

Evidence-based practice

Behaviour and enclosure use of captive parma wallabies (*Macropus parma*): an assessment of compatibility within a mixed-species exhibit

Jessica Rendle^{1,2}, Samantha J. Ward³, Wanda McCormick^{1,4}

¹Moulton College, Animal Welfare and Management, Moulton, Northamptonshire, UK

²Current Address: College of Veterinary Medicine, Murdoch University, Western Australia

³Animal, Rural and Environmental Sciences, Nottingham Trent University, Nottingham, UK

⁴Current Address: Anglia Ruskin University, Cambridge, UK

Correspondance: Jessica Rendle; J.Rendle@murdoch.edu.au; +61 (0) 8 9360 6718

Keywords: animal welfare, behaviour, enclosure use, mixed species exhibits, parma wallaby.

Article history:

Received: 25 Jul 2016

Accepted: 14 Mar 2018

Published online: 30 April 2018

Abstract

Many zoos choose to house parma wallabies (*Macropus parma*) in mixed-species exhibits and a successful combination of species can provide a source of enrichment. However, there are potential health and welfare concerns, so it is important to consider species compatibility. This study investigates the effects of mixed-species housing on the parma wallaby. Parma wallabies at Dudley Zoological Gardens were observed for nine days in two different housing systems: mixed species (MS), with Patagonian mara (*Dolichotis patagonum*), and single species (SS). Scan sampling of all individuals, across a range of behaviours, was carried out for 90 minutes across the day. Differences in foraging behaviour were observed, with wallabies housed in the MS exhibit foraging significantly less than the SS group (W27=899.0, P<0.01). Wallabies in the MS enclosure performed a novel behaviour, agonistic directional urination that was not observed in the SS group. Enclosure use was analysed using a Spread of Participation Index (SPI); values revealed MS wallabies utilised less of their enclosure, with a notable preference for areas not frequented by the mara (W27=899.0, P<0.05). The results suggest that the MS wallabies are affected by the presence of the mara, both behaviourally and in enclosure use, which could be indicative of a negative welfare state. This study provides evidence of species incompatibility, a potential issue for the welfare of captive parma wallabies and the successful maintenance of this species in captivity. Careful and continual monitoring of species within mixed-species enclosures is recommended.

Introduction

It is important to determine the correct environment in which to house macropods in captivity. The specific requirements for each species will differ, but in general should reflect those of their counterparts in the wild, whilst being enriching (Hosey et al. 2009). Enrichment can come in many forms, including physical, sensory, social and cognitive (Hosey et al. 2009), and the mixing of species within an exhibit is believed to provide a more dynamic environment for its inhabitants (Buchanan-Smith 2012). Mixed-species exhibits can also be advantageous to the zoo by creating a more efficient use of enclosure space (Dalton and Buchanan-Smith 2005).

Mixed-species exhibits have become standard practice amongst zoos worldwide with a range of taxa being successfully managed in this way (Dorman and Bourne 2010). However, as these exhibits become more popular (Clark and Melfi 2012), there is an increasing need to draw on information of interspecific interactions to assess compatibility, and ultimately the welfare, of species being kept in this type of enclosure.

This study aimed to investigate the effects of a mixed-species enclosure type on the behaviour of a population of captive parma wallabies, at a UK zoo, when housed together with the Patagonian mara (*Dolichotis patagonum*).

Table 1. Parma wallaby behavioural ethogram.

Behavioural category	Description
Looking	Head raised, on two feet, eyes fixed
Foraging	Head down actively ingesting food or investigating, or head raised and ingesting food directly from plant source
Self-grooming	Scratching or manipulating of fur with paws or orally
Aggression	All aggressive behaviour, inter- & intraspecific (lunging, chasing, 'boxing' with front paws) where one animal is displaced
Affiliative social behaviour	Allogrooming, nose-to-nose greeting and sniffing of any part of the body where an animal is not displaced
Locomotion	Hopping and pentapedal (walking on four limbs and tail)
Lying down	With side of body in contact with the ground, with back legs to the side
Head quiver	Shaking/vibration of the head (Coulson 1989), slight quick horizontal movements of the snout (Ganslober 1995)
Out of sight	Animal out of view, obscured by vegetation/ enclosure furniture/design or in the house

Developed from Coulson (1989); Blumstein et al. (1999); Ord et al. (1999) and personal observation.

Methods

Subjects, housing and husbandry

Two groups of parma wallabies were observed at Dudley Zoological Gardens in May 2013. The wallabies had been separated into two distinct groups for management purposes some months earlier. One group of sexually mature wallabies (3♂ 0♀ 0UNK) were housed within a mixed-species exhibit (MS) along with Patagonian mara (1♂ 2♀ 0UNK). The single species group (SS) comprised wallabies of potentially mixed sexes (0♂ 4♀ 3UNK) and ages. No changes were made to standard husbandry routines whilst the study took place.

This study was given ethical clearance by Dudley Zoological Gardens and Moulton College Ethics Committee. This manuscript was produced in accordance with the ARRIVE Guidelines where applicable.

Behavioural observations

An ethogram, developed from the literature (Coulson 1989; Blumstein et al. 1999; Ord et al. 1999) and personal observation, was used to catalogue various behaviours previously observed in this species (Table 1). In addition to these categories, subjects could also be scored as 'out of sight'. Instantaneous group scan sampling at 30 second intervals was used to record behaviour, during three 30-minute observation sessions (morning, midday and afternoon) at alternate enclosures (SS and MS), for nine days, resulting in a total of 27 observation sessions. Animals were fed at approximately 1700 daily so this time period was omitted from observation to avoid the effects of anticipatory behaviours (Boulos and Legothetis 1990; Waite and Buchanan-Smith 2001).

Enclosure use

To explore enclosure use, instantaneous scan sampling was conducted at 60 second intervals during the same 30-minute period used to record behaviour. Wallaby and mara locations within the enclosure were recorded on a map, previously plotted with 'furniture' (e.g. trees, housing) and divided into zones (Figure 1). Zones in both MS and SS enclosures were demarcated as similarly as possible, using aspects common to both enclosures, e.g. the house. However, due to the uneven landscape within the MS enclosure, zones were also defined by natural features in the enclosure that obstructed viewing of the wallabies. Figure 1 and Table 2 outline the differences between the SS and MS enclosures. Zone 1 (the house), in both the MS and SS enclosures, was of similar structure and function, enabling analysis of wallaby use to be compared between enclosure types.

Behavioural analysis

To account for the difference in group size, the number of observations recorded per behavioural category was divided by the number of individuals in the group. This was undertaken per observation session (morning, midday and afternoon), and in addition, data from the three sessions were pooled to provide data for the entire study period. Statistical analysis was performed using SPSS Version 24 and a Mann-Whitney U test was performed for each behavioural category, per enclosure type. Numerous tests

Table 2. Zone geography for each zone for both the single-species (SS) and mixed-species (MS) exhibits.

Zone	MS geographical features	% MS enclosure	SS geographical features	% SS enclosure
1	Enclosed wooden 'house'.	3.3	Enclosed concrete 'house'. Zone 1 includes gravelled area, adjacent to the house.	23.0
2	Highest peak in enclosure, predominantly flat, with few bushes.	15.2	Small, open-sided shelter, located within Zone 3.	0.5
3	Small, heavily vegetated area, significant shrub coverage, steeply sloped.	3.0	Grass-covered paddock, single, established tree.	17.5
4	Sloped area with large clusters of vegetation, number of large trees.	17.9	Grass-covered continuation of Zone 3 and closest to the visitor barriers.	19.0
5	Large mound surrounded by dips and troughs of earth, very little vegetation.	9.8	Grass-covered continuation of Zone 4, next to the visitor barrier, single established tree.	21.0
6	Little vegetation and steep mounds.	7.1	Grass-covered continuation of Zone 5.	19.0
7	Even vegetation, two mara burrows, small pool (approx. 1.5m ²), steep mounds. Area out of sight from observers.	43.7	N/A	

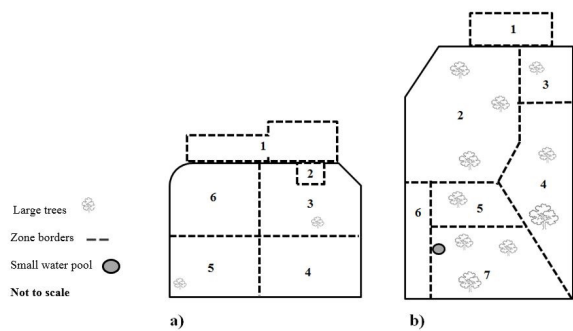


Figure 1. Maps of the a) single-species and b) mixed-species enclosures depicting the division of the zones used for calculating the SPI values. There were 19 trees of varying size in the MS enclosure, however only the largest ones have been included in this map for clarity. Not to scale.

were possible on this set of data; therefore, a Bonferoni correction was applied. A measure of significance was taken at $P < 0.05$.

Enclosure use analysis

To determine the wallabies' enclosure use, two separate analyses were performed, one for zone use and one for use of available space. Statistical analysis was carried out using MINITAB 13.2. The Friedman test was used to investigate differences between the time of day and zone; the Mann-Whitney U test was used to investigate differences between mara and wallaby zone use. Finally, to determine wallaby and mara use of available space, a modified

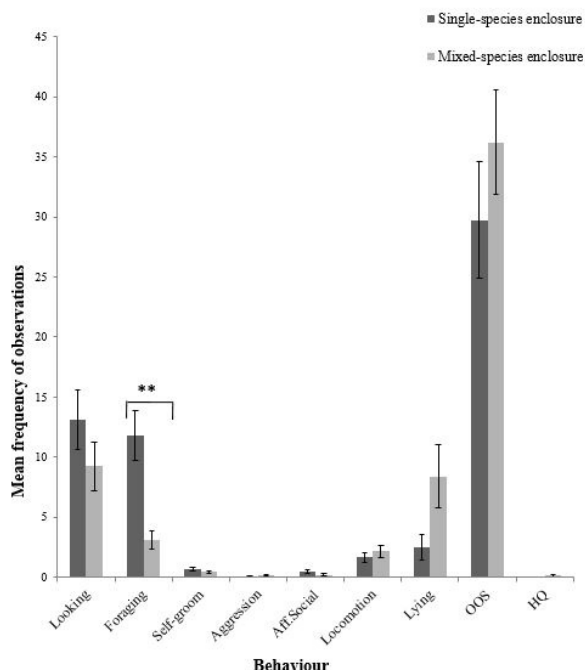


Figure 2. Mean frequencies of behaviour observed, per individual, for total study period for parma wallabies housed in single-species and mixed-species enclosures. HQ=head quiver, Aff. Social=affiliative social behaviour, OOS=out of sight. Error bars represent $\pm SE$ (**= $P < 0.01$).

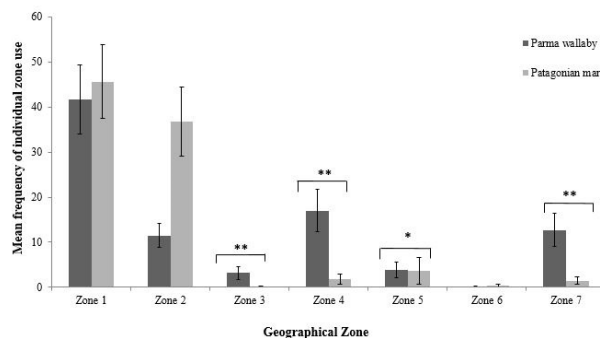


Figure 3. Mean frequency of individual zone use for the parma wallaby and Patagonian mara (in the mixed-species enclosure) for the total study period. Error bars represent $\pm SE$ (*= $P < 0.05$, **= $P < 0.01$).

Spread of Participation Index (SPI) was calculated, allowing for the inclusion of unequal zones (Plowman 2003). Further assessment of the SPI values was undertaken by performing a Mann-Whitney U test.

Results

Behaviour

The SS wallabies spent significantly more time foraging compared to wallabies in the MS group ($W_{27}=899.0$, $P < 0.01$) (Figure 2). There was no significant difference ($P > 0.05$) between the two enclosures for 'looking', 'locomotive', 'self-grooming', 'aggressive' and 'social affiliative' behaviours.

The time of day had no significant effect on the mean frequency of observed behaviours ($P > 0.05$). The least observed behaviour was the 'head quiver'; however, due to insufficient data, analysis on this behavioural category could not be performed. The head quiver was only observed in the MS wallabies throughout the entire study.

Enclosure use

Mixed-species zone use

A number of significant differences were identified in specific zone use between the two species sharing the MS enclosure (Figure 3). The wallabies used Zone 3 (heavily vegetated) ($W_{27}=854$, $P < 0.01$), Zone 4 (some vegetation) ($W_{27}=895.5$, $P < 0.01$) and Zone 7 (out of observer's sight) ($W_{27}=881$, $P < 0.01$), significantly more than the mara. A significant difference was also identified between wallaby and mara use of Zone 5 (mounds) ($W_{27}=838$, $P < 0.05$). Zone 1 (the house) received the highest individual mean frequency of use, with both species using it almost equally. Mara use of Zone 2 (raised with little vegetation) almost equalled that of Zone 1 (36.81 ± 8.09); a clear difference in mean frequency compared to wallaby use (11.52 ± 2.58), yet not statistically significant.

Time of day significantly affected wallaby zone use ($S_3=14.98$, $P=0.02$). Zone 1 was used most during the midday period, and Zone 6 only during the morning. Zone 4 (sloped, vegetated) was similarly used throughout the day.

During the morning period, the wallabies spent significantly more time in the vegetated Zone 3 ($W_9=115$, $P < 0.01$) and out of sight in Zone 7 ($W_9=118.5$, $P < 0.01$) than the mara. During the afternoon period, the wallabies were observed significantly more in the sloped Zone 4 than were the mara ($W_9=108$, $P < 0.05$).

Single-species zone use

The wallabies did not use different zones of the single species enclosure significantly differently at different times of day ($S_3=8.33$, $P>0.05$). There was no significant difference between the use of Zone 1 by the two groups of wallabies ($P>0.05$).

SPI results

The wallabies use more of the enclosure (SPI=0.46) than do the mara (SPI=0.74) in the mixed-species exhibit. A significant difference in SPI values (enclosure use) was identified ($W_{27}=615$, $P=0.03$). Use for both species was at its greatest during the morning sessions (wallaby SPI 0.29, mara SPI 0.65). A significant difference was found in SPI values (enclosure use) between the MS wallabies and mara during the morning session ($W_9=62.5$, $P=0.05$). SPI values for the three different observation periods of the day indicate that the SS wallabies use their enclosure significantly more during the morning (SPI=0.23) than at any other time of day (midday SPI=0.49, $W_9=47$, $P=0.0007$; afternoon SPI=0.27, $W_9=61.5$, $P=0.03$). The SPI values for both groups of wallabies identified that enclosure use is highest during the morning (SS SPI=0.23; MS SPI=0.29) and lowest at midday (SS SPI=0.49; MS SPI=0.63). Wallabies housed in the single-species enclosure used more of their enclosure than those housed in the mixed-species enclosure, during every period of the day; although no significant difference between SPI values was found ($P<0.05$). SPI values for the total study period were pooled, resulting in a value of 0.33 for SS wallabies and 0.46 for MS wallabies; there was no significant difference between the SPI values for the two groups of wallabies ($P<0.05$).

Discussion

Behaviour

The pattern of active behaviours observed by the wallabies generally supports previous findings, with most of their time spent foraging (Maynes 1977; Ord et al. 1999). Primarily a grazing animal (Maynes 1977; Read and Fox 1991), parma wallabies will also feed on tougher, more fibrous, dicotyledonous plants (Vujcich 1979), much like those found in abundance in the MS enclosure. Studies have shown that the more fibrous the food, the less time they spend foraging, in part caused by the need to invest more time in mastication (Lentle et al. 2004), an effect which was reflected here. In addition, the SS wallabies, although in a smaller enclosure, had a greater availability of grass and spent more time 'foraging'. These results support the findings of Lentle et al. (2004) that wallabies spend more time feeding when eating grass than when their food source comprises other, more fibrous, plants. Therefore, the reduction in foraging behaviour may be associated with a lack of preferred grazing material. The SS wallabies had restricted access to the house during the day, but retained access to the grassy paddock. This action may have resulted in a change of behaviour of the SS group, but may also explain the significantly greater foraging behaviour observed in the SS group.

Foraging behaviour differs between genders, with male wallabies spending substantially more time feeding (Ord et al. 1999). This is contrary to the current study's results, which demonstrate that the males in the MS group forage far less than the predominantly female SS group. Yet, as group size increases, so too does time allocated to foraging (Blumstein et al. 1999), and the SS group ($n=7$) was more than twice the size of the MS group ($n=3$). However, this could also be dependent on other factors, such as the age of individuals within each group (Fisher and Goldizen 2001), enclosure design and availability of foraging material. In addition, the SS group comprised adult females and joeys, therefore the increase in foraging behaviour could be the result of the doe's additional nutrient requirements if lactating

(Hume 1999). As group size increases, so too does the chance of feeding competition (Watts 1985), which could have contributed to the observed difference in foraging behaviour; however, this factor is not substantiated.

The results for 'aggressive' or agonistic encounters, although statistically not significant, were greater in the all-male MS wallabies than in the SS group. Yet, in mixed-species exhibits, aggressive encounters can be both intra- and interspecific. Interspecific encounters have been rarely documented in macropods (Gansloßer 1995); however, during this study wallaby aggression was directed at the mara on three occasions. One incident, apparently initiated by a wallaby, opened with a head quiver, seemingly directed at the mara, promptly followed by the displacement and pursuit of the mara. It could be argued that the head quiver, in this specific case, was a deimatic behaviour. This hypothesis is supported by previous suggestions that the head quiver is a form of conflict (Herter et al. 1985). However, it has also been noted as an indication of stress (Gansloßer 1995). It is also interesting to note that throughout the study period, the head quiver was only observed in the all-male MS enclosure. Understanding the rationale behind the head quiver requires further investigation.

There were also male-specific 'aggressive' behaviours. The spraying of urine is commonly described as agonistic behaviour in other macropod species (e.g. red kangaroo *Macropus rufus*) (Russell 1985). This behaviour has not previously been reported in the parma wallaby; however, the spraying of urine by an MS wallaby was observed during this study, directed at a mara. The behaviour occurred on displacement of the wallaby, thus suggesting that this behaviour was performed agonistically. However, the body position of the wallaby when directing urine differed from the upright position commonly used by larger macropods: the wallaby was leaning forwards and the spray was directed backwards, occurring on displacement. Arguably, therefore, this behaviour may be indicative of fear; further research is required to investigate and assess the implications of this alternative explanation.

Enclosure use

The MS enclosure zones varied in size, furniture and use. Zone 1 (the house) was the most frequented of all zones within the MS enclosure. There were some significant differences in overall use of specific zones, the most marked being in the overall use of Zones 3, 4 and 7. In particular, Zones 3 and 4 were densely covered with vegetation and had the highest concentration of trees and shrubs, emulating the natural habitat of parma wallabies (Read and Fox 1991). These areas also provided an abundance of foraging opportunities, albeit of the less-preferred forage for the species (grass) (Lentle et al. 2004); a factor that could offer a possible explanation for increased use of these zones. The MS wallabies foraged significantly less than their SS counterparts, indicating these zones may have been chosen for another reason other than to forage, for example, because of displacement. There was also a significant difference in use of Zone 7. The mara very rarely used this zone and it is unclear what resource the wallabies may have been seeking; it is possible the zone was used because it was an area not frequented by the mara.

For a prey species like the parma wallaby (Miller 2001), Zones 2 and 5 may be geographically more preferable due to their raised, flattened positions and the lack of vegetation thus increasing visibility. Equally, mara also have a preference for such open spaces (Baldi 2007) and they may have dominated the wallabies for access of this area as they used Zone 5 significantly more and there was a visible (but non-significant) difference in mean frequency of use for Zone 2. The mara may use scent marking as a possible tactic to discourage the wallabies from the preferred zones (Taber and

Macdonald 1992), a behaviour commonly performed by rodents (Hurst 2005). Macropods are aversive to particular scents, and avoidance will take precedence over other behaviours, such as foraging (Lentle et al. 2003; Parsons and Blumstein 2010). The possible displacement of the wallabies from particular areas of the enclosure strengthens concerns regarding the compatibility of the parma wallabies and the Patagonian mara.

Enclosure use may be altered as a response to human visitors (Birke 2002; Choo et al. 2011; Downes 2012). Although visitor-effects were not considered in the study, the SPI and zone-use results highlight that the wallabies used the side of the enclosure with the least human traffic, on the busiest days, indicating a possible visitor-effect on enclosure use. This hypothesis is further supported by increased 'locomotive' behaviours and evidence of disturbance (Parsons and Blumstein 2010) and has also been observed in other species (e.g. gorillas, Wells 2005). The weather may also have influenced the wallabies' use of their enclosure. On the wettest days, the wallabies in both enclosure types remained largely in, or within close proximity to, Zone 1 (house).

The increase in enclosure use in the SS wallabies could also be explained due to the presence of joeys (Jarman 1991; Fisher and Goldizen 2001). Females are less likely to spend time in open clearings to avoid predation (Fisher and Goldizen 2001); with three joeys present in the SS group, such a strategy is possible, potentially explaining why Zone 6, nearest the house (Zone 1), was so important. Due to the greater population of wallabies, coupled with the smaller size and grassy nature the SS enclosure, there may be depletion in grazing material necessitating migration around the enclosure to improve grazing potential. It therefore could be suggested that a smaller enclosure is more highly used. In contrast, Clubb and Mason (2003) suggest that restricted space may be a causal factor in the development of stereotypic behaviours. However, if there is enough space to enable the animals to perform their natural behaviours and the social grouping is sufficient, then it is possible that having a larger exhibit with 'extra' space is not necessary.

Finally, evidence of interspecific aggression arising from this study should not be ignored; careful and continual monitoring of animals within the mixed-species enclosure is advised.

Conclusion

An animal's behaviour and enclosure use is the result of a combination of factors. The size of the enclosure is not necessarily the most important factor, it is rather how the animal uses it. Natural behaviours and anticipated enclosure use can be encouraged through the provision of environmental enrichment, such as mixing of species; however, if this enrichment is in the form of a mixed-species exhibit, species must be compatible. The subtle differences in enclosure use and behaviour observed in this study have contributed to identifying a possible incompatibility between Patagonian mara and parma wallabies and warrants further investigation. The significantly reduced foraging behaviour by wallabies in the mixed-species enclosure, coupled with the reluctance to use those areas of the enclosure most frequented by the mara, could be cause for concern. Appreciation of the subtle signs of incongruity such as differences in behaviour and use of available space within the enclosure, cannot be underestimated and should be acted upon accordingly. Careful and continual monitoring of animals within the mixed-species enclosure is advised. Effects of such actions are influential to species conservation and to animal welfare.

Acknowledgements

The authors would like to thank Dr David Beeston and staff at Dudley Zoological Gardens, for their help and assistance

throughout the study. The Moulton College Ethics Committee, the academic team at Moulton College who provided approval and support for the study. We would also like to thank New South Wales Department of Environment and Heritage, especially Shane Ruming, for exceptional guidance.

References

- Baldi R. (2007) Breeding success of the endemic mara *Dolichotis patagonum* in relation to habitat selection: Conservation implications. *Journal of Arid Environments* 68: 9–19.
- Birke L. (2002) Effects of browse, human visitors and noise on the behaviour of captive orang-utans. *Animal Welfare* 11: 189–202.
- Blumstein D.T., Evans C.S., Daniel J.C. (1999) An experimental study on behavioural group size effects in tammar wallabies, *Macropus eugenii*. *Animal Behaviour* 58: 351–360.
- Boulos Z., Logothetis D.E. (1990) Rats anticipate and discriminate between two daily feeding times. *Physiology & Behaviour* 48: 523–529.
- Buchanan-Smith H.M. (2012) Mixed-species exhibition of Neotropical primates: analysis of species combination success. *International Zoo Yearbook* 46: 150–163.
- Choo Y., Todd A., Li D. (2011) Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behaviour Science* 133(1): 78–86.
- Clark F.E., Melfi V.A. (2012) Environmental enrichment for a mixed-species nocturnal mammal exhibit. *Zoo Biology* 31(4): 397–413.
- Clubb R., Mason G.J. (2004) Pacing polar bears and stoical sheep: testing ecological and evolutionary hypotheses about animal welfare. *Animal Welfare* 13: 33–40.
- Coulson G. (1989) Repertoires of social behaviour in the Macropodidae. In: Grigg G., Jarman P., Hume I. (eds). *Kangaroos, Wallabies and Rat-Kangaroos*. Chipping Norton: Surrey Beatty and Sons Pty. Ltd. p. 457–473.
- Dalton R., Buchanan-Smith H.M. (2005) A mixed-species exhibit of Goeldi's monkeys and pygmy marmosets (*Callimico goeldi* and *Cebuella pygmaea*) at Edinburgh Zoo. *International Zoo Yearbook* 39: 176–184.
- Dorman N., Bourne D.C. (2010) Canids and ursids in mixed-species exhibits. *International Zoo Yearbook* 44: 75–86.
- Downes K. (2012) Is there a visitor effect on behaviour and enclosure use of mixed bird species in a zoo enclosure? *The Plymouth Student Scientist* 5(1): 38–60.
- Fisher D.O., Goldizen A.W. (2001) Maternal care and infant behaviour of the bridled nailtail wallaby (*Onychogalea fraenata*). *Journal of Zoology* (London) 255: 321–330.
- 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.
- Herter U., Schneider I., Gansloßer U. (1985) Some remarks on the behavioural repertoire of the parma wallaby, *Macropus parma* Waterhouse. *Zoologischer Anzeiger - A Journal of Comparative Zoology*. 215(5/6): 287–297.
- Hosey G., Melfi V., Pankhurst S. (2009) *Zoo Animals: Behaviour, Management and Welfare*. Oxford: Oxford University Press.
- Hurst J.L. (2005) Scent marking and social communication. In: McGregor P.K. (ed.) *Animal Communication Networks*. Cambridge: Cambridge University Press. p. 219–243.
- Hume I.D. (1999) *Marsupial Nutrition*. Cambridge: Cambridge University Press.
- Jarman P.J. (1991) Social Behaviour and Organisation in the Macropodoidea. *Advances in the Study of Behaviour* 20: 1–50.
- Lentle R.G., Haslett S., Hume I.D., Stafford K.J., Kennedy M., Springett B.P. (2003) Foraging behaviour in tammar (*Macropus eugenii*) and parma (*Macropus parma*) wallabies. *Australian Journal of Zoology* 51: 297–305.
- Lentle R.G., Hume I.D., Stafford K.J., Kennedy M., Springett B.P., Browne R., Haslett S. (2004) Temporal aspects of feeding events in tammar (*Macropus eugenii*) and parma (*Macropus parma*) wallabies. Food acquisition and oral processing. *Australian Journal of Zoology* 52: 81–95.
- Maynes G.M. (1977) Distribution and aspects of the biology of the parma wallaby, *Macropus parma*, in New South Wales. *Australian Wildlife Research* 4(2): 109–125.
- Miller A. (2001) *Parma wallaby (Macropus parma): resource manual*. Rhode Island, USA: Roger Williams Park Zoo.
- Ord T.J., Evans C.S., Cooper D.W. (1999) Nocturnal behaviour of the parma wallaby, *Macropus parma* (Marsupialia: Macropodidae). *Australian*

- Journal of Zoology* 47: 155–167.
- Parsons M.H., Blumstein D.T. (2010) Familiarity breeds contempt: Kangaroos persistently avoid areas with experimentally deployed dingo scents. *PLoS ONE* 5(5): 1-7 <https://doi.org/10.1371/journal.pone.0010403>.
- Plowman A.B. (2003) A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science* 83: 331–336.
- Read D.G., Fox B.J. (1991) Assessing the habitat of the parma wallaby, *Macropus parma* (Masupialia: Macropodidae). *Wildlife Research* 18(4): 469–477.
- Taber A.W., MacDonald D.W. (1992) Spatial organisation and monogamy in the mara *Dolichotis patagonum*. *Journal of Zoology* 227: 417–438.
- Vujcich V. (1979) *Feeding ecology of the parma, Macropus parma Waterhouse, and tammar Macropus eugenii Desmarest, wallabies on Kawau Island*. [MSc Thesis]. Auckland: University of Auckland.
- Waite C., Buchanan-Smith H.M. (2001) What time is feeding? How delays and anticipation of feeding affect stump-tailed macaque behaviour. *Applied Animal Behaviour Science* 75: 75–85.
- Watts D.P. (1985) Relations between group size and composition and feeding competition in mountain gorilla groups. *Animal Behaviour* 33(1): 72–85.
- Wells D.L. (2005) A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science* 93: 13–17.