THE IMPORTANCE OF AGE/SEX CLASS RELATIONSHIPS FOR CAPTIVE-BREEDING – A REVIEW OF MACROPODOIDEA (KANGAROOS, WALLABIES AND RAT-KANGAROOS) AS A CASE STUDY

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In this paper social relationships (as defined by Hinde) between age/sex classes of kangaroos, wallabies and rat-kangaroos are reviewed and characterized by frequencies, direction and, where possible, intensity of behavioural interactions, by their patterning in sequences and by distance regulation. Male social organization in the wild for larger non-solitary species is organized in an age/size-related hierarchy. Frequent interactions among equal-sized males stabilize this hierarchy and large males by their simple presence deter younger ones from courting.

Depending on social organization in the wild, the presence of one or more males, sometimes males from different age classes, is desirable from the animal welfare standpoint.

The structure of breeding groups can be greatly improved in terms of welfare and breeding optimization, when a diversity of social relationships are as close to natural conditions as possible.

Keywords: aggression, animal welfare, courtship, ethology, Macropodidae, mating system, Potoroidae, social behaviour, social organization.

Introduction

The superfamily Macropodoidea (macropodoids) is made up of two families: Macropodidae (macropodids) consisting of kangaroos and wallabies; and Potoroidae (potoroids), the rat kangaroos. Species of this superfamily, particularly the larger wallabies and kangaroos, are among the 'typical' animals that visitors expect to find even in zoological gardens of modest size.

Several species, for example the Tammar wallaby *Macropus eugenii*, are also important laboratory animals for reproductive physiology and genetics. Accordingly recommendations for husbandry and captive breeding can easily be found (see Collins 1973; several authors in Evans 1982; Green 1986; Williams 1990).

Most of these husbandry papers recommend keeping only one adult male with the females and removing male offspring after weaning. The reasons given for these suggestions are 1) that males might be more aggressive towards each other in the presence of females and 2) that females might be more stressed, particularly in oestrus, when courted by several males.

These general recommendations, however, do not recognize obvious differences in mating systems and social organization. The social systems of macropodoids have recently been reviewed, from different angles, by Croft (1989), Jarman (1991), Jarman and Coulson (1989)

and Gansloßer (1989; 1993a; in press). About sixty living species ranging in size from 1kg to 90kg inhabit nearly all terrestrial habitats in the Australian faunal region – from rainforest to arid zones. The small species living in more or less closed habitats are often solitary, whereas larger species in open grasslands tend to form larger, but loose aggregations. When comparing mating systems and social organization, basically three mating types occur depending on spatial distribution and predictability of females (see Gansloßer in press; Gansloßer & Jarman 1984). Category A are small nocturnal species from closed habitats where males and females both inhabit individual home ranges. Due to the animals' small size and the dense vegetation, chances for male/male encounters are rare, both courtship and aggressive patterns are direct, and rather unritualized. Males are really solitary in this category and often behave very aggressively towards each other in the presence of females (even though bachelor groups can be kept away from the breeding colony (own unpublished observation)).

The remaining species with other mating systems are characterized by males forming a size-related linear hierarchy – as size is related to age, the largest male is also normally the oldest (Jarman 1983) – and access to oestrus females is restricted to the largest male present. There is, however, an important difference between the two remaining categories. Category B are species where the presence of females is predictable due to some important resource, for example rock caves for rock-wallabies (*Petrogale sp*), open pasture next to forest edge for pademelons (*Thylogale sp*). The top-ranking males tend to monopolize these 'female-rich' areas by keeping lower-ranking males away towards the periphery. In category C due to the unpredictable ranging behaviour of females, males are 'roving males' (Clutton-Brock 1989). Only females approaching oestrus are defended by the highest-ranking male present who forms a consort relationship with her.

Keeping females of these species with only one male therefore seems unsatisfactory. The ability of animals to develop social relationships that come as near to their natural situation as possible, both in quantity and in complexity is certainly desirable. Females that are provided with possibilities of mate choice, and males that are able to develop relationships with conspecifics of different age classes, certainly are living in a more enriched environment. The value of social relationships for individuals has been discussed, for example, by Kummer (1978) with regard to social dynamics and individual strategies, and by Mason (1976; 1978; 1986) with regard to the ontogenetic course of socialization processes. These and many other publications demonstrate that social relationships form an important part of a mammal's environment. Depriving an animal of this part of its environment should be carefully considered from the animal welfare point of view. In his critical evaluation of 'behavioural enrichment' of Zoo exhibits, Robinson (1993) explicitly states that 'by minimizing aggression, fighting and unpredictability . . . may unwittingly be doing our animals a disservice' and 'by ignoring behavioural appetites for aggression, competition and rivalry which could mean that some animals are deprived of major consummatory behaviours in zoo conditions'. The example of a male red kangaroo fighting an emu (see below) clearly points in that direction. Resources for female macropodoids are not only food but often other habitat structures, for example shelters. Competition among males, as explained, is dependent on what type of organization the species forms. At least for category C there should be well-developed mechanisms for solving these daily conflicts without too much energy expenditure and risk. Correlations between behavioural repertoire, social interactions and social systems

have been discussed, for example, by Coulson (1989) and Gansloßer (1989; 1993a; in press).

The following paper intends to present data both published and unpublished, to address the following assumptions:

- Age/sex class relationships in macropodoids, as expressed by frequencies, patterning and direction of interactions, differ in relation to the species-typical social system.

- Male/male relationships, both within and between age classes, are stable in those species that have a non-solitary social system, and thus there is no need to separate all surplus males from breeding groups.

- Male/female relationships in sexually dimorphic species vary in quality in relation to the degree of sexual dimorphism. In highly dimorphic species, the female's mate choice is an important part of female/male relationships. Females should not be deprived of it.

- In many non-solitary species, several males in one group can even reduce tensions and lead to a more stable structure.

Some remarks on data and sources

The following review includes published material, dissertations and theses as well as unpublished data from ongoing research at my study group. Both captive and free-ranging conditions are covered.

Whenever possible, data from behavioural interactions and relationships in general were compared for captive and free-ranging animals. These comparisons never revealed any obvious differences in types or distributions of interactions. Compare, for example, data on *M. rufus* by Croft (1981a) to Gansloßer & Wilhelm (1986), Wilhelm & Gansloßer (1989): the descriptions of behavioural elements and the context in which they occur are very similar. Relationships between age/sex-classes are also characterized by the same differences in frequencies: a comparison of data on *M. rufus* as well as on *M. rufogriseus* (Johnson 1985; Jones 1987) shows the rates of interactions in captivity are higher, but relations between rates (eg frequency of large male vs medium male fights) are comparable. Comparisons by other authors on other species (eg S C Barker personal communication 1983; P M Johnson personal communication 1983 on *P. assimilis*; Coulson 1989) showed similar consistencies between the data sets. Therefore, data from captive and free-ranging animals have not been discussed separately.

Elements that are performed only by one age or sex class are regarded as specific for this class, or specific for a particular relationship if they are directed only from one class of actors towards one class of recipients. Elements that are performed by one class of actors more often than expected from random are termed typical for this class, or typical for the relationship between two classes if they are performed from one class of actors towards one class of recipients more often than expected.

Typical elements of age/sex class relationships

Agonistic elements are either heavily aggressive with a serious risk of injury, or only mildly so (perhaps threatening), or highly ritualized, predictable and part of a so-called 'sparring-fight' among equally sized animals. Data for this distinction and for the distribution among age-sex classes are given in Gansloßer (1989). Unritualized, potentially dangerous elements

are: Attack from lateral (AL) or behind (AH), Biting (B), Chasing (C) because it can lead to AH, Kicking (K), and Throwing down (TD) if it is followed by B or K. Even these are not immediately dangerous when part of a rather fixed behavioural sequence, which the opponent can counter in kind, such as C, K or TD.

Table 1 **Abbreviations and definitions of elements cited in the text (see Gansloßer 1989).**

A	Attacking: one animal jumps upon another one
AF	Frontal attack
AL	Lateral attack
AH	Attack from behind
B	Biting
BX	Boxing: a prolonged fight, mostly consisting of rapid, rigid sequences of wrestling, pushing and kicking
C	Chasing: rapid, bipedal hops
F	Fleeing: rapidly moving away, normally in bipedal hopping gait
K	Kicking with hindlegs
KLi	Kicking while lying on one's side
TD	Throwing down: causing another animal to lose balance by making it tumble, or throwing it over in a wrestling bout
WR	Wrestling: two animals standing upright, trying to make each other fall by vigorously pushing and pressing with their forelimbs

AL, AH and B are radically missing in the larger species of wallabies and kangaroos, and are typical (out of 18 species of macropodoids) for male relationships only in: *Dorcopsis luctuosa* (Gansloßer & Schappert in press); tree kangaroos, mostly *Dendrolagus inustus*, *Den. goodfellowi* (Gansloßer 1979); *Thylogale* sp (Clancy 1983); *Petrogale* sp (Bleistein *et al* 1994); and to some extent *M. rufogriseus* (eg Johnson 1989; Murböck 1977); as well as the more primitive species of potoroids (Johnson 1980). Studies of free-ranging (Croft 1981a, b; Southwell 1981) as well as captive (Gansloßer & Wilhelm 1986) larger macropodids, also show that medium-sized males (and small and/or subadult males) tend to keep to themselves, with little contact with larger males or females. This further reduces the chance of serious injuries or stress.

In male/female relationships, potentially dangerous elements only occur in potoroids (see below), *Dendrolagus* sp, *D. luctuosa*, *Thylogale* sp, some *Petrogale* sp, and rarely in *M. rufogriseus* or *M. agilis* (Gansloßer 1989).

In relationships involving subadult animals and adult males, the injurious elements are performed less than expected in every species of macropodid for which we calculated the rates (Gansloßer unpublished). In our potoroids (*Bettongia penicillata, Aepyprymnus rufescens*) they only occur around sexual maturity (Gansloßer & Lissowsky unpublished data).

Analysing rates of aggression with respect to age-class differences (Wilhelm & Gansloßer unpublished data) for red kangaroos, shows that most aggressive acts involve subadult, or small males, whereas adult males have only a low frequency of agonistic behaviour towards females. When further separating adult males into medium and large males (see Gansloßer 1989; in press) the occurrence of potentially dangerous aggressive acts, both between males as well as towards females, is almost totally restricted to medium males. Studies on free-ranging species (eg Croft 1981a, b; Southwell 1981; see Gansloßer in press) also mention that large males are courting in a more 'gentle', less aggressive way — and females react more aggressively when courted by medium males. Large males on the other hand interrupt prolonged courtship by medium males, or medium males themselves often restrain from displaying in the presence of large males (Gansloßer in press; Krettinger 1990)

Ethologists have conducted long and lively discussions on whether there is 'appetence for aggression', ie a tendency to fight, that animals find rewarding when it is consummated. Rasa (1981) reviews studies of this problem, and presents data on several species that obviously seek out situations associated with fighting and displaying. She also mentions cases of aggressive actions directed towards other objects when no suitable opponent is present. At least one example for this redirection was observed in a kangaroo study: Wilhelm (1984) observed a group of red kangaroos, consisting of one male, several females and subadults, housed together with a pair of emus in a zoo. The male kangaroo almost daily approached the emu from frontal position, directed displaying elements towards it and started to embrace and kick it, like an opponent male kangaroo. Sparring fights are a regular feature of the social life, particularly among medium males, of free-ranging kangaroos and large wallabies (see Croft 1981a, b; Kaufmann 1974, 1975; Krettinger 1990). As Robinson (1993) claims, depriving them of these opportunities certainly is a severe and, as our data show, unnecessary restriction. Only a few zoos have opportunities to keep bachelor groups of kangaroos in large, attractive enclosures. Surplus males are mostly kept alone in small cages, further depriving them of social contacts. This certainly is an undesirable situation both in terms of welfare and from the management aim of producing socially competent individuals (Gansloßer 1993b).

In the context of sexual behaviour and courtship, the one potentially stressful element is the mating chase (eg Johnson 1985 for *M. rufogriseus*; Kaufmann 1974 for *M. parryi*). The female approaching oestrus suddenly starts a dash, and rapidly hops away from the courting males over a distance of up to several hundred metres, often in a circle or semi-circle back to the starting point (Gansloßer in press). The mating chase is the only part of high intensity courting which is performed by all males present, whereas the other courting patterns are a prerogative of the largest, highest-ranking male currently present. The highest-ranking male is closely behind the female and the other males follow him in reverse order of hierarchy, ie second-ranking behind him, lowest-ranking at the end. As mentioned, the mating chase is initiated by the female's dash not by the males, and it seems to be an important part of female mate choice. It also occurs when only one adult male is present, and there is no evidence of it being longer, more rigorous or more stressful to the female if other males join in (our unpublished observations on several species). More important from a welfare point

than removing surplus males, is that the enclosure is large enough and structured accordingly to facilitate this chase and any obstacles that may cause injury are removed.

Agonistic behaviour between the sexes during courting is normally restricted to hitting and wrestling, however, bites can occur (see Gansloßer 1989). Two facts have to be considered in this context: both in free-ranging and in captive kangaroos and large wallabies, aggression between the sexes depends on the male's age and size (eg Croft 1981a, b; Gansloßer in press; Southwell 1981); females react more aggressively towards younger males than towards larger males, and medium-sized males are more vigorous and more aggressive in courting than large males. Croft (1981b) and Krettinger (1990) have compared courting in free-ranging *M. robustus* between large and medium males. Large males tend to have more stereotyped or otherwise ritualized patterns (ie with less variation), often without direct contact to the female's body, and perform more predictable sequences. Similar observations on differences were made (unpublished) in our studies on captive *T. billardierii, M. parma* and others, with one important modification (Gansloßer 1992): intensity increases during the course of courting when the less ritualized, more rigorous patterns (eg scratching and pulling the female instead of patting her) occur. This again is connected to the particular male's status; females tend to accept older/larger males more easily for copulation, which means that these males often 'do not need' to revert to high-arousal patterns.

On the other hand the less dimorphic species, ie rock-wallabies, small wallabies etc, perform mutual grooming in courtship – the female also grooming the male. For example *D. luctuosa* (Gansloßer & Schappert in press), *P. inornata* (Horsup 1986), *M. parma* (Herter unpublished observations), and *M. robustus* (Osazuwa 1978) which is the only large species with female/male grooming; whereas in large, more dimorphic species only the male is active in grooming. This could be, as Walther (1974) suggests for antelopes, a mechanism to reduce tensions in those species in which sexes are more similar, and more prone to 'misunderstand' each other.

Frequency and intensity of interactions between age/sex classes obviously change in the presence of an oestrus female. In a study of eight male and four female *M. rufogriseus* in Dortmund Zoo, Dörsam (1983) found increases of slightly as well as heavily agonistic patterns between males and an increase in heavily agonistic elements between male and female. The increase in heavily agonistic elements between the sexes is mostly due to an increase in the rate of hitting by the female and embrace/wrestling by the male, which have close connections in sequential analysis to the courting elements of head-pressing, patting etc (see Gansloßer 1992).

Potential indicators of stress

Macropodoids perform several behaviour patterns that are easily identified in connection with stress and/or excitement (Coulson 1989; Gansloßer 1979; Immelmann 1965). Head quivering (slight quick horizontal movements of the snout) occurs in arousal of different origin, for example when exploring novel situations or conspecifics. Tail-lashing is mostly performed by small- to medium-sized species. Salivating and extensive licking of the forearms is seen in high arousal as well as under heat-stress. All these patterns regularly occur during courting. However, when observed for prolonged times without the presence of currently exciting stimuli, they may be indicators of an individual being under permanent, potentially harmful stress.

Comparison between different groups

When reviewing data from groups of different size and composition (Table 2 gives some examples) it is evident that group size, and number of animals per age/sex class, can influence rates of agonistic behaviour within as well as between classes. However, no consistent trend is obvious and in some cases even with more males present, the rates are lowered. In no case did we find dramatic increases with an increasing number of males that would justify removal of some males.

Table 2 **Rates of aggressive behaviour in different group compositions, elements per observation hour.**

Only potential injurious elements (see text above) have been included. Statistical tests could only be performed for *M. rufogriseus* and *M. rufus* and did not reveal significant differences (*M. rufogriseus*: *U* test, *M. rufus*: Wilcoxon-Wilcox). lm = large male; mm = medium male

Species	Source	Enclosure size	Group composition only adults given	Total observation hours	♂♂	♂♀	♀♂	♀♀
Dorcopsis muelleri	Schappert 1985 and unpublished data	~150m²	1♂ 4♀	80h		0.21	0.97	0.22
			2♂ 5♀	22h	0.2	0.13	0.13	0.1
			2♂ 4♀	20h	0.32	0.37	0.28	0.1
			3♂ 4♀	53h	0.15	0.14	0.22	0.3
Macropus parma	unpublished data	~300m²	1♂ 3♀	50h		0.06	0.09	0.08
			2♂ 3♀	20h	0.3	0.07	0.14	0.15
Macropus rufogriseus	Jones 1987	~300m²	4♂ 2♀ (2 lm 2 mm)	250h	0.24	0.3	0.07	0.003
		~125m²	2♂ 2♀ (2 mm)	50h	0.5	0.33	0.07	
Macropus fuliginosus	unpublished data	~250m²	3♂ 2♀ (1 lm 2 mm)	34h	0.3		0.03	
			1♂ 3♀ (lm)	64h			0.06	0.02
Macropus rufus	Wilhelm 1984	~300m²	4♂ 4♀ (1 lm 3 mm)	20h	3.2	0.17	0.03	0.02
		(same enclosure)	1♂ 4♀ (1 mm)	53h		0.1	0.04	0.03

Returning to the original assumptions stated in the introduction, it could be shown that agonistic behaviour between males and females when expressed in rates, ie acts per animal per time unit, obviously is not independent of group composition. However, in large species with a more gregarious social system, there is no consistent increase with increasing number

of males, and in no cases did increasing numbers of males lead to dramatic or potentially dangerous levels of male/male or male/female aggression.

It seems to be that in species with a type C mating system, ie 'roving males' (Clutton-Brock 1989), the animals' social disposition allows the formation of a hierarchy, independent of particular sites, that allows them to live in multi-male captive groups as well. Problems can arise in small enclosures with type B species, where the high-ranking males exclude the lower-ranking ones from the sites preferred by females.

Anecdotal evidence (unpublished observations) from other macropodoid collections suggests that even in smaller species, such as *Thylogale* spp or *Petrogale* spp, multi-male groups can be kept provided that the enclosures include shelters and hiding places for all animals (see Clancy 1983; Nicholls 1972). Aggression between sexes mostly involves small and/or subadult males. This can be caused not only by courting but might also involve some elements of play-fighting, as small and/or subadult males still direct play-fights towards females, even in free-ranging conditions (Krönert 1991).

Concluding remarks

The importance of living in a species-typical network of social relationships has been discussed in general by many authors, for example Hendrichs (1978), Hinde (1976, 1983) and Kummer (1975; 1978). Hendrichs (1978) explicitly states that '. . . the state of a social tension that is necessary for the functioning of a social organization is termed "social tonus" here. It can be increased by moderate influences which would be detrimental in stronger doses . . . . The interaction of social tonus and tonus-organization provides the individuals with a state of "elevated calmness" between laxity and excitedness that is necessary for the social life of the population' (my translation).

In conclusion it is not only possible, but desirable from the welfare as well as captive propagation point of view, to keep more than one male in breeding groups of most medium-to large-sized macropodoids, provided that information about their social system in the wild is carefully integrated into husbandry schemes. As a further benefit, the sight of sparring kangaroo males can also be quite attractive for visitors and can easily be used for educational programmes, for example, on dominance and its consequences in the life of mammals.

Acknowledgements

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