorong Wildlife Park		√
Talune Wildlife Park		√
Trowunna Wildlife Park		√
Zoo Doo	√	
Ballarat Wildlife and Reptile Park	√	
Currawong Bush Park		√
Gumbuya Leisure Park		√
Healesville Sanctuary		√
Melbourne Zoo	√	√
Werribee Zoo		√
Birdland Animal Park	√	
Coffs Harbour Zoo		√
Mogo Zoo		N/A
Fleays Wildlife Park		√
Lone Pine Koala Sanctuary	√	
Qld Reptile and Fauna Park		√
South Bank Parklands	√	√
Territory Wildlife Park		√
Bannamah Wildlife Park	√	√
Caversham Wildlife Park and Zoo	√	
Greenough Wildlife & Bird Park		√
Perth Zoological Gardens		√
Adelaide Zoo	√	√
Cleland Wildlife Park		√
Dundee's Wildlife Park		√
Urimbirra Wildlife Park		√
Auckland Zoo		√
Totals	**9**	**21**

Appendix 5 Total Numbers of Each Species Maintained by Respondents to the Questionnaire

Table A.5: Total number of individuals of each species held by each respondent

		Bonorong Wildlife Park	Talune Wildlife Park	Trowunna Wildlife Park	Zoo Doo	Ballarat Wildlife and Reptile Park	Currawong Bush Park	Gumbuya Leisure Park	Healesville Sanctuary	Melbourne Zoo	Werribee Zoo	Birdland Animal Park	Coffs Harbour Zoo	Mogo Zoo	Taronga Zoo	Western Plains Zoo	Currumbin Sanctuary	Fleays Wildlife Park	Lone Pine Koala Sanctuary	Qld Reptile and Fauna Park	South Bank Parklands	Territory Wildlife Park	Bannamah Wildlife Park	Caversham Wildlife Park and Zoo	Greenough Wildlife & Bird Park	Perth Zoological Gardens	Adelaide Zoo	Cleland Wildlife Park	Dundee's Wildlife Park	Urimbirra Wildlife Park	Urimbirra Wildlife Park	Auckland Zoological Park	Wellington Zoological Gardens
M. r. banksianus	75											2	4		2	5	17		15	4	10												
M. r. rufogriseus	150	30	Y	60	7			18	8	6	15													6									
P. tridactylus	11	6	Y							2					2		1																
M. parma	54								10	5			6								3			2					2				
M. Eugenii	68						1	4					2											4			7	10					
M. parryi	34									4						16	6	2		1	5												
M. dorsalis	17									5							5			1	6												
M. agilis	19																5					11		2			1						
M. giganteus	332	20		35			9	50	5	16	12	15	16	3	2	10	67		40	2	2												
M. fuliginosus	261					96		6	9	15					6	10							10	25	6	12	5	41					
M. robustus	153								5	2			15			17	82					1	3	15	4	1	3	5					
M. antilopinus	33									7												18				8							
M. bernardus	4																					4											
M. rufus	267					9		5	13	6	17	5	16		8	17	26		20	2		19	3	25	6	6	9	19	1				
B. penicillata	15														5								4				6						
B. gaimardi	14	3		11																										40	40		
B. lesueur	2																									1	1			10	10		
A. rufescens	6												1				1						4							10	10	12	4
L. conspicillatus	1																					1								40	40		
L. hirsutus	16															13																	
O. unguifera	6																					2		4									
O. fraenata	3																	3												6	6	10	
P. lateralis	4																									4							
P. pencillata	4								4																								
P. xanthopus	105									4					3	10										2	18	23		25	25		3
P. brachyotis	2																					2								20	20		
P. concinna	1																					1											
T. stigmatica	21									5							2	8			6												
T. billardierii	80	12	Y	15	3				8															2									

		Bonorong Wildlife Park	Talune Wildlife Park	Trowunna Wildlife Park	Zoo Doo	Ballarat Wildlife and Reptile Park	Currawong Bush Park	Gumbuya Leisure Park	Healesville Sanctuary	Melbourne Zoo	Werribee Zoo	Birdland Animal Park	Coffs Harbour Zoo	Mogo Zoo	Taronga Zoo	Western Plains Zoo	Currumbin Sanctuary
T. thetis	27														3		
S. brachyurus	51					30				8					3		
W. bicolour	121						2	4	6	3		12	4			23	
D. goodfellowi	9									3					2		4
D. matschiei	12																
D. luctuosa	15									4							7
	1993	71	0	121	10	135	12	87	68	95	44	34	64	3	36	121	223

	Fleays Wildlife Park	Lone Pine Koala Sanctuary	Qld Reptile and Fauna Park	South Bank Parklands	Territory Wildlife Park	Bannamah Wildlife Park	Caversham Wildlife Park and Zoo	Greenough Wildlife & Bird Park	Perth Zoological Gardens	Adelaide Zoo	Cleland Wildlife Park	Dundee's Wildlife Park	Urimbirra Wildlife Park	Urimbirra Wildlife Park	Auckland Zoological Park	Wellington Zoological Gardens
T. thetis	6			6			2						35	35		
S. brachyurus						3			7							
W. bicolour	Y	20		8		4	3				15	9	8	8		
D. goodfellowi																
D. matschiei									6	6						
D. luctuosa									2	2						
	19	95	10	46	59	31	90	16	49	58	113	12	194	194	22	7

Appendix 6 Total Numbers of Males and Females Maintained by Respondents to the Questionnaire

Table A.6: Total numbers of males and females of each species held at each responding wildlife park or zoo

	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
M. r. rufogriseus	51	78	7	15	26	34	2	5			6	7	2	5	2	3	6	9														
M. r. banksianus	19	41																	1	1	1	3				2	2	3	9	8		
M. parma	14	26											2	8	1	4					2	4										
M. eugenii	37	25							1		1	1									1	1										
M. parryi	13	12													2	1											4	4	3	3	1	1
M. dorsalis	4	11													3	1														5		
M. agilis	6	11																											4	1		
M. giganteus	87	135	5	12	16	19			3	6	4	12	2	3	9	7	6	6			4	9	1	2		2	5	5	27	40		
M. fuliginosus	49	70									2	4	3	6	·2	4									2	4	3	2				
M. robustus	51	79											0	5	1	1					4	11					3	6	39	43		
M. antilopinus	7	24													3	4																
M. bernardus	3	1																														
M. rufus	78	121									2	1	3	9	3	2	11	6	2	3	4	12			2	6	5	9	13	13		
P. tridactylus	5	6	2	4											2										1	1				1		
B. penicillata	5	10																							2	3						
B. gaimardi	3	9		1	3	8																										
B. lesueur	1	1																														
A. rufescens	3	3																			1									1		
L. conspicillatus	1	0																														
			Bonorong Wildlife Park		Trowunna Wildlife Park		Zoo Doo		Currawong Bush Park		Gumbuya Leisure Park		Healesville Sanctuary		Melbourne Zoo		Werribee Zoo		Birdland Animal Park		Coffs Harbour Zoo		Mogo Zoo		Taronga Zoo		Western Plains Zoo		Currumbin Sanctuary		Fleays Wildlife Park	

	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
M. r. rufogriseus																												
M. r. banksianus				4	2	8																			3	3	1	9
M. parma					1	2													1	1			4	6	2		2	2
M. eugenii															5	2	4	6					25	15				
M. parryi				1	3	2																						
M. dorsalis				1	1	4																						
M. agilis							2	9								1												
M. giganteus				2																			4	8			1	2
M. fuliginosus									3	7	1	5	5	7	3	2	23	17					2	12				
M. robustus								1	1	2		4		1	1	2	2	3										
M. antilopinus							3	13					1	7														
M. bernardus							3	1																				
M. rufus				2			7	7	1	2	2	4		6	3	6	12	4	1				8	27				
P. tridactylus																												
B. penicillata									2	2					1	5												
B. gaimardi																												
B. lesueur														1	1													
A. rufescens									2	2																		
L. conspicillatus							1																					
	Lone Pine Koala Sanctuary		Qld Reptile and Fauna Park		South Bank Parklands		Territory Wildlife Park		Bannamah Wildlife Park		Greenough Wildlife & Bird Park		Perth Zoological Gardens		Adelaide Zoo		Cleland Wildlife Park		Dundee's Wildlife Park		Monarto Zoological Park		Urimbirra Wildlife Park		Auckland Zoological Park		Wellington Zoological Gardens	

	D. luctuosa	*D. matschiei*	*D. goodfellowi*	*W. bicolour*	*S. brachyurus*	*T. thetis*	*T. billardierii*	*T. stigmatica*	*P. concinna*	*P. brachyotis*	*P. xanthopus*	*P. pencillata*	*P. lateralis*	*O. fraenata*	*O. unguifera*	*L. hirsutus*
	8	4	4	56	7	8	37	11	1	1	44	0	2	2	1	7
	7	7	5	30	12	16	33	8	0	1	56	4	2	1	1	9
Bonorong Wildlife Park							4									
							6									
Trowunna Wildlife Park							6									
							9									
Zoo Doo																
Currawong Bush Park				2												
Gumbuya Leisure Park				2												
				1												
Healesville Sanctuary				3			2									
				2			3					4				
Melbourne Zoo			1	2	2			2			4					
	4		2	1	4			3								
Werribee Zoo																
Birdland Animal Park																
Coffs Harbour Zoo				3												
				1												
Mogo Zoo																
Taronga Zoo			1		1	1										
			1		2	2					3					
Western Plains Zoo				11							10					5
				12												8
Currumbin Sanctuary	5		2					2								
	2		2													
Fleays Wildlife Park						2		2						2		
						3		4						1		
Lone Pine Koala Sanctuary				20												
Qld Reptile and Fauna Park																
South Bank Parklands				2		2		5								
						4		1								
Territory Wildlife Park									1	1					1	
										1					1	
Bannamah Wildlife Park				2	1											
				2	2											
Greenough Wildlife & Bird Park																
Perth Zoological Gardens	1	3			3						2		2			
	1	3			4								2			
Adelaide Zoo	2	1									6					
		4									12					
Cleland Wildlife Park				6							4					
				6							14					
Dundee's Wildlife Park				6												
				3												
Monarto Zoological Park											18					2
											27					1
Urimbirra Wildlife Park				3		3	25									
				5		7	15									
Auckland Zoological Park																
Wellington Zoological Gardens																

Appendix 7 Reproductive Status of Collections

Table A.7: Reproductive status of individual collections of macropods in all responding wildlife parks and zoos

Species Name	Bonorong Wildlife Park	Talune Wildlife Park	Trowunna Wildlife Park	Zoo Doo	Ballarat Wildlife and Reptile Park	Currawong Bush Park	Gumbuya Leisure Park	Healesville Sanctuary	Melbourne Zoo	Werribee Zoo	Birdland Animal Park	Coffs Harbour Zoo	Mogo Zoo	Taronga Zoo	Western Plains Zoo	Currumbin Sanctuary	Fleays Wildlife Park	Lone Pine Koala Sanctuary	Qld Reptile and Fauna Park	South Bank Parklands	Territory Wildlife Park	Bannamah Wildlife Park	Caversham Wildlife Park and Zoo	Greenough Wildlife and Bird Park	Perth Zoological Gardens	Adelaide Zoo	Cleland Wildlife Park	Dundee's Wildlife Park	Monarto Zoological Park	Urimbirra Wildlife Park	Auckland Zoological Park	Wellington Zoological Gardens
M. r. rufogriseus	Y	Y	Y	Y			Y	Y	Y	Y													Y									
M. r. banksianus											Y	Y		N	Y	N	?	Y	N	Y										Y	Y	
M. parma								Y	Y			Y								Y			Y							Y	Y	N
M. eugenii						N	Y					N											Y			Y				Y		
M. parryi									Y						Y	Y	N		N	Y												
M. dorsalis									Y							N	?		N	Y												
M. agilis																N	?				N		Y			N						
M. giganteus	Y	Y	Y			N	Y	N	Y	N	Y	Y	N	N	N	Y	?	Y	N	N										Y		N
M. fuliginosus					Y		N	Y	Y					Y	Y							Y	Y	N	Y	N				Y		
M. robustus								N	Y			Y			Y	Y					N	Y	Y	N	N	Y						
M. antilopinus									Y												N				Y							
M. bernardus																					N											
M. rufus					Y		Y	Y	Y	N	Y	Y		N	N	Y	?	Y	N		N	N	Y	N	N	Y				Y		
P. tridactylus	Y	Y							N					Y		N																
B. penicillata														N								Y				Y						
B. gaimardi	N		Y																													
B. lesueur																									N	N						
A. rufescens												N				N						Y										
C. campestris																																
L. conspicillatus																					N											
L. hirsutus															Y														Y			
O. unguifera																					N		Y									
O. fraenata																	Y															
P. lateralis																									Y							
P. pencillata								N																								
P. xanthopus									N					N	N										N	Y	Y		Y			
P. brachyotis																					N											
P. concinna																					N											
T. stigmatica									Y							N	Y			Y												
T. billardierii	Y	Y	Y	Y				Y															Y							Y		
T. thetis														Y			Y			Y			Y							Y		
S. brachyurus					Y				Y					Y								Y			Y							
W. bicolour						N	N	Y	Y		Y	N			Y		?	Y		N		Y	Y							Y		
D. goodfellowi									Y					N		Y																
D. matschiei																									N	Y						
D. luctuosa									N							N									Y	N						

Appendix 8 Ages of Macropodoids Maintained in Captivity

	Bonorong Wildlife Park				Trowunna Wildlife Park			Zoo Doo				Ballarat Wildlife And Reptile Park			Currawong Bush Park			Gumbuya Leisure Park			
	A	SA	YAF	PY	A	SA	YAF	A	SA	YAF	PY	A	SA	PY	A	SA	YAF	A	SA	YAF	PY
M. parma																					
M. eugenii															1			2		1	1
M. parryi																					
M. dorsalis																					
M. r. banksianus																					
M. r. rufogriseus	22	7	1	15	43	11	6	6	1		1							13	2		3
M. agilis																					
M. giganteus	17	2	1	12	27	5	3								4	3	2	16	14	10	10
M. fuliginosus																		4	2		
M. robustus																					
M. antilopinus																					
M. bernardus																					
M. rufus												2	3	2				3		1	
P. tridactylus	6																				
B. penicillata																					
B. gaimardierii	1		1	1	8	3															
A. rufescens																					
L. conspicillatus																					
O. unguifera																					
O. fraenata																					
P. pencillata																					
P. xanthopus																					
P. brachyotis																					
P. concinna																					
T. stigmatica																					
T. billardierii	10	2		6	5	10				3											
T. thetis																					
S. brachyurus																					
W. bicolour															2			2	2		
D. goodfellowi																					
D. luctuosa																					

	Healesville Sanctuary				Melbourne Zoo		Werribee Zoo	Birdland Animal Park		Coffs Harbour Zoo				Mogo Zoo	Western Plains Zoo		Fleays Wildlife Park				Qld Reptile and Fauna Park
	A	SA	YAF	PY	A	YAF	A	A	PY	A	SA	YAF	PY	A	A	PY	A	SA	YAF	PY	A
M. parma	7	2		3	5					5	1										
M. eugenii										2											
M. parryi					3	1									8	8	1	1			1
M. dorsalis					4	1															1
M. r. banksianus										3	1										4
M. r. rufogriseus	7		1		5	1	15														
M. agilis																					
M. giganteus	3	2			16		12	2		10	3		3	3							2
M. fuliginosus	6	2	1		6	1									5	5					
M. robustus	5				2					8	5	2			9	8					
M. antilopinus					7																
M. bernardus																					
M. rufus	12		1		5	1	17	5	3	10	2	4			14	3					2
P. tridactylus					2																
B. penicillata																					
B. gaimardierii																					
A. rufescens										1											
L. conspicillatus																					
O. unguifera																					
O. fraenata																	2	1			
P. pencillata	4																				
P. xanthopus					4																
P. brachyotis																					
P. concinna																					
T. stigmatica					5												3	2	2	1	
T. billardierii	5		3																		
T. thetis																	3	1	1	1	
S. brachyurus					6	2															
W. bicolour	4	1	1	2	3					4											
D. goodfellowi					3																
D. luctuosa					4	1															

	South Bank Parklands				Territory Wildlife Park				Bannamah Wildlife Park				Greenough Wildlife & Bird Park		Adelaide Zoo		Cleland Wildlife Park				Dundee's Wildlife Park		Auckland Zoological Park
	A	SA	YAF	PY	A	SA	YAF	PY	A	SA	YAF	PY	A	SA	A	PY	A	SA	YAF	PY	A	SA	A
M. parma	2		1																		1	1	2
M. eugenii																	7	2		1			
M. parryi	4	1		1																			
M. dorsalis	4	2		1																			
M. r. banksianus	8	1	1	2																			10
M. r. rufogriseus																							
M. agilis					11																		
M. giganteus																							
M. fuliginosus									6	2	2	3	5	1			41	4	5	1			
M. robustus						1			3				4				4	1					
M. antilopinus					16			2															
M. bernardus					2	2																	
M. rufus					14		5	5	3				6				8	2	3	3	1		
P. tridactylus																							
B. penicillata									2	2		1											
B. gaimardierii																							
A. rufescens									4			1											
L. conspicillatus						1																	
O. unguifera						2																	
O. fraenata																							
P. pencillata																							
P. xanthopus															5	1	12	6		5			
P. brachyotis					2																		
P. concinna					1																		
T. stigmatica	5	1		1																			
T. billardierii																							
T. thetis	5	1		1																			
S. brachyurus									3														
W. bicolour									3	1		1					8	4	2	1	5	4	
D. goodfellowi																							
D. luctuosa																							

Appendix 9A Places of Acquisition of New Stock For Wildlife Parks and Zoos

Table A.9A: Places of acquisition for wildlife parks and zoos

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	Captive breeding, injured and orphaned from the wild.
Talune Wildlife Park	Captive breeding and donations of injured and orphaned animals.
Trowunna Wildlife Park	Captive bred and hand reared orphans.
Zoo Doo	Public donations and captive breeding.
Ballarat Wildlife and Reptile Park	Surplus lists from other zoos and parks.
Currawong Bush Park	Melbourne Zoological Board/Healesville Sanctuary.
Gumbuya Leisure Park	Captive breeding.
Healesville Sanctuary	From other zoos and parks, orphans from the wild.
Melbourne Zoo	Other zoos. Captive breeding. Australasian Species Management Plan.
Werribee Zoo	Melbourne Zoo.
Birdland Animal Park	Bred own, from other parks or injured or orphaned from the wild.
Coffs Harbour Zoo	Breed own or acquire from other zoos.
Mogo Zoo	Hand reared.
Taronga Zoo	Captive breeding. Other zoos. Australasian Species Management Plan.
Western Plains Zoo	Captive breeding. Other zoos. Australasian Species Management Plan.
Currumbin Sanctuary	Captive breeding. Other zoos. Australasian Species Management Plan.
Fleays Wildlife Park	From other zoos and captive breeding.
Lone Pine Koala Sanctuary	Exchange with other parks.
Qld Reptile and Fauna Park	Orphans not able to be released.
South Bank Parklands	Other parks or orphans from the wild.

Wildlife Park/Zoo	Response
Territory Wildlife Park	Orphans from the wild or from aboriginal community after hunts.
Bannamah Wildlife Park	From other zoos and parks. Western grey kangaroos are donated as injured and orphaned from the wild.
Caversham Wildlife Park and Zoo	From parks across Australia.
Greenough Wildlife & Bird Park	From C.A.L.M. carers and members of the public.
Perth Zoological Gardens	Captive breeding. Other zoos. Australasian Species Management Plan.
Adelaide Zoo	Captive breeding. Other zoos. Australasian Species Management Plan.
Cleland Wildlife Park	From other zoos and parks and injured and orphaned from the wild.
Dundee's Wildlife Park	Donations from the public.
Monarto Zoological Park	Captive breeding. Other zoos. Australasian Species Management Plan.
Urimbirra Wildlife Park	Other parks and zoos in South Australia or other zoos as required.
Auckland Zoological Park	Captive breeding.
Wellington Zoological Gardens	Australasian Species Management Plan.

Appendix 9B Management of Excess Stock

Table A.9A: Management of excess stock

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	Self regulating (fighting), release into wild.
Talune Wildlife Park	Culling
Zoo Doo	All animals are retained as they are not suitable for release.
Currawong Bush Park	Euthanased, vasectomise male *M. giganteus*.
Gumbuya Leisure Park	Trade with other parks, release into sanctuary.
Healesville Sanctuary	Trade with other zoos and parks.
Melbourne Zoo	Other zoos or culled.
Werribee Zoo	Vasectomise males.
Birdland Animal Park	Controlled breeding, sent to other parks, culling.
Coffs Harbour Zoo	Other zoos - Australasian Species Management Plan.
Mogo Zoo	Other zoos - Australasian Species Management Plan.
Taronga Zoo	Other zoos - Australasian Species Management Plan.
Western Plains Zoo	Other zoos - Australasian Species Management Plan. Release into the wild as part of captive breeding program.
Currumbin Sanctuary	Goodfellow's tree-kangaroo bred for release into secure environments. Culling. Other zoos - Australasian Species Management Plan.
Fleays Wildlife Park	Trade with other zoos, release.
Lone Pine Koala Sanctuary	Exchange with other parks
South Bank Parklands	Traded with other parks.
Territory Wildlife Park	Fostered to carers for rehabilitation and release.
Bannamah Wildlife Park	Trade with other zoos and parks.
Caversham Wildlife Park and Zoo	Trade with other parks.
Greenough Wildlife & Bird Park	Excess stock are avoided by controlling the intake of new stock.
Perth Zoological Gardens	Culling. Other zoos - Australasian Species Management Plan.
Adelaide Zoo	Culling. Other zoos - Australasian Species Management Plan.
Cleland Wildlife Park	Culling, selling to other parks and zoos and placements with carers.
Monarto Zoological Park	Culling. Australasian Species Management Plan.
Auckland Zoological Park	Euthanase joeys as required. Other zoos.
Wellington Zoological Gardens	Other zoos - Australasian Species Management Plan.

Appendix 10 Types of Enclosures Maintained by Respondents to the Questionnaire

Table A.10: Types of enclosures maintained by wildlife parks and zoos reposnding to the questionnaire

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	The potoroos and bettongs live in the nocturnal house. These enclosures are approximately 4.5 x 3 m each. Forester kangaroos, Bennett's wallabies and Tasmanian pademelons free-range over an area of 5-6 acres.
Talune Wildlife Park	Forester kangaroos, Bennett's wallabies and Tasmanian pademelons free-range over an area of several acres. Young pademelons and Bennett's wallabies are housed in small, rectangular enclosures in small numbers. Long-nosed potoroos are housed in a small glass enclosure in a nocturnal house.
Trowunna Wildlife Park	Forester kangaroos, Bennett's wallabies and Tasmanian pademelons are free-ranging across 38 acres. Bettongs are held in two other enclosures.
Zoo Doo	Tasmanian pademelons are held in 3 x 5 metre enclosures that they share with rabbits and guinea pigs. Bennett's wallabies on display (no more than 2) are held in a small pentagonal enclosure. Additional Bennett's wallabies are free-ranging over a large paddock.
Ballarat Wildlife and Reptile Park	The Kangaroo Island kangaroos free range. The red kangaroos and quokkas each have large, square paddocks.
Currawong Bush Park	Animals free-range over a 1.5 ha rectangular enclosure of natural bush land.

Wildlife Park/Zoo	Response
Gumbuya Leisure Park	Kangaroos free-range over enclosures from 1 to 10 acres in size. Wallabies are kept in a fenced and roofed enclosure approximately 1 acre in size.
Healesville Sanctuary	Enclosure 1 is 4 acres and roughly diamond shaped. Enclosure 2 is 3 acres and the same shape. Enclosure 3 is a 1 acre square enclosure.
Melbourne Zoo	Several enclosures of varying sizes and shapes, all irregular.
Werribee Zoo	Free-range on 4 ha.
Birdland Animal Park	Four rectangular enclosures, 40 x 30 m, 20 x 20m, 85 x 40 m and 30 x 45 m.
Coffs Harbour Zoo	Enclosures are approximately 3500 m^2, except for the rufous bettong, which is in an enclosure approximately 20 m^2 in size. Enclosures are roughly square or rectangular in shape.
Mogo Zoo	Eastern grey kangaroos free-range on one acre of sloping land bordered by Red Pandas on one side and tigers on the other, but with no visual contact with the tigers.
Fleays Wildlife Park	*T. stigmatica* are on 0.2 ha. *T. thetis* are on 0.4 ha. *O. fraenata* and *M. parryii* are each on 0.15 ha.
Lone Pine Koala Sanctuary	Free-ranging on 170ha of back reserve of Redbank.

Wildlife Park/Zoo	Response
Qld Reptile and Fauna Park	Free-ranging over a 3 acre, square enclosure that contains other smaller exhibits within its boundaries.
South Bank Parklands	Paddocks are mostly rectangular. One is a free-range, four hectare area with an external boundary fence only. Another is 50 x 50 m, a third is 20 x 20 m and another 1 hectare in size. None of these is open to the public. An oval enclosure containing a rainforest exhibit is open to the public; this is .3 hectares in size.
Territory Wildlife Park	Walk-through macropod exhibit is divided into 3 areas with a path that visitors are required to remain on. The first area is 70 x 100 m, the next 80 x 130 m and the last 100 x 50 m. All irregularly shaped to avoid corners. Smaller holding enclosures are off public display.
Bannamah Wildlife Park	Large macropods free-range over 1 hectare; the enclosure is rectangular. Swamp wallabies are in a rectangular enclosure 150 x 50 m. Quokkas are in a similar enclosure and all other macropods are in "aviary" type enclosures.
Greenough Wildlife & Bird Park	50 x 25 metre rectangular.
Adelaide Zoo	
Cleland Wildlife Park	Six macropod enclosures of varying shapes range from 2 to 5 acres.
Dundee's Wildlife Park	450 m^2 enclosure.

Wildlife Park/Zoo	Response
Urimbirra Wildlife Park	2 x 1 hectare.
	1 x 8 hectares.
	2 x .75 hectares.
	3 x .25 hectares.
Auckland Zoo	1 ovoid enclosure approximately 350-400 m^2.

Appendix 11 Numbers of Visitor Inclusive and Visitor Exclusive Enclosures Maintained by Respondents to the Questionnaire

Table 3.10: Number of visitor inclusive or visitor exclusive enclosures

Wildlife Park/Zoo	Visitor Exclusive	Visitor Inclusive
Bonorong Wildlife Park	2	3
Talune Wildlife Park	2	2
Zoo Doo	3	0
Ballarat Wildlife and Reptile Park	2	1
Currawong Bush Park	0	1
Gumbuya Leisure Park	4	2
Healesville Sanctuary	0	3
Melbourne Zoo	7	1
Werribee Zoo	0	Drive Through
Birdland Animal Park	3	1
Coffs Harbour Zoo	3	1
Mogo Zoo	1	0
Western Plains Zoo	0	1
Currumbin Sanctuary	1	1
Fleays Wildlife Park	0	4
Lone Pine Koala Sanctuary	0	1
Qld Reptile and Fauna Park	0	5
South Bank Parklands	4	1
Territory Wildlife Park	0	3
Bannamah Wildlife Park	5	1
Caversham Wildlife Park and Zoo	4	1
Greenough Wildlife & Bird Park	0	1
Cleland Wildlife Park	0	6
Urimbirra Wildlife Park	3	5
Auckland Zoo	0	1
Totals	**44**	**47**

Appendix 12 Numbers of Wildlife Parks and Zoos that either Permit or Prevent the Feeding of Exhibited Animals

Table A.12: Parks and zoos that permit or prevent feeding of individuals on exhibit

Wildlife Park/Zoo	Yes	No
Bonorong Wildlife Park	√	√
Talune Wildlife Park	√	
Trowunna Wildlife Park	√	√
Zoo Doo	√	
Ballarat Wildlife and Reptile Park	√	
Currawong Bush Park		√
Gumbuya Leisure Park	√	
Healesville Sanctuary	√	
Melbourne Zoo		√
Werribee Zoo		√
Birdland Animal Park	√	
Coffs Harbour Zoo	√	
Mogo Zoo	√	
Taronga Zoo		
Western Plains Zoo		
Currumbin Sanctuary	√	
Fleays Wildlife Park		√
Lone Pine Koala Sanctuary	√	
Qld Reptile and Fauna Park		√
South Bank Parklands		√
Territory Wildlife Park		√
Bannamah Wildlife Park	√	√
Caversham Wildlife Park and Zoo	√	
Greenough Wildlife & Bird Park	√	
Perth Zoological Gardens		
Adelaide Zoo		
Cleland Wildlife Park	√	
Monarto Zoological Park		√
Urimbirra Wildlife Park	√	
Auckland Zoological Park		√
Totals	**17**	**12**

Table 3.10: Number of visitor inclusive or visitor exclusive enclosures

Wildlife Park/Zoo	Visitor Exclusive	Visitor Inclusive
Bonorong Wildlife Park	2	3
Talune Wildlife Park	2	2
Zoo Doo	3	0
Ballarat Wildlife and Reptile Park	2	1
Currawong Bush Park	0	1
Gumbuya Leisure Park	4	2
Healesville Sanctuary	0	3
Melbourne Zoo	7	1
Werribee Zoo	0	Drive Through
Birdland Animal Park	3	1
Coffs Harbour Zoo	3	1
Mogo Zoo	1	0
Western Plains Zoo	0	1
Currumbin Sanctuary	1	1
Fleays Wildlife Park	0	4
Lone Pine Koala Sanctuary	0	1
Qld Reptile and Fauna Park	0	5
South Bank Parklands	4	1
Territory Wildlife Park	0	3
Bannamah Wildlife Park	5	1
Caversham Wildlife Park and Zoo	4	1
Greenough Wildlife & Bird Park	0	1
Cleland Wildlife Park	0	6
Urimbirra Wildlife Park	3	5
Auckland Zoo	0	1
Totals	**44**	**47**

Appendix 13 Most Popular Times for Visitors to Wildlife Parks and Zoos Responding to the Questionnaire

Table A.13: Most popular times for visitors to Wildlife Parks and Zoos that responded to the questionnaire

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	Summer (Nov-March) and weekends and public holidays during winter.
Talune Wildlife Park	11am to 3pm daily.
Currawong Bush Park	Weekends.
Gumbuya Leisure Park	Weekends, sunny days, school holidays.
Healesville Sanctuary	Weekends, sunny days, school holidays.
Melbourne Zoo	Weekends, sunny days, school holidays.
Werribee Zoo	Sunny holiday Sundays and public holidays.
Birdland Animal Park	Weekends 10am to 3pm and school holidays 9:30am to 5pm.
Coffs Harbour Zoo	School holidays.
Mogo Zoo	School holidays, especially Christmas. Steady business throughout the year.
Qld Reptile and Fauna Park	Weekends and school and public holidays.
South Bank Parklands	Steady business throughout the year and during the day. Peak times during the days are 10am to 2pm. Peak periods during the year are Sundays and school and public holidays.
Territory Wildlife Park	Peak business is in the mornings due to the position of the exhibit near the entrance gate. During the year, peak visitation is during the dry season (May, June and July).
Bannamah Wildlife Park	Busiest periods are between 10am and 1pm and between November and May, depending on good weather.
Caversham Wildlife Park and Zoo	No discernable pattern.
Greenough Wildlife & Bird Park	Business is seasonal, with the busiest periods falling in the cooler months, between April and October.
Cleland Wildlife Park	Mid-afternoon and through the warmer months.
Urimbirra Wildlife Park	Christmas through to Easter.
Auckland Zoo	11.30am to 2pm daily.

Appendix 14 Times at Which Managers of Captive Macropods Notice Greatest Activity in their Animals

Table 3.13: Times at which captive macropods are noted by their managers to be more active.

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	Early mornings and late afternoon (before 9am and after 3pm).
Talune Wildlife Park	When visitors with feed are present.
Zoo Doo	Evenings and through the night.
Currawong Bush Park	Evening.
Gumbuya Leisure Park	Early morning, early afternoon and evenings.
Healesville Sanctuary	Morning and late afternoon.
Melbourne Zoo	Early morning and late afternoon.
Werribee Zoo	Morning and evening.
Birdland Animal Park	Dawn and dusk and cool, fine days.
Coffs Harbour Zoo	Feed time.
Mogo Zoo	AM and PM.
Qld Reptile and Fauna Park	Mornings except for the *M. dorsalis* individual who is more active around late afternoon.
Territory Wildlife Park	Early morning and late afternoon.
Bannamah Wildlife Park	In the early morning.
Caversham Wildlife Park and Zoo	On and off all day on cloudy days and before 10am and after 4pm on sunny days.
Greenough Wildlife & Bird Park	Feeding time and windy weather.
Cleland Wildlife Park	Cooler parts of the day.
Dundee's Wildlife Park	Early morning and late afternoon. Animals graze throughout the day.
Urimbirra Wildlife Park	Mornings and late afternoon.
Auckland Zoo	During morning feeding times.

Appendix 15 Key Management Issues Nominated by Current Managers of Captive Macropods

Table 3.14: Key management issues nominated by current macropod managers.

Wildlife Park/Zoo	Response
Bonorong Wildlife Park	As males get older, it is important to keep them separate as fighting will always lead to death. They may also become aggressive to visitors. Must keep male numbers to a minimum, especially as all females breed and have pouch young every season.
Trowunna Wildlife Park	Feeding, diet, hygiene, handling, preventative medicine, stocking rates, sex ratios.
Zoo Doo	Habitat enrichment, managing stock to exhibit natural behaviours over visitor expectations. Two animals are displayed to the public together to minimise stress from low stocking rates.
Currawong Bush Park	Managing a sustainable population size for the enclosure area. Balancing mimicking natural habitats and allowing natural behaviours against visitor expectations to touch and feed the animals, and training them to the extent that they are not stressed by the artificial environment/circumstances while still maintaining an element of naturalness/wildness. Changing visitor perceptions to allow phasing out of such enclosures/wildlife parks.
Gumbuya Leisure Park	Maintain natural environments, so stocking rates are important. Have unlimited water resources to maintain good pasture growth if stock levels are managed in line with enclosure sizes. Feed supplementation is carried out regardless of pasture condition.
Healesville Sanctuary	Stocking rates, controlled breeding, preventative medicine, updating diets and feeding practices regularly.
Melbourne Zoo	Primarily husbandry and housing.

Wildlife Park/Zoo	**Response**
Werribee Zoo	Provision of plenty of room. Keeping stocking rates low relative to amount of available pasture/contaminant loads from animals. Control breeding. Neuter males if required to keep unnatural sex ratio. Provide adequate cover for wallabies - need to be able to get away behind sight barriers.
Birdland Animal Park	Space, good feed, privacy, undue stocking rates, shelter.
Coffs Harbour Zoo	Regular worming, altering the amount of food supplement depending on available enclosure vegetation. General cleaning away of faecal matter.
Mogo Zoo	Only 3 hand reared animals, so no overstocking and no pressure gives relaxed animals.
Fleays Wildlife Park	Attention to diet, understanding of social order. Important to have one dominant male with clear superiority. Daily visual health checks and knowledge of individuals' normal behaviour, especially in rarer wallabies, to assist in early diagnosis.
Lone Pine Koala Sanctuary	To be able to be released in the wild.
Qld Reptile and Fauna Park	Good husbandry and happy, healthy kangaroos and wallabies. Currently building a walk-through exhibit with feeding by visitors, acquiring several new species and getting some males on breeding loans from another zoo. Also hoping to develop an off-display area for research and captive breeding of an endangered species for re-release into the wild.

Wildlife Park/Zoo	Response
South Bank Parklands	Large, well-planted (grass, shrubs) enclosures. Minimal disturbance, but regular familiarisation procedures. For example, put feed out at the same time each day and, where possible, handle or touch animals, perform pouch checks, etc. Pademelons require dense cover to retreat to and shady areas. Young pademelons can get through standard 2" chain wore fences. Hessian clipped up around perimeter fence when new stock arrive to reduce injuries. Sedation while moving any macropods is almost mandatory.
Territory Wildlife Park	Adhere to a manageable stocking level with regards to animal husbandry and exhibit presentation (try to keep the exhibits as natural as possible without them looking totally degraded). Type of feed is important; need to maintain a high nutritional level to combat the stress of humidity and parasitism during the wet season. Regular drenching is important to prevent build up of parasites due to inability to rest exhibit areas. Adequate shelter needs to be provided as protection from monsoonal weather and to keep food dry. Hygiene of feed areas i.e. removal of faecal material and cleaning of water troughs is important to reduce parasite levels and infections. Tetanus vaccinations and identification implants for all macropods
Bannamah Wildlife Park	Stocking rates. Managing the ratio of males to females. Well balanced diet. Enclosures should contain areas of retreat for macropods.
Caversham Wildlife Park and Zoo	Mostly stocking and feeding. Wallabies need vitamins and not over-feeding.

Wildlife Park/Zoo	**Response**
Greenough Wildlife & Bird Park	Minimising stress experienced by exhibited animals. Animals are removed if they don't mix with existing groups. Also, macropods must be able to cope with visitor interactions. These types of interactions are managed so that animals are not forced to directly interact with visitors. Males are desexed to control breeding and reduce aggressive interactions. Provision of a variety of types of feed without overfeeding.
Cleland Wildlife Park	Accurate population counts for managing stocking rates. Good pasture. Shelter from the elements, especially for *M. rufus* in the cold, wet weather. Staff experience.
Dundee's Wildlife Park	Female to male ratios, providing micro-habitats within the enclosure and the type and amount of feed. Also, settling animals into a new environment was a key concern.
Urimbirra Wildlife Park	The behaviour of macropodoids towards people in walk-through exhibits. Striking a balance in stocking rates between high enough levels to satisfy visitor expectation and low enough numbers to minimise environmental damage. The provision of appropriate feed types. Bread is banned, but browsing on enclosure vegetation is encouraged through management practices. Adequate roughage must be available.