Anim. Behav., 1973, **21**, 449–456

DOMINANCE AND ASSOCIATION AMONG MEMBERS OF A CAPTIVE AND A FREE-RANGING GROUP OF GREY KANGAROOS (*MACROPUS GIGANTEUS*)

BY T. R. GRANT*

Department of Zoology, University of Sydney, Sydney, Australia

Abstract. Dominance relationships and the degree of association between members of groups of eastern grey kangaroos (*Macropus giganteus*) were investigated by observing a small group in captivity and a larger free-ranging group. Only decisive aggressive interactions were used as a criterion of dominance, and the number of times individuals occurred together were used as a measure of association. A dominance hierarchy in which the male assumed the highest rank was found in the captive group, while in the wild hierarchies were found separately among both males and females in the group. A low level of positive association existed between members of both the groups studied and the data indicated that in general the free ranging animals tended to move about at random with respect to each other. In the captive group dispersion about the enclosure was regular but became more random during the day in winter and spring.

Caughley (1964) and Kirkpatrick (1966) studied the social behaviour of the eastern grey kangaroo, a species of macropodid inhabiting dry sclerophyll forest, open woodland and scrub in eastern Australia. These authors concluded that the only positive social interactions were between mothers and young and that other groupings were merely feeding aggregations. Caughley (1964) asserted that social hierarchies did not appear to exist in either the red or grey kangaroos he studied.

More detailed observations by Russell (1970b) showed that a form of dominance existed in two groups of red kangaroos in captivity and observations in various parts of New South Wales, Australia convinced me that some degree of sociality also existed in the grey kangaroo. The aim of the investigation reported in this paper was to determine the nature of both negative (dominance) and positive (association) relationships in the eastern grey kangaroo, *Macropus giganteus*.

Methods

During the winter and spring of 1971 and the summer of 1972 seven kangaroos (one male and six females) were observed in captivity. At each of these seasons the animals were watched for 12 to 14 hr at a time, making up five complete 24-hr periods.

These animals were kept at the Cowan Field Station of the University of New South Wales in an enclosure of approximately 550 m^2. They were fed on lucerne hay and poultry pellets from separate food hoppers and were observed from a tower situated a few yards outside the enclosure.

During the night dim lighting was supplied by three red filtered lamps (200 W). The animals were fitted with white collars which allowed them to be seen more easily. Reflective symbols (Ealey & Dunnett 1956) rivetted to these facilitated rapid individual recognition.

Two pouch young vacated the pouch during the summer and were observed, one for the rest of the period and the other until its death in early February 1972.

Only one of the captive adults had been reared by its mother. The rest had been hand reared at the station or elsewhere.

In the field, thirteen to twenty-three kangaroos were observed when they came out to feed on a small grassy flat in the Nadgee Nature Reserve on the south coast of New South Wales (approximately 37°25′ S; 49°58′ E). The group consisted of three mature females, three young at foot and a variable number of mature males. Observations were made using 7×50 field glasses and although none of the animals was marked most could be recognized by their natural markings, their colour and their size. The full moon supplied most of the light necessary for night observations and additional light was supplied from a red-filtered spotlight. As in work on the captive group, data were recorded on a portable tape recorder or check sheets.

*Present address: School of Zoology, University of New South Wales, Kensington, Australia.

Sade (1967) stressed that aggressive interactions themselves rather than their cause or context formed the only distinct criterion of rank in rhesus monkeys and in this study aggressive interactions were used as an indication of individual animals in the groups. In the grey kangaroo these interactions usually began with a threat in which one or both animals raised themselves high on their hind legs. This was usually followed by the protagonists cuffing at each other's chests with their fore paws, and in the case of male–male interactions kicks were delivered with the hind limbs while the animals balanced on their tails. These interactions were scored on a 'win/loss' basis and two different scores were calculated to allow ranking of animals. Encounters were only considered in which one animal (the 'loser') broke off the contact by moving away from the other (the 'winner'). Occasionally threat alone caused a retreat and these were also taken to be 'decisive' interactions.

The 'success score' (Russell 1970b) was computed by dividing the number of successful encounters an animal was involved in by the total number in which it took part.

The 'points score' was calculated on each animal's success in its interactions with each other animal. Two points were given if it was successful in over 50 per cent of its encounters with another animal, one point was given in the case of a tie and none if less than half were successful.

By scoring the number of times each animal occurred within 120 cm of another at set 15-min intervals in the enclosure a measure of association between individuals was obtained. Because distances were difficult to estimate in the field the numbers of times animals were seen moving together onto the feeding area or away from it were recorded instead of animals standing together. From these data the frequency of occurrence of groups of various sizes was also obtained. Variance/mean ratios were calculated for each observation period to test the type of dispersion observed. A variance/mean ratio of 1 indicates randomness, one of more than 1 showing clumping and less than 1 regular spacing (Southwood 1966).

Attempts were made to correlate rank with age, weight, aggressiveness and sexual activity. In all these correlations Spearman's Rank Correlation Coefficient (Siegel 1957) was calculated.

Throughout this paper the terms 'pouch young' and 'young at foot' are used when referring to the young while it is in the pouch or permanently out of it. These terms are less ambiguous than the word 'joey' which refers to a young at either of these stages in its life.

Results

Dominance

Only adults were considered in the dominance relationships in the captive group as the young were out of the pouch for only part of one observation period.

The male in the captive group was dominant over the females. He was beaten by the largest female in two encounters soon after the introduction of all the animals into the same enclosure, but his 'success score' of 1·00 in the two later periods of observation indicated his dominance in the group (Table I).

Table I. Success Scores, Points Scores and Ranks of Adult Animals in the Captive Group for Each Observation Period

No.	June–July 1971				Sept.–Oct. 1971				Jan.–Feb. 1972			
	S.S.	R	P.S.	R*	S.S.	R	P.S.	R*	S.S.	R	P.S.	R*
♀2	0·14	7	3	6	0·00	7	2	6	0·00	6=	4	6
♀3	0·28	4	5	4	0·24	5	5	4	0·28	4	8	4
♀4	0·25	6	1	7	0·37	4	4	5	0·15	5	6	5
♀5	0·27	5	4	5	0·13	6	1	7	0·00	6=	3	7
♂6	0·86	2	11	1	1·00	1	11	1	1·00	1	11	2
♀7	0·78	3	9	3	0·74	3	9	3	0·52	3	10	3
♀8	0·87	1	10	2	0·94	2	10	2	0·96	2	12	1
Decisive encounters	149				149				74			

* S.S. = Success Score; P.S. = Points Score; R = Rank.

Table II. Correlation Coefficients (r_s) and Probabilities Obtained for Correlations of Ranked Success and Points Scores Within and Between Observation Periods for the Animals in Captivity

	Success Score/Points Score			June–July/Sept.–Oct.		June–July/Jan.–Feb.		Sept.–Oct/Jan.–Feb.	
	J–J	S–O	J–F	S.S.	P.S.	S.S.	P.S.	S.S.	P.S.
r_s	0·93	0·93	0·93	0·86	0·86	0·94	0·71	0·98	0·94
P	<0·01	<0·01	<0·01	<0·05	<0·05	<0·01	<0·05	<0·01	<0·01

Below the male, two of the largest females dominated, one (no. 8) over the other (no. 7), and both over the remaining group of four females. This subordinate group was subject to changes in rank and the numbers of interactions between them was low.

Significant correlations were found between the two rankings in each period and between rankings for consecutive periods (Table II) but ranked ages failed to show any correlation with the dominance ranks established. The main factor associated with dominance appeared to be weight (r_s values always significant). The number of encounters an animal initiated was used as a measure of aggressive tendency in the captive kangaroos and it was found that among the females the most aggressive animals tended to be the most dominant (r_s always $>0{\cdot}84$ $P<0{\cdot}01$).

In the free-ranging group no aggressive interactions occurred between the males and females and so the sexes were considered separately.

One female appeared to dominate the female group at Nadgee (Table III). This represented the only dominance in this group which consisted of only three mature animals and two young at foot.

Dominance in the males was more marked,

Table III. Success Scores, Points Scores and Ranks of Both Males and Females in the Free-Ranging Group of Kangaroos

Males					Females				
No.	S.S.	Rank	P.S.	Rank	No.	S.S.	Rank	P.S.	Rank
1	0·50	5	11	4=	1	1·00	1	8	1
2	0·00	9=	10	6=	2	0·75	3	7	2
3	0·00	9=	9	10	3	0·42	4	4	3=
4	0·53	2	17	1	4	0·83	2	4	3=
5	0·68	4	10	6=	5	0·17	6	4	3=
6	0·25	6=	8	11=	*♂2	0·33	5	1	6
7	0·25	6=	11	4=					
8	0·75	3	13	3					
9	1·00	1	15	2					
10	0·00	9=	10	6=					
11	Seldom seen								
12	0·00	9=	10	6=					
13	0·25	6=	8	11=					
Decisive encounters		32				22			

*'Foster' young at foot of female 1 which was only involved in encounters with females.

although the comparative infrequency of decisive encounters between animals in the wild (thirty-two male–male) produced a number of ties in the data as shown in Table III. Again there seemed to be a high-ranking group with a number of subordinate animals below it which showed little interaction amongst themselves. The two scoring criteria reversed the leadership in the males but a significant correlation (r_s 0·88; $P<0·01$) still existed between the two ranking schemes.

The visual estimate of size was very approximate but was found to be correlated (r_s 0·89 and 0·77 $P<0·01$) with rank. Dominance did not seem to be related to sexual activity, although on four occasions one male was observed chasing males away from the female he was accompanying.

Some animals were seen more frequently than others. This could have been the fault of the observer but it was unlikely that animals were not observed if they were present over an entire observation period which lasted from the time animals began entering the clearing in the afternoon until they returned to the bush the next morning. The most commonly seen males were the most dominant ones (r_s 0·98 and 0·59; $P<0·01$ and 0·05).

Aggression by females towards the young of others was noted frequently in the captive group (the two young were involved in sixty-nine aggressive encounters) but only two instances of this were seen in the group at Nadgee. No defence of the young by the mother was ever seen. The young generally retreated from any encounter with an adult other than their mothers.

Association

The matrices in Tables IV and V show that the strongest associations in the captive group were between mothers and their young. Apart from this, associations between females were

Table IV. Matrices of Association Between Pairs of Animals Together in Captivity

	2	3	4	5	♂6	7	8
2/	161	105	139	123	120	78	116
3/	119	196	128	99	96	83	
4/	101	123	107	104	86		
5/	131	99	113	84			
♂6	111	106	131				
7/	185	67					
8/	183						

June–July 1971
480 observations

	2	3	4	5	♂6	7	8
2/	176	68	106	108	109	70	74
3/	141	216	100	105	100	102	
4/	133	83	113	98	100		
5/	203	79	90	81			
♂6/	117	163	126				
7/	151	101					
8/	216						

Sept.–Oct. 1971
480 observations

	2	3	4	5	♂6	7	8	Young 9	Young 10
2/	235	76	97	109	62	44	59	27	79
3/	216	136	55	83	51	90		36	53
4/	96	104	198	73	104			41	71
5/	33	112	61	41				22	263
♂6/	127	76	71					36	55
7/	45	57						189	49
8/	253							36	35
9/								47	7
10/								10/	25

Jan.–Feb. 1972
480 observations of adults ♂
288 observations of young ♀9
394 observations of young ♀10

often stronger than between females and the male. The association did not change markedly over the three study periods, although in the summer a weakening of the association between most animals did occur.

In the wild animals again the most common association was between the mother and her young at foot. The young at foot which had just vacated the pouch (female 5) had a closer relationship with its mother than its older sibling (female 4). The remaining females formed a loose group with which the males were associated to varying degrees. No relationship existed between dominance ranks and degree of association of the males with females, but a correlation (r_s 0·86, $P<0·01$) was found between this association and sexual activity in the males.

The male no. 2 was a young which had lost its mother and was fairly closely associated with the female group.

The results of variance/mean ratio tests of dispersion (Table VI) indicated that animals in the group in captivity showed a tendency to be regularly spaced in the enclosure and those in the field to be spaced at random. The dispersion changed in the captive animals between day and night, with the pattern being more close to random during the day. The animals at Nadgee seldom moved off the feeding area at night and so separate variance/mean ratios could not be computed for these.

Single animals were the most common 'group' observed in both the captive and free-ranging kangaroos (56 to 72 per cent of groups) and groups of two made up 15 to 24 per cent of the groups seen throughout the study (Table VII).

Table V. A Matrix of the Association Between Pairs of the Free-Ranging Kangaroos

				Young			Young											
	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	12	13
1/	1	21	10	45	54	7	16	1	3	4	7	0	3	0	2	0	3	3
2/	5	9	19	20	3	9	2	10	4	11	0	2	0	2	0	2	6	
Females	3/	10	8	10	3	5	1	9	4	10	0	0	2	0	0	0	3	
Young	4/	3	45	7	17	1	1	3	6	0	3	0	2	0	3	4		
	5/	0	6	17	1	3	4	6	0	1	1	2	0	3	3			
		1/	15	4	1	2	2	3	0	3	0	3	0	1	4			
	Young	2/	2	1	0	0	5	0	3	0	1	0	3	3				
		3/	0	1	1	1	0	1	0	0	0	0	0					
			4/	8	6	9	1	1	0	0	0	0	2					
				5/	2	8	0	1	0	0	0	0	0					
					6/	16	0	1	0	2	0	0	5					
				Males		7/	9	0	0	0	0	0	0					
							8/	5	0	0	0	0	0					
								9/	20	0	0	0	0					
									10/	3	0	1	3					
										11/	0	0	0					
											12/	2	1					
												13/	0					

Nov.–Dec. 1971
241 observations

Table VI. Variance/Mean Ratios

	Total period	Day	Night
Cowan:			
June–July 1971	0·7453	0·8448	0·4331
Sept.–Oct. 1971	0·6212	0·9214	0·3731
Jan.–Feb. 1972	0·6291	0·6911	0·6360
Nadgee:			
Nov.–Dec. 1971	0·9161	—	—

Table VII. Frequency of Observation of Groups of Various Sizes (expressed as a percentage of the total groups observed)

	Cowan			Nadgee
Group	June–July 1971	Sept.–Oct. 1971	Jan.–Feb. 1971	Nov.–Dec. 1971
1	56·3	61·1	72·0	59·7
2	22·8	23·7	15·4	21·0
3	10·5	8·3	7·0	10·1
4	6·8	3·3	3·5	5·0
>4	3·4	3·3	2·1	4·6

Discussion

Hierarchial organization existed within the captive group of grey kangaroos and the stability of this organization was indicated by the correlations between the ranks based on each criterion from one observation period to another. There appeared to be similar organization between females and between males in the group at Nadgee. The dominance structure was apparently maintained by aggressive interactions in both situations and significant correlations between the two ranking schemes gave evidence of the reality of the relationships.

The largest animals were the most dominant. Russell (1970b) found this to be the case in red kangaroos. She also found that rank was correlated with age. In the group studied in captivity here no such correlation was found even when the male, which was the youngest animal, was removed from the grouping. It should probably be pointed out that this is not the anomaly it seems as the size of a kangaroo does not necessarily reflect its age. This is especially true in females in captivity where size is influenced by the way animals are reared. The male in this group initiated very few aggressive interactions but the females were more aggressive and the most dominant tended to be the most aggressive.

Packer (1969) noted hierarchies which led to a reduction in the incidence of fighting in groups of quokkas (*Setonix brachyurus*) in captivity. Very few encounters between grey kangaroos involved only a display of threat but the generally low level of aggression (0·13 to 0·18 decisive encounters per animal per hour in captivity and 0·022 per animal per hour in the wild) may indicate the establishment of an accepted hierarchy leading to the avoidance of situations involving contact between individuals. The higher incidence of aggression in the enclosure was most likely a result of enforced proximity preventing avoidance of dominant animals by the subordinate ones.

The function of such organization is obscure. There was some evidence of the high ranking animals gaining preference at feeding places in the enclosure. The significance of this type of organization may not be evident except in times of stress (Russell 1970b), when the dominant animals would be at an advantage. Field observations before and after a period of stress (e.g. drought) would have to be carried out in order to determine the validity of this suggestion. No copulation was observed in the field, and it is possible that dominance may be of importance in governing access to females during oestrus. Sexual activity of the males in the group at Nadgee was not related to the dominance hierarchy, but the observations of a dominant male chasing others away from a female gives support to the suggestion above.

In the group at Nadgee the males most commonly seen were the dominant ones. The feeding area where the observations were made was perhaps the best in the whole reserve, consisting of improved pasture from an abandoned farm. On two occasions an unidentified male was chased out of the clearing by one of the high ranking males from the group. I suggest that the dominant males and the females (which were present in all observation periods) probably were the resident population and others which were seen less frequently were animals from outside the group which sometimes used the same feeding area.

The development of a structure of social dominance in a captive group of animals does

not indicate that the animals form socially organized groups in the wild but it does indicate some potential for social organization in the species. Grey kangaroos showed this potential in captivity and restricted evidence from field work suggests that it is realized in the wild.

Some positive association seemed to exist within the groups of kangaroos studied. This association was strongest between females and their young but in the captive group two pairs of females had a close association with each other (nos. 2 and 5 and nos. 3 and 4). These animals frequently indulged in mutual and allogrooming (fifty-four instances in nos. 2 and 5 and forty-six in nos. 3 and 4). One of these relationships could have been sexual behaviour as contacts often took on some of the characteristics of normal sexual activity. Despite this, however, the evidence suggests that individuals of this species are capable of forming associations with other individuals.

Despite the association between these two pairs there appeared to be an avoidance of each other by members of the group (variance/mean ratios of $<1{\cdot}00$). This tendency was reduced during the day in the first two observation periods as the animals fed during the first and last few hours of daylight and congregated at the food hoppers. During the winter and part of the spring periods some animals also lay down near each other in the patches of sunlight which filtered through the trees. During the summer regular dispersion existed throughout the day.

The association between individuals also declined in the summer. At this stage of the year the animals began to make depressions in the ground in which they lay during the heat of the day. Russell (1970a) observed this digging behaviour in the red kangaroo and suggested it might serve to remove hot surface soil before the animal lay down. My observations did not support this view for the grey kangaroos as most of the scraping was carried out after the animal lay down. Occupation of these discrete depressions may have served to facilitate heat loss from single lying animals. The function of this behaviour is not clear but it does explain the 'antisocial' behaviour observed in the summer, which reduced the degree of association measured.

The free-ranging kangaroos showed much less association and moved fairly randomly on and off the feeding area at Nadgee.

The predominance of single animals in observations of groups in both situations indicated the looseness of any association which may have existed in the wild group of grey kangaroos.

Kangaroos do not appear to exhibit the complex social organization seen in the grazing eutherian species (ungulates). The rigid herd structure seen in many ungulates (e.g. black-tailed deer, Dassmann & Taber 1956; elk, Altman 1963; wildebeest, Estes 1969; and zebra, Klingel 1969) does not exist in the grey kangaroo, but rather the basic social units in this species is the solitary male and the female with her young at foot from one or more breeding seasons. The evidence presented here indicates that these units may be held together by some positive association and by the development and maintenance of a hierarchy of dominance within a group feeding in the same area.

Acknowledgments

This work was carried out while I held a University of Sydney Post-Graduate Research Studentship. I wish to thank the School of Zoology, University of New South Wales for the use of their facilities at Cowan and Ranger David Hope for allowing me to work on the Nadgee Nature Reserve. Dr P. F. Sale, Dr A. C. Hodson and Dr E. M. Russell read and criticized the manuscript in its various stages of preparation. Mr Bryan Shadbolt is also acknowledged for his assistance in attending and maintaining the kangaroos at Cowan.

REFERENCES

Altman, M. (1963). Naturalistic studies of maternal care in the moose and elk. In: *Maternal Behaviour in Mammals* (Ed. by H. L. Rheingold). New York: Wiley.

Caughley, G. (1964). Social organisation and daily activity of the red and grey kangaroo. *J. Mammal.*, **45**, 429–436.

Dassmann, R. F. & Taber, R. D. (1956). Behaviour of Columbian black-tailed deer with reference to population ecology. *J. Mammal.*, **37**, 143–164.

Ealey, E. H. M. & Dunnett, G. M. (1956). Plastic collars with patterns of reflective tape for marking nocturnal mammals. *C.S.I.R.O. Wildl. Res.*, **1**, 59–62.

Estes, R. D. (1969). Territorial behaviour of the wildebeest. *Z. Tierpsychol.*, **26**, 284–370.

Kirkpatrick, T. H. (1966). Studies of Macropodidae in Queensland. 4. Social organisation in the grey kangaroo (*Macropus giganteus*). *Qld J. agric. anim. Sci.*, **23**, 316–322.

Klingel, H. (1969). The social organisation and population ecology of the plains zebra (*Equus quagga*). *Zool. Afr.*, **4**, 249–263.

Packer, W. (1969). Observations on the behaviour of the marsupial *Setonix brachyurus* (Quoy and Gaimard) in an enclosure. *J. Mammal.*, **50**, 8–20.

Russell, E. (1970a). Observations on the behaviour of the red Kangaroo (*Megaleia rufa*) in captivity. *Z. Tierpsychol.*, **27**, 385–404.

Russell, E. M. (1970b). Agonistic interactions in the red kangaroo (*Megaleia rufa*). *J. Mammal.*, **51**, 80–88.

Sade, D. S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In: *Social Communication Among Primates* (Ed. by S. A. Altman), pp. 99–115. Chicago: University of Chicago Press.

Siegel, S. (1957). *Nonparametric Statistics for Behavioral Sciences*. New York: McGraw-Hill.

Southwood, T.R.E. (1966). *Ecological Methods*. London: Methuen.

(*Received* 31 *May* 1972; *revised* 10 *November* 1972; *MS. number:* 1147)