

## CHAPTER EIGHT

### Social Interactions and Reproductive Success of Males

#### 8.1 Introduction

The previous two chapters described how female red-necked wallabies care for their infants, and form enduring associations with them. Adult male wallabies make no parental investment (sensu Trivers 1972) and any association between fathers and their offspring is purely accidental. This is also true of many other species of mammals, and Trivers (1972) has argued powerfully that in species such as these males will be selected to increase their reproductive success by mating with as many females as possible in an unselective fashion, while the females allocate their reproductive effort to the care of individual offspring, and should tend to discriminate against males who may have inferior genotypes. Therefore, although variations in the reproductive success of females will primarily be determined by differences in their abilities to nurture individual offspring (often in competition with other females for resources essential to this task), variations in the reproductive success of males will be due to differences in their abilities to find and gain access to mates, as well as to disparities in the mothering abilities of those mates (Hrdy and Williams 1983). This contrast in the way in which the pressures of sexual selection and natural selection fall on males and females can account for much of the observed sexual dimorphism in animals (Arnold 1983, Trivers 1972).

In many species the most important proximate factor determining whether a male will be able to mate or not is his position in a social dominance hierarchy. Social dominance, particularly among males, is a pervasive phenomenon in animal societies, and male dominance rank usually correlates positively with involvement in mating and, ultimately, reproductive success. Dewsbury (1982) showed that this

correlation is practically universal amongst mammalian species, although some exceptions have been noted in primates and rodents. It is presumably because body size to some extent determines an individual's potential for social dominance that the males of so many species of polygynous mammals have become larger than the females (Ralls 1977, Clutton-Brock *et al.* 1977, Clutton-Brock, Guinness and Albon 1982, Alexander *et al.* 1982). There are, however, many subtleties in this relationship. For example, Jarman (1983) has shown that in some species of polygynous ungulates males reach a maximal body size quite early in their adult lives and thereafter remain unchanged in size, while in others, and in many species of macropods, males may continue to grow throughout their lives. This difference seems to be related to the manner in which males go about using their dominance to guarantee access to mates. In territorial species of ungulates males are able to mate with any females who become receptive within their territories, so that males need only acquire sufficient social (and physical) stature to enable them to claim a piece of ground used by females, and they are assured a measure of reproductive success (although this will, of course, vary somewhat with the attractiveness of the territory to females). However, in species in which for one reason or another males do not defend territories, and therefore experience a freer association with other males and with females, fine differences in the dominance ranks of males could have a very much larger effect on the rate at which they accumulate matings. It is in these latter species that males may continue to grow throughout life and where very old and large males are the most successful at warding off threats and interruptions from other males while they court and mate with oestrous females (Jarman 1983).

The comparatively free mixing of the sexes and age classes in the macropods, together with the fact that so many of them have males who continue to grow throughout their lives and associate together in groups when following oestrous females (Jarman 1983), suggests that it is essential that we have detailed information on dominance rankings and mating success in relation to body size in order to appreciate the workings of sexual selection in the males of their species. This chapter presents such information for red-necked wallabies. I follow

Dewsbury (1982) in defining dominance as the ability to prevail over others in aggressive encounters when access to resources is not in dispute, and then assess the utility of dominance rank as a predictor of the degree to which a male will gain access to resources (in this case, the resources are oestrous females). I also look for correlations between dominance rankings and body size rankings, analyse changes in the behaviour of males as they change their position in the hierarchy, and describe spatial variations in the degree to which high-ranking males have sexual access to oestrous females.

## 8.2 Non-reproductive agonistic interactions

This section presents data on those interactions between males which took place when no oestrous or near-oestrous females were present. Something of interactions around oestrous females will be said in section 8.3.

8.2.1 *Description of interactions.* Interactions varied in kind from simple displacements, when one animal approached another, who moved aside; to fights, when the two stood and faced one another, and sparred, kicked and so on (see below). Intermediate kinds of interactions, as when one male placed his paws on the other's shoulders while displacing him, very rarely occurred, so that the distinction between fights and displacements is an easy one to draw in practice. I saw a total of 93 interactions in which the identities of both participants were known. Of these, 50 (54%) were fights and 43 (46%) were displacements. The intensity and vigour with which both kinds of interactions were played out varied considerably. Some displacements were very casual : one male would saunter up to another, who stepped a few paces aside; while at other times the dominant individual rushed at the subordinate and chased him for a short distance. Less often, the two males stayed close together, staring intently at one another for several seconds, until one lost heart and withdrew; I saw only two displacements of this kind, both were between large, high-ranking males.

Fights were escalated displacements, when one male approached

another, who refused to move aside. Fights would often be preceeded by a short period in which the two males crouched feeding side by side only two or three metres from one another. Typically, after no more than a few minutes of such unusually close association the two males would abruptly stand and begin to groom themselves. The grooming that presaged fighting was often exaggerated in fashion, and the males paid unusual attention to their chests, arms and shoulders. The longest bout of such grooming that I observed lasted for five minutes. In that case, a medium-sized male had cautiously approached a slightly larger male. As he approached, the smaller male started grooming very vigorously and was nibbling his fur and making sudden jumps as if annoyed by biting flies. His jumps and starts took him closer still to the other male, who then also stood up and began grooming. Usually the interacting males began to groom almost simultaneously, so that I was unable to tell which of them had initiated the grooming bout. After several seconds or minutes of grooming one male would jump at the other and the fight proper would begin. These kinds of preliminaries were most likely to precede fights between males who were similar to one another in size.

All fights were similar to the extent that the males stood erect facing one another with their heads thrown back, and grappled and sparred with their forearms. The grappling seemed to have several purposes. Each male tried to place his forearms above and over the other's, so that he could reach far enough to claw his opponent's face and neck, and also grab his ears. It was probably to protect their eyes and faces that the males kept their heads thrown back while fighting, and I saw no male with injured eyes or scarred cheeks, although many of them had notched or tattered ears. By keeping his forearms above his opponent's one male was sometimes also able to hug the other around the shoulders and pin his arms to his sides, and from this position push him backwards or throw him to the side. Hugging was seen in 16% of fights, usually between large males. If one male had a significant advantage in height and reach over his opponent, he was sometimes able to place his paws on the other's shoulders and press him down, and then perhaps deliver a sideways swipe at his head and shoulders.

Fighting males would often momentarily cease grappling with their opponents and kick them. Male red-necked wallabies kick by throwing themselves into the air and delivering a downwards blow with their hind feet to their adversaries midriff, unlike kangaroos, which prop on their tails as they kick. In 63% of the observed fights, one or both of the males did some kicking. In the fights when only one of the males kicked (38% of all fights) the loser was ten times more likely than the victor to have been the kicker. Males who were being overpowered in a grappling contest sometimes broke out of it by kicking wildly and throwing themselves away from their opponent - such kicks appeared to cause no hurt to the winning male, and tended to come with increasing frequency towards the end of a fight. Kicking could also be employed offensively and was used so by closely matched males. When kicking offensively males tended not to jump wildly but stayed in close to their opponents and delivered short, direct and often audible blows. Male macropods have thickened skin over their abdomens, presumably to shield them from such kicks (Jarman pers. comm.). That offensive kicks were sometimes decisive is suggested by the observation that some males who had been kicked appeared to be very short of breath, as if winded, at the end of a fight, and that powerful kicks were delivered relatively infrequently, and in the later stages of fights. When being decisively beaten, either because he was being overreached and thrown off balance in grappling or was receiving hard kicks, a male would usually try to terminate the fight by breaking away from his opponent and by adopting a typical feeding crouch with his back to the winning male. Males in this position would sometimes also make exaggerated feeding movements - this posture and activity seemed to pacify the winning male, who rarely continued to harass the loser.

In very few of these interactions did the males behave in a stereotyped or ritualised way. I saw only two displays which were repeated with little variation by different males. In 6.4% of the observed fights, one of the males crouched over a tussock, rubbing his chest over it from side to side and pulling grass from it with his forepaws. While doing this, a male would tense his forearms and shoulder muscles while pointing his muzzle up into the air, and

sometimes lift himself part-way out of his crouch so as to have his forearms fully extended in front of him. These movements served to display the musculature and length of the males arms and shoulders, and may also have left some of his scent on the tussock, although I could detect no scent on tussocks which had been treated in this way. I refer to this display as 'grass-pulling', although I once saw a male go through these actions over bare ground. I saw only large males (size ranks 6.6 or above, average of 3.0) doing this, and only during or before interactions in which they were dominant. On one occasion I saw a small male (rank 17.7) produce a tentative version of some of these actions. The second kind of display, which I refer to as 'high-standing' was seen twice, during grooming sessions which preceded interactions between large males. These males briefly drew themselves up to an exaggerated height by standing on their toes, while also inflating their chests. In each of these interactions, one only of the males produced this display, and did not repeat it.

*8.2.2 Body size and dominance rank.* Most of the interactions which I observed had clear outcomes, and I assumed the winner of each to be dominant to the loser, unless the results of other interactions suggested otherwise. Sixty-seven of the observed interactions were from pairs whom I had seen interacting on more than one occasion, and only 2 (3%) of these were inconsistent with the hypothesis that the relationships between males remain stable over time (some reversals in dominance were documented in 1984, and are described below). Table 8.1 shows that large males were usually dominant to small males. Although a number of instances of males dominating others slightly larger than themselves were recorded, they accounted for only 21% of the interactions. The correlation between dominance and body size was more specifically demonstrated for two reasonably large sets of males, within which a number of interactions sufficient to establish unambiguous dominance rankings was seen. One of these sets included almost all of the males from the northern part of the study area, the other included about half of the males from the central section. The dominance rankings in each were converted to a standard ten-point scale, and plotted against the standard body size ranks in Fig. 8.1. Both correlations were significant ( $r_s=1.00$ , 4 d.f.;  $P<0.01$ ;  $r_s=0.89$ ,

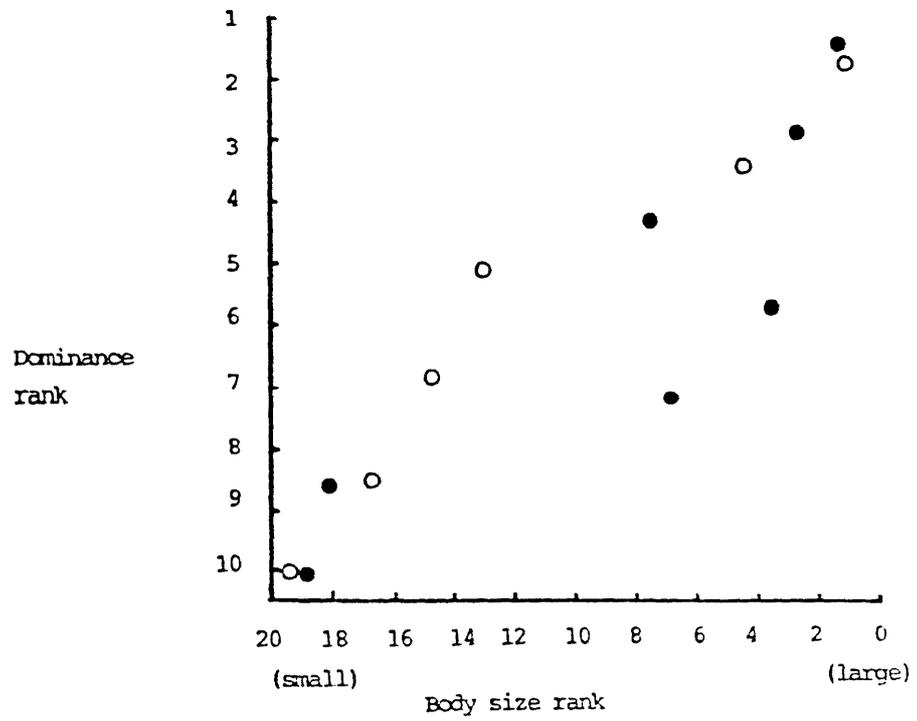


Fig. 8.1 Relationships between body size ranks and dominance ranks in two sets of male wallabies. Open circles are northern males, closed circles are central males.

5 d.f.;  $P < 0.01$ ), although some instances remain of males being dominant to others who were slightly larger than themselves.

For the remainder of this chapter, I shall use the body size ranks of males as approximate indices of their dominance ranks.

### 8.2.3 *Characteristics of the dominance hierarchy.*

*Frequencies of interaction.* When males were associating they interacted with a frequency of 1.45 interactions/wallaby.hour (n=38.5 wallaby hours of observation of associating males not with oestrous females). The frequency with which males interacted with others varied with their size (see Fig. 8.2). Small males interacted rarely, but interaction frequencies increased with body size, falling off slightly for very large males (I showed in the previous chapter that the proportion of time spent by males with other males did not vary significantly with body size, therefore these frequencies are good indicators of the variation in total interaction rate with size. Males spent, on average, 30 % of their time with other males). The numbers of interactions in which males of each of five size classes of equal breadth (as plotted in Fig. 8.2) were involved differed significantly from the numbers expected had interaction frequency not varied with body size ( $\chi^2=11.0$ , 4 d.f.,  $P < 0.05$ ). A more complete analysis of the effect of body size on interaction frequency is presented in Table 8.2, which compares observed with expected numbers of interactions according to the sizes of both males. The table shows that large males interacted with other large males much more often than expected from the time they spent together, large and medium males interacted with moderate frequency, while in all other combinations of size classes interactions were infrequent ( $\chi^2=27.95$ , 5 d.f.,  $P < 0.001$ ).

*Partner preferences.* That proportion of the interactions in which any male took part that he himself had initiated also increased with body size (see Fig. 8.3), with very large males the only ones who initiated more than half of their encounters (the difference was significant  $\chi^2=33.51$ , 4 d.f.,  $P < 0.01$ , when tested as for interaction frequency). The mean size rank of the males with whom any individual initiated encounters tended to increase with the initiator's body size, although, as Fig. 8.4 shows, the trend is not consistent with

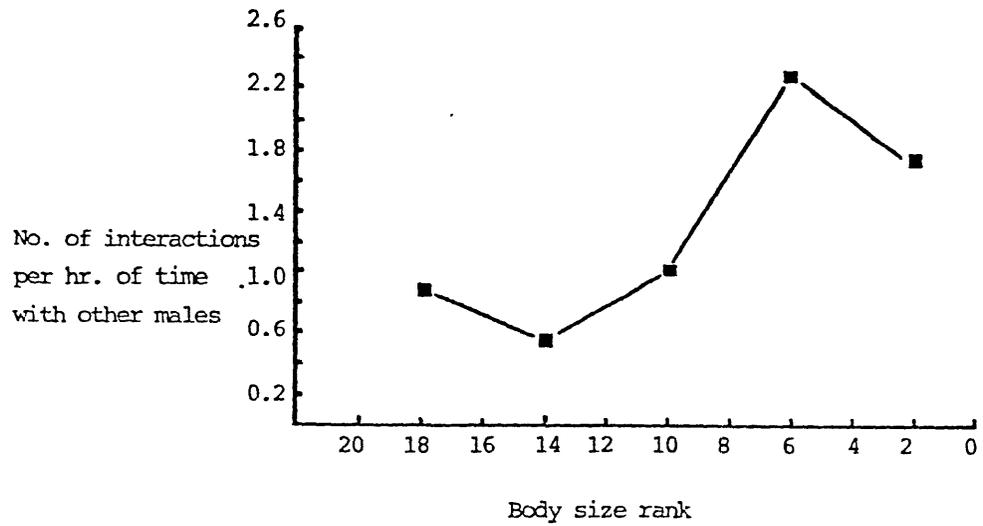


Fig. 8.2 Relationship between body size in males, and frequency of interaction with other males.

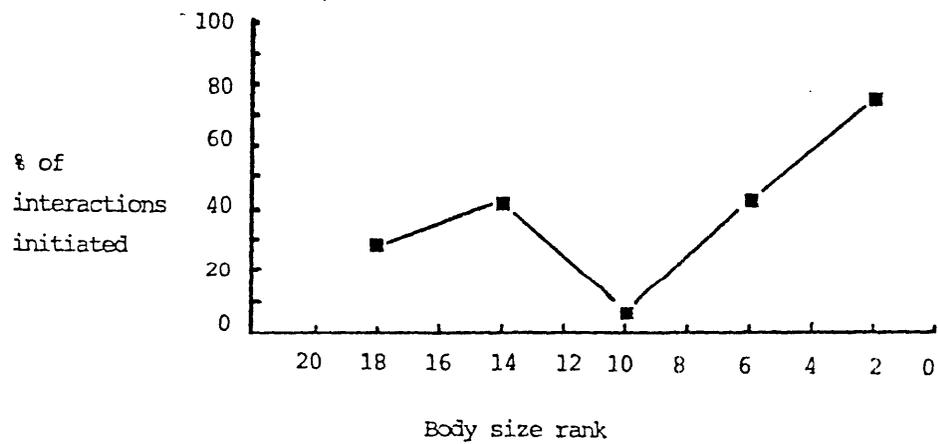


Fig. 8.3 Relationship between body size of males, and the proportions of their interactions which they initiate.

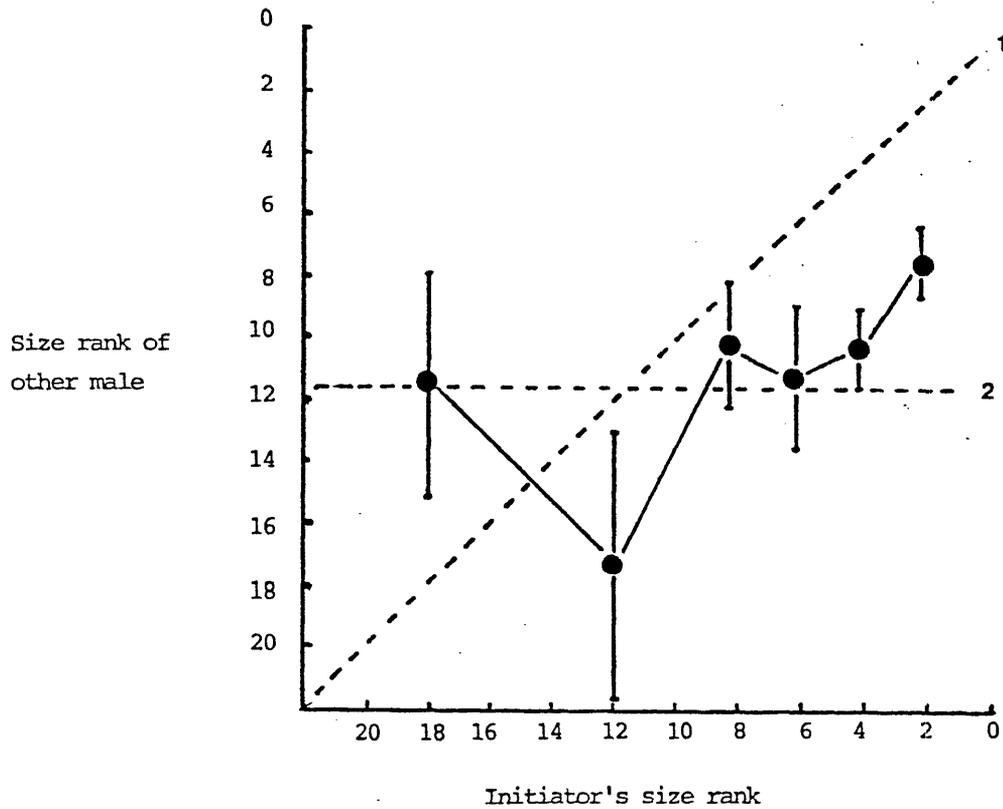


Fig. 8.4 Relationship between body size of males and the size ranks of the males (means with 95% C.I.s) with whom they initiate agonistic interactions. Dashed line 1 is the trend expected if males initiated interactions with males of their own size, dashed line 2 is the trend expected if males initiated interactions randomly.

the hypothesis that males sought encounters with other males of their own size. Males of most size ranks preferred to initiate encounters with males smaller than themselves. This was not true of very small males, for whom there is no evidence that they initiated encounters in other than a random fashion; and is only equivocally true of males in the upper range of the medium size class, who apparently preferred to interact with males only slightly smaller than themselves. The most striking feature of Fig. 8.4 is the narrowing of the size range of a male's preferred interaction partners as his own size increased: small males provoked a wide range of other males, whereas very large males consistently sought encounters only with males in a narrow band of sizes approximately five size ranks below themselves.

*Interaction type.* The probability that an interaction between any two males would escalate into a fight varied both with the relative and absolute sizes of the males. The great majority of interactions between males very different to one another in size were displacements, whereas the outcomes of interactions between more closely matched males were more likely to be decided by fighting (see Table 8.3,  $\chi^2=6.15$ , 2 d.f.,  $P<0.05$ ). Table 8.4 shows also that interactions between medium males and between small males were more likely to be fights than were interactions between large males. The data on interactions within the medium and small classes had to be combined before a test of this trend could meet the criterion of minimum expected frequencies required for  $\chi^2$ ; when this was done the differences proved to be significant ( $\chi^2=4.07$ , 2 d.f.,  $P<0.05$ ).

*Reversals of dominance status.* Reversals in the dominance relationships within three dyads of males were recorded during this study. One male (Max) was a member of each of these dyads. He was a large male (size rank of 5.9 in 1983) who lived in the central part of the study area and was known to be subordinate to four other large males there. Two of these others were males who had not yet reached breeding status (see below), the other two were larger and monopolised the mating in that area. The male closest to Max in size and immediately above him in dominance status frequently initiated fights with him (I saw nine fights between the two up to the end of 1983) and was always able to defeat him, until the two fought very bitterly in

February of 1984. That fight lasted for only two minutes, but left both males exhausted, and involved much tight hugging, throwing and hard kicking (especially from Max), and was clearly won by Max. Observations made by myself and K. Higginbottom (pers. comm.) later in 1984 showed that Max had by then also become dominant over two of the other males to whom he had been subordinate earlier in the study, and had begun to enjoy uninterrupted courtship of females.

### 8.3 Body size and sexual access to oestrous females

Males of a wide range of body size ranks were seen in the company of oestrous females. However, there was a very clear pattern in the amount of time males of various sizes spent with such females (see Fig. 8.5). Males in the top three or four size ranks spent a good deal of time with oestrous females, while most males in the three size ranks below them spent almost none, although smaller males often had high frequencies of association with females in oestrus. The bimodality of this distribution was not due to any lack of interest by middle-ranking males in sexually attractive females, but came about because the very largest, most dominant males selectively excluded from the group of males following an oestrous female those males closest to themselves in rank, while allowing markedly smaller males to remain on the periphery of the group. Interactions between males following oestrous females will be described in detail in the next chapter; for now I wish to note that only males in the right hand peak of the distribution of Fig. 8.5 were consistently able to remain close to oestrous females without fear of displacement by larger or more dominant males, and that males who were able to achieve this formed in any year, a small proportion of the adult male sector of the population. In 1981, only 18.7% (3 of 16) of the males present were breeding males; the proportions for 1982 and 1983 were 16% (4 of 25) and 20% (5 of 25) respectively. The mean size ranks of these males were 2.2, 2.6 and 2.6 in 1981, 1982 and 1983 respectively. Although very few matings were seen, the control these males exerted over oestrous females indicates that they must have accounted for almost all of the matings in the population (see following chapter).

Although the ages of none of the older males in the study

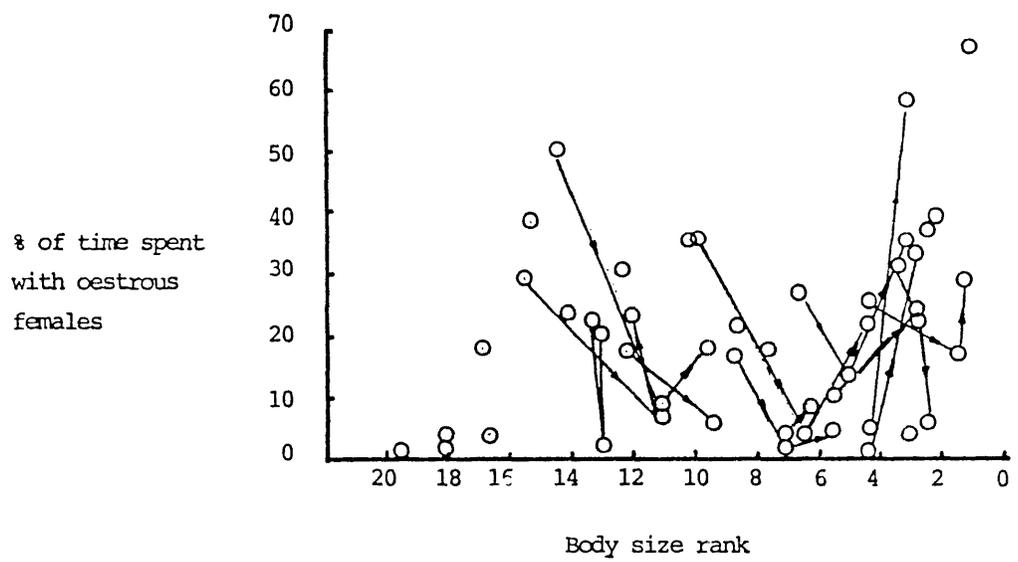


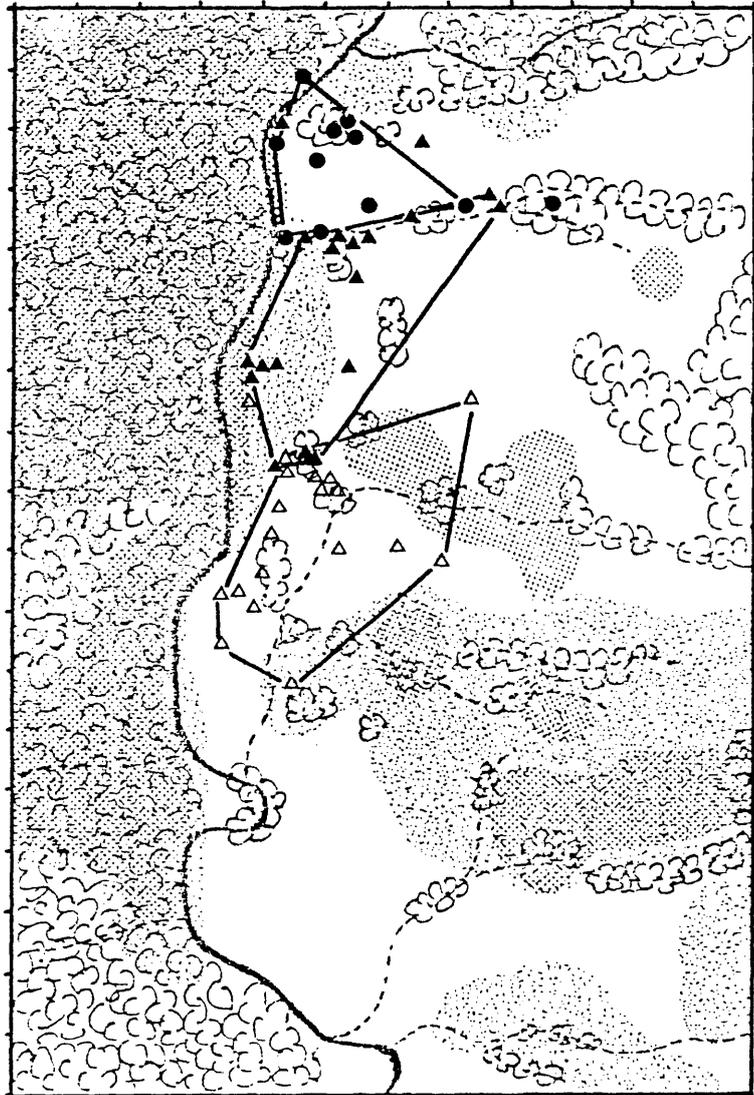
Fig. 8.5 Relationship between body size and the proportions of their time spent with oestrous females. Lines join estimates for the same males in successive six-month periods.

population were precisely known, the data discussed in Chapter 2 would suggest that all of the breeding males were at least seven years old.

#### 8.4 Spatial partitioning of access to mates by dominant males

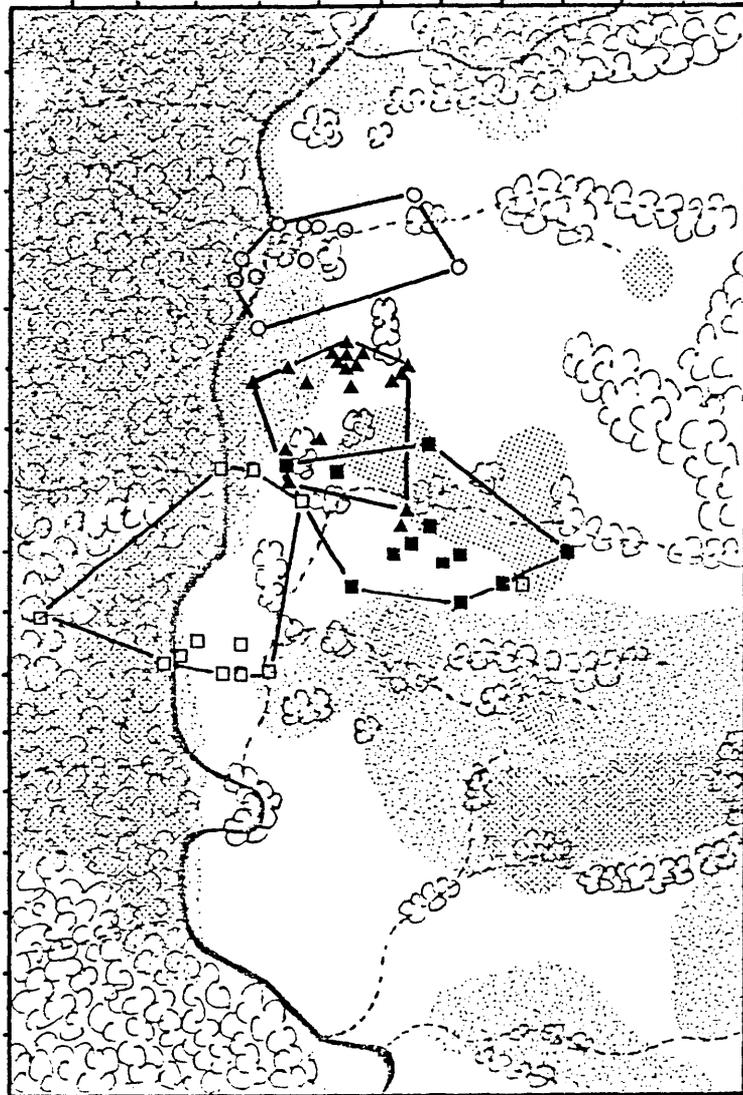
Part of the reason for the clarity of the distinction between breeding and non-breeding males was that large, breeding males usually did not interfere with one another, at least over the short term, and used separate mating areas or, as I shall call them, 'dominions' (this term is discussed below). In Fig. 8.6 to 8.8 are plotted the locations of the sightings of breeding males with oestrous females in each year of the study (a total of eight males, and 12 male years). In 1981 and 1982 there was a nearly complete separation of the areas over which each of the breeding males was seen to court oestrous females, as shown by the lack of overlap between the polygons describing the males' dominions (these polygons included 95% of the sightings of each male with oestrous females). In 1983, three males had large, non-overlapping dominions, and two males had (apparently) very small dominions wholly or partly within the dominions of the other three males. These latter two males are both interesting cases. One of them (Jack) had suffered a decline in his dominion size over the three years of the study, and was not seen to do any courting of oestrous females in 1984 (K. Higginbottom, pers. comm., and my observations). During 1983, Henslowe, who had been Jack's southern neighbour, extended his dominion to the north, until it completely covered Jack's. I twice saw Henslowe displace Jack early in 1983. One of these displacements was a particularly intense encounter; the following account of it is taken from my field notes :

- 1845: Jack, Henslowe and Max standing near one another.  
Henslowe and Jack 7 m apart, Henslowe and Max 15 m  
apart, Jack and Max 8 m apart.
- 1852: Max leaves.
- 1855: Jack stands up and grooms himself, Henslowe starts  
grooming also, both groom rather exaggeratedly for  
approx. 30 seconds, then Henslowe goes over to Jack,  
they look at one another. Jack grooms again, then



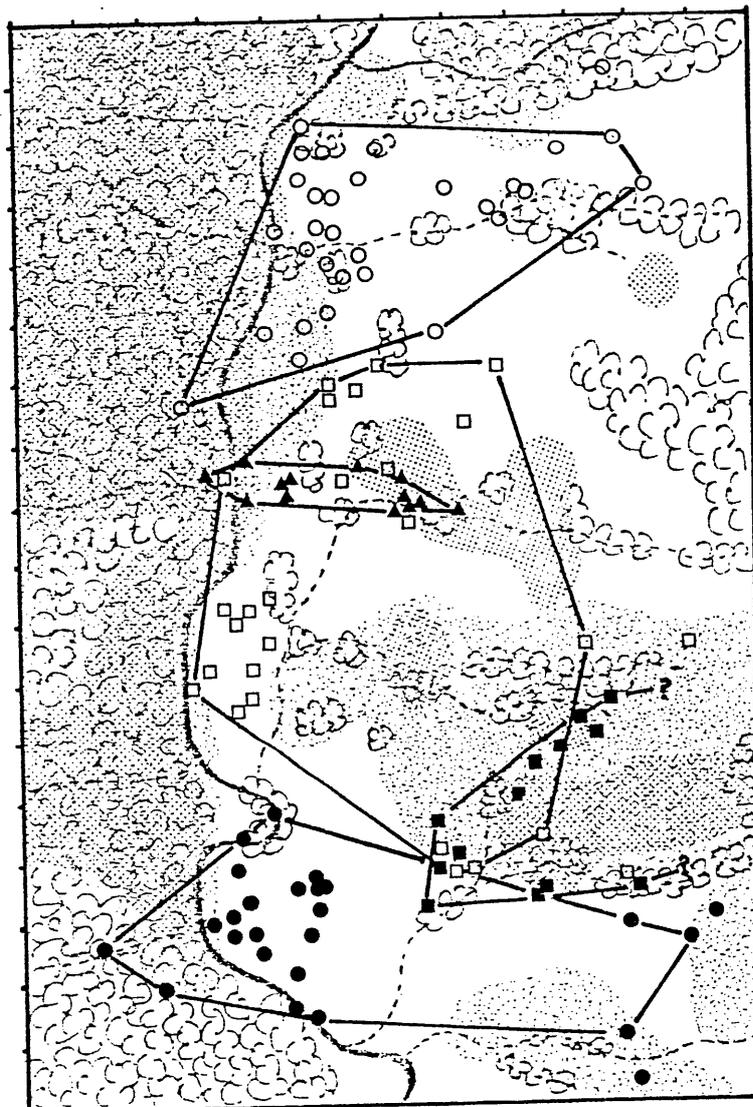
- Milo
- ▲ Tallow
- △ Jack

Fig. 8.6 Distribution of sightings of dominant males courting oestrous females, 1981.



- Perssimonn
- ▲ Jack
- Henslowe
- Theo

Fig. 8.7 Distributions of sightings of dominant males courting oestrous females, 1982.



- Perssimonn
- ▲ Jack
- Henslowe
- Geebung
- Nankeen

Fig. 8.8 Distribution of sightings of dominant males courting oestrous females, 1983.

stares at Henslowe again. Henslowe is crouched very low, looking very solid and threatening, staring (glaring) steadily at Jack. After several more seconds of this, Jack hops quickly away, leaving Henslowe, joins Max. Jack stands beside Max, rubs his chest on a tussock, moves in front of Max, and they grapple with their forearms...

Jack defeated Max in that encounter (although Max came to dominate Jack in 1984) but Henslowe had prevailed over him very easily. Interactions between breeding males were seen very rarely.

Some of the sightings I made of Jack courting females around the time this interaction took place, and later in 1983, and which I used to map his 1983 dominion, may actually have been instances of him inappropriately following females already mated by Henslowe - his true dominion in 1983 may have been vanishingly small.

The second male with a small 1983 dominion, Nankeen, was often seen courting oestrous females either near the joint border of Henslowe's and Geebung's dominions, or near the eastern edge of Henslowe's dominion. It is possible that he also courted oestrous females farther to the east, out of my study area.

The dominions of breeding males remained spatially discrete in spite of the fact that their home ranges often overlapped extensively. Dominions were, on average, only 31.4% of the males' 95% home ranges (mean dominion size=9.16 ha; mean home range size=28.9 ha; n=12 wallaby years). Of the total number of a male's sightings in a given year, a mean of 47.2% were outside his dominion. When out of their dominions, males deferred to the locally dominant male, in a similar fashion to non-breeding large males. If a breeding male found an oestrous female outside his dominion who was not being followed by the locally dominant male, he courted her until that male found and displaced him, and thereafter kept contact with the female only from some distance, or not at all.

I do not have enough data to accurately estimate the average length of time spent by dominant males as dominion-holders. However, none of the males held his dominion for more than two years. one did

so for only six months, and the others held this status for between one and two years. I therefore suggest the average duration of tenure in dominions to be somewhere between one and two years.

### 8.5 Discussion

Male red-necked wallabies' dominance ranks are largely determined by their relative body sizes, although the imprecision of this relationship suggests that other factors, such as differences in the fighting skills of individual males, and the tactics they use to elevate their status, also have some influence on dominance orders. Similar results have been found by Kaufmann (1974a) for whiptail wallabies, and also by Grant (1973) for eastern grey kangaroos. However, in quokkas the dominance rankings of males are correlated with their ages rather than their body weights (Kitchener 1972). Very close correlations between age and dominance status have also been found among female bison *Bison bison* (Rutberg 1983) and horses *Equus caballus* (Wells and Goldschmidt 1979). It is therefore plausible that observed correlations between body size and dominance rank could be incidental to associations between age and size, together with direct effects of age on dominance rank. However, the correlation between age and weight for adult male wallabies is so loose (see Fig. 1.2) that it could not significantly affect a correlation between body weight and dominance.

The simplest interpretation of this relationship between body size and dominance rank is that large males acquire dominance because their size gives them some advantage over smaller males in aggressive interactions. However, it is possible that to some extent, the causation in this relationship may run in the opposite direction: dominance status may influence body size. Dittus (1977) showed that subordinate male toque monkeys *Macaca sinica* feed less efficiently than dominants and that males who lose status subsequently lose weight. It therefore seems likely that in this species an individual's dominance position during its growth period could influence its growth rate and the ultimate size it might reach. It has also been shown that aggressive interactions influence levels of circulating hormones in mammals, and that these changes may be more

long-lasting in subordinate than in dominant individuals. Following aggressive encounters, plasma levels of adrenal corticoids rise, while levels of testosterone and gonadotropin may fall (Harding 1981). To the extent that plasma concentrations of hormones which influence growth rates and the duration of growth in males may vary in this fashion, an individual's body size could be partly determined by the outcomes of his past encounters with other males. Only with long-term data on the growth rates and social status of known individuals, ideally in conjunction with monitoring of their hormone levels, will we be able to know whether effects of this kind are important. If there is an effect of the outcomes of a male red-necked wallabies' interactions with other males on his hormone balance, it could provide an elegant explanation for the observation that males tend to initiate encounters with slightly smaller males : they may be, in effect, trying to suppress, by inducing hormonal changes in them, males slightly below their own status, while avoiding conflicts which could lastingly diminish their own confidence and aggression.

The data that I have presented in this chapter indicate that the dominance relationships between males of similar size tend to be more stable among large than among smaller males. The evidence for this is that interactions between large males are more likely to be displacements than are interactions between medium or small males, which usually escalate into fights. In a displacement, one of the interacting males immediately behaves submissively, as if reluctant to dispute the other male's higher status. Other trends suggest that the most important period for the establishment of fine differences in rank between males may be during the time that breeding males are excluding them from groups of males following oestrous females; that is, as they are passing from the medium size class into the large size class, and may be within a year or two of becoming breeding males. Males interact with their highest frequency, and are most likely to provoke similarly-sized males, when they are of this size. They are also, at this stage in their lives, selectively aggressed by the most dominant, breeding males. Other data (in the previous chapter) show that very large males do not associate most frequently with similarly-sized males (as do all smaller males), but with males

several size ranks below their own ranks. I interpret these trends in the following way : as one means of guaranteeing their own continued access to oestrous females, breeding males suppress males who are queueing to enter the breeding pool, while those queueing males seek to consolidate what status they have, and gain advantage over their peers by provoking them, or being drawn into fights with them, at relatively high frequencies. Evidently, the most important means by which non-breeding large males entered the breeding pool was by stepping into a space left by a breeding male who had died or disappeared. This happened three times during my study. The dominant male in the northern part of the study area in 1981, Milo, was succeeded by his immediate subordinate, Perssimonn, only after Milo disappeared at the end of 1981. Likewise, Henslowe and Theo had both been present in Tallow's dominion in 1981, but each of them took up sections of it only when Tallow disappeared. The only male who remained alive in the study area after his dominion had passed to another male was Jack, and his dominion had not been usurped by a younger male, but had been taken over by a neighbouring dominion-holder (Henslowe). I saw no clear indications that males first acquire dominions by challenging and vanquishing their owner. Under these circumstances, those males who have some prospect of acquiring a dominion will be most likely to do so if they can be dominant to other males who are also waiting to take over dominions.

Quite apart from the interest attached to the ways in which males come into the possession of their dominions, the dominions themselves are intriguing phenomena. Their existence shows that dominance in large male red-necked wallabies is site-dependent. In some parts of their home ranges they enjoy uncontested access to oestrous females, while elsewhere they defer to one or other of their peers. Although there is no overt defence or advertisement of dominions, no restriction on the movement through them of any class of wallaby, nor even any strong tendency for breeding males to stay within their own dominions, the boundaries between them are often very distinct. There are two important questions to ask about this site-fixity of dominance. Firstly, why are some males not dominant throughout their entire home ranges? and secondly, why do males not exclude other males

from the areas in which they are dominant?

Large males are potentially able to inflict quite serious injuries on one another in fights; any large male who tried to dominate all of the other large males whose home ranges overlapped his own would place himself at the risk of serious injury, or at least exhaustion, and the consequent complete loss of his potential to achieve any matings with females. Clearly, however, males will be selected to contest sexual access to some females, and fight hard to win mating rights over at least some of the females potentially available to them. Having achieved this, the risks of total reproductive failure undergone by a male attempting to expand his area of dominance to include all of a large home range might outweigh the proportional increase in access to mates that would follow were he successful. Probably the only males who could comfortably expect to become supremely dominant throughout their home ranges would be those who, for some reason, were clearly superior in size, vigour or prowess in fighting to all of their neighbours, a circumstance which seems not to have arisen during this study.

There may be a number of reasons why the dominions are not defended and used exclusively. To begin with, because male red-necked wallabies usually travel alone, a male who attempted to evict all other males from his dominion and to keep them out would have to deal with each intruder separately; this would compound the difficulty of his task. This cannot be the whole explanation though, because males of some asocial species of ungulates ecologically similar to the red-necked wallaby successfully defend territories (e.g. Klipspringer *Oreotragus oreotraus* Dunbar and Dunbar (1974), roe deer, Bramley 1970). Probably, male red-necked wallabies do not defend territories because, given that males can - without being seriously threatened by other local males - stay close to females who come into oestrous in their dominions, the extra costs and risks incurred through active exclusion of those males from the whole dominion may not be worthwhile. In addition to this, strict defence of the dominion would oblige dominant males to spend almost all of their time there, but by moving outside their dominions, males have the opportunity to surreptitiously mate with other females, find out about weaknesses or

disappearances of other dominion-holding males, and perhaps to expand their own dominions into the spaces.

I have used the word 'dominion' here with some reservations. The term was introduced by Brown (1975) to describe an area within an individual's home range wherein it is dominant, but from which it does not attempt to completely exclude other individuals. This kind of spatial organisation of dominance has been observed in males of the dragonfly *Leucorrhinia intacta*, who select perches on which they await receptive females and from which they chase rival males. The probability that a perching male will chase another male varies with the intruder's distance from the perch, and his behaviour : males are more likely to be chased if they approach the perching male closely, and if they hover rather than fly past him. Males are also more likely to chase intruders when the total intruder pressure is low (Wolf and Waltz 1984). In the black and white colobus monkey *Colobus guereza* population studied by Oates (1977a), groups have extensively overlapping home ranges, but each group is more likely to displace other groups in the core area of its own home range than at the periphery. Ungulates illustrate a diverse array of styles of territoriality, which range from strict defence to territorial advertisement without exclusion. The first type is displayed by blue duikers *Cephalophus monticola* (Dubost 1980). Territorial impala *Aepyceros melampus* males will allow bachelor males to pass through their territories provided they do not interact with females (Jarman 1979); while territories of the white rhinoceros *Ceratotherium simum* are often occupied by a satellite subordinate male as well as the dominant territory-holder (Owen-Smith 1975). In Grevy's zebra *Equus grevyi* dominant males establish discrete areas within which they advertise their dominance and defend oestrous females from other males, but from which they do not exclude any conspecifics (Klingel 1974). The partiality, or complete lack, of exclusion of rivals by dominant individuals from their areas of dominance in these species contrasts with the behaviour of many passerine birds to which the term 'territorial' was first applied in a biological context. In great tits *parus major*, for example, breeding pairs occupy sharply defined, discrete areas from which they vigorously exclude all other

conspecifics (Krebs 1971).

As Kaufmann (1983) and others have recognised, there is in reality an indivisible continuum of forms of spatial organisation of dominance between the classical territoriality of passerine birds, and non-exclusive, unadvertised areas of dominance, such as I have described for red-necked wallabies. Kaufmann's definition of territoriality - as 'a fixed portion of an individual's or groups range in which, through social interactions, it has priority of access to one or more critical resources over others who have priority elsewhere or at another time' - embraces the whole of this continuum. While recognising the utility of this definition, I feel that, given the confusion surrounding the meaning of the word 'territory' (see Kaufmann 1983) it should be retained for application only to systems which approximate the classical form of territory, while the word 'dominion' can be applied to systems towards the other end of the continuum.

Table 8.1 Matrix of agonistic interactions between male wallabies (individuals are ranked according to body size). Entries are the absolute numbers of interactions seen.

WINNER	LOSER																																
(Large)	Milo	Henslowe	Tallow	Jack	Tristania	Geebung	Theo	Perssimonn	Colo	Gillgully	Max	Hubert	Pademelon	Marlo	Django	Pipo	Bobuck	Pedro	Oldbuck	Beetle	Seradoc	Took	Silkie	Toona	Dama	Paladin	Carrabeen	Walpajirri	Gymnopedie	Niggle	Aepy		
Milo	X							2																									
Henslowe		X									1	2																					
Tallow			X				1			1																							
Jack				X					9	2	6				7	1																	
Tristania					X					2				1																			
Geebung					1	X																											
Theo							X		1																					1			
Perssimonn								X							3					2													
Colo									X	3						7									1								
Gillgully										X																							
Max											X	1		1									1			1	1						
Hubert												12	X	2										3	3	2				1			
Pademelon														X																			
Marlo															X																		
Django																X																	
Pipo																	X				1												
Bobuck																		X															
Pedro																			X														
Oldbuck																				X	1												
Beetle																					X	1	1										
Seradoc																						X											
Took																							X										
Silkie																								X									
Toona																									X								
Dama																									1	X		2	2				
Paladin																											X						
Carrabeen																												X					
Walpajirri																													X				
Gymnopedie																														X			
Niggle																															X		
Aepy																																X	

(small)

TABLE 8.2: Number of interactions (observed/expected) between males of the major size classes ( $\chi^2 = 27.9$ , 5 d.f.,  $P < 0.001$ )

	Large males	Medium males	Small males
Large males	19/ 7.1		
Medium males	9/11.3	1/3.9	
Small males	3/ 6.3	0/3.9	1/3.3

TABLE 8.3: Relationship between the difference in size of interactees and the likelihood that interactions will escalate into fights ( $\chi^2 = 6.15$ , 2 d.f.,  $P < 0.05$ )

	Size difference (number of body size ranks)		
	0-4	4-8	> 8
Percentage of interactions resulting in fight	47.1	54.1	10.0
n (interactions)	51.0	32.0	20.0

TABLE 8.4: Relationship between body size classes of interactees and interaction type (observed/expected number of fights)

	Large males	Medium males	Small males
Large males	18/17.60		
Medium males	10/10.63	6/2.80	
Small males	1/ 6.00	3/3.20	5/2.8

## CHAPTER NINE

### Courtship and Mating

#### 9.1 Introduction

From the previous chapter, it is clear that differences between male wallabies in size and dominance status determine their abilities to defend access to oestrous females. However the distribution of mating success among males could also be influenced by strategies employed by females to increase the likelihood that the males with whom they mate will possess certain traits. Do female red-necked wallabies choose their mates?

This chapter analyses courtship in red-necked wallabies, and shows how the females influence its character and the identities of the successful males.

#### 9.2 Duration of oestrus

In this chapter I use the term 'oestrus' to refer to the period, preceeding and including the time at which a female mates, in which she is unusually attractive to males and is continuously followed by them. Female red-necked wallabies spend, on average, less than 30% of their time with males. However, approximately three weeks after her young permanently leaves the pouch, each female passes through a period of at least four days during which she is constantly followed and courted by males (her 'consorts'). Some aspects of the females' behaviour also change during this time. Oestrous females tended to become unusually nervous and flighty, particularly towards the end of oestrus; a few became very jumpy and groomed themselves sporadically as if troubled by biting flies. The behaviour of males following oestrous females suggested that these females also emitted a characteristic scent. This was indicated by the males' eagerness to approach and sniff oestrous females around the pouch and cloaca, and more clearly by the way in which males who had become separated from

oestrous females carefully sniffed the air and ground as they searched for them. Once, I watched two males relocating an oestrous female from whom they had become separated, while I kept her in sight : the males independently followed the female's path almost exactly, sniffing the ground carefully and regularly as they went, until each came to her after following her scent for approximately 250 m.

To measure the duration of a female's oestrus it was necessary not only to observe her regularly while she was fully oestrous, but also to locate her during the days immediately before her period of oestrus began and immediately after it ended, so as to precisely determine the dates of her first and last days in oestrus. It was often difficult to find females as regularly as this. Another methodological difficulty in measuring the duration of oestrus was that, because my field trips were usually slightly less than two weeks long, I was more likely to observe the entire course of short rather than of long bouts of oestrus : this problem could lead me to underestimate the true average duration of oestrus. I was able to determine first and last dates in oestrus for five females, these bouts of oestrus lasted four, five, six, seven and eight days (median=six days, mean=six days). However, another six oestrus periods which were incompletely recorded lasted at least six days each, and a seventh persisted for at least eight days. I therefore conservatively estimate the average duration of oestrus as seven days. Using this estimate as a rule-of-thumb, I was able to divide bouts of oestrus which were incompletely recorded into early (first four days) and late (last three days) phases, and this forms the basis for much of the quantitative analysis which follows.

The estimate of average duration of oestrus arrived at above refers only to adult females who were breeding without pause. Oestrus may have been even more prolonged in females breeding for the first time, or returning to breeding after a period of reproductive inactivity. I was not able to thoroughly document durations of oestrus for such females, but I did see males consorting with one of each of these classes of females over periods of at least ten days.

I saw only four matings, each of which took place during the last day of oestrus. It seems that females were closely followed and

guarded by males for no more than about twelve hours after they first permitted mating. The small number of matings seen also leads me to suspect that mating is largely nocturnal.

### 9.3 Interactions between males and oestrous females

When females were in oestrus, they interacted with the males who were following them at a frequency of 1.57 interactions per hour (n=21 hours of systematic observations of oestrous females and consorting males). This compares with a frequency of male-female interactions of 0.6 per hour of observation of non-oestrous females in groups with males (n=20 hours). The frequency with which females interacted with their consorting males increased through the course of the female's oestrus : during early oestrus, interactions occurred with a frequency of 0.57 per hour, while during late oestrus they occurred with a frequency of 2.07 per hour.

Interactions between males and oestrous (and non-oestrous) females were invariably instigated by the male, and most often involved him approaching her very closely and briefly sniffing her cloaca and pouch area. Oestrous females usually stood still for such inspections, and were much less likely than were non-oestrous females to move away from or actively rebuff males who approached and inspected them. I once saw an oestrous female pass urine while a large male had his muzzle near her cloaca, and the male take some of the urine into his mouth. This male did not show any discernible signs of flehmen, nor did any of the other male wallabies whom I watched sniffing females. Flehmen has been observed in other species of *Macropus*, but it is performed less conspicuously by them than it is by male ungulates (Coulson and Croft 1981). It is possible that females allowed males to taste their urine more frequently than this single observation would suggest. The animals I observed were often partly obscured in long grass, and some subtle features of their interactions could easily have passed unnoticed.

A male would sometimes approach a female from the front, press his chest against hers, and rub his chest from side to side across her chest. I refer to this behaviour as 'chest-rubbing'. The movements and postures involved in chest-rubbing are in many ways similar to

those used in grass-pulling (see previous chapter) and were also sometimes performed *in vacuo*, i.e. in front a female but without actual contact. Males usually initiated this kind of interaction when they rejoined an oestrous female after a separation from her, or when making an initial inspection of a female, and were thus especially excited or aroused.

Although I did not see females actively courting or soliciting males, two females were observed to respond to the approaches of their dominant male consorts by grooming them over the shoulders and back with paws and mouth. These females only groomed males during the last two or three days of oestrus; for the rest they, and the other oestrous females, remained indifferent to, if not mildly alarmed by, the attentions of the males.

Large, dominant males, who were able to stay in closest proximity to oestrous females, usually interacted with them cautiously, as if wary of alarming them and putting them to flight. Lower-ranking males, who attempted to interact with females whenever circumstances allowed (see below) were likely to do so in a hasty, excited and sometimes rough manner.

These measures and descriptions of interaction frequency and type probably under-estimate the intensity of courtship in red-necked wallabies. The most impressive characteristic of this courting is the attentiveness and determination with which males follow oestrous females, and the fact that some males stay as close as they possibly can to a single female for many days on end.

#### **9.4 Dynamics of groups of consorting males**

When in oestrus, females were usually followed by small groups of males : the median number of males with oestrous females was 2, the mean number was 2.55 (n=106 sightings of oestrous females). The number of males following each female tended to increase as her oestrus progressed (see Fig. 9.1); during their final two days of oestrus some females were being followed by as many as seven males. Typically, a single large male remained closest to the female, and a number of considerably smaller males followed this male and the female (these two classes of males are referred to as 'dominant' and

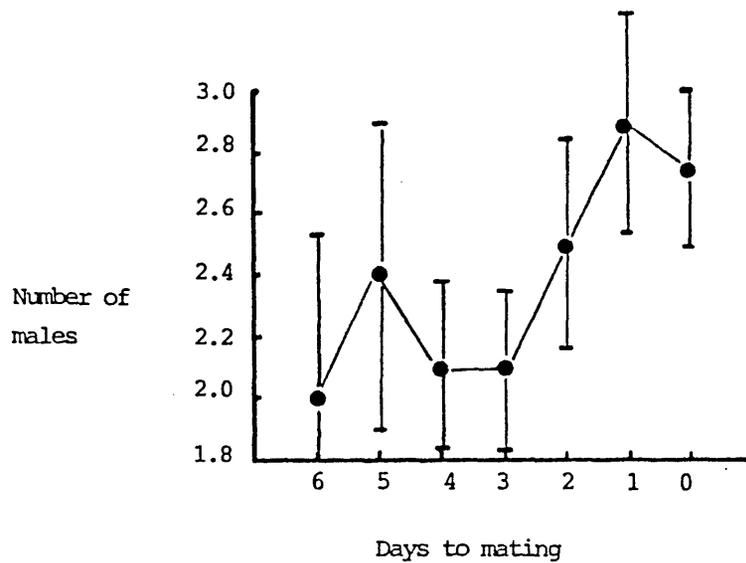


Fig. 9.1 Relationship between day of oestrous, and number of males following the female (means, with 95% C.I.s).

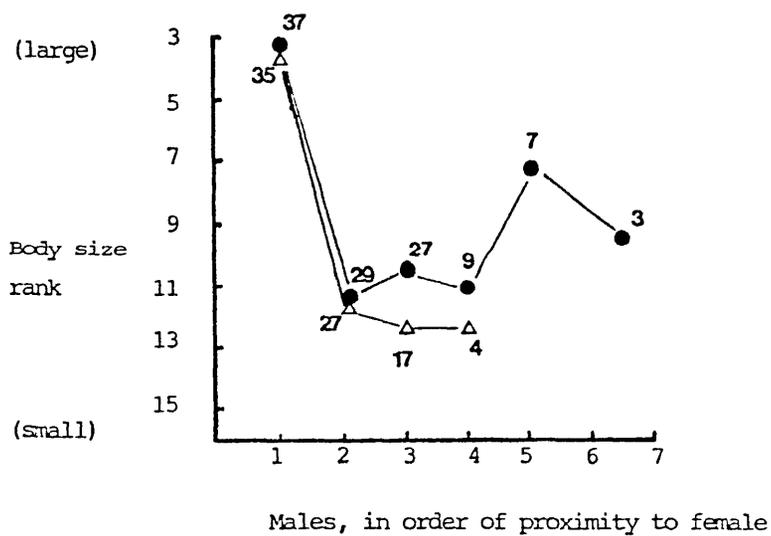


Fig. 9.2 Mean size ranks of males, in order of proximity to oestrous females (sample sizes = no. of sightings). Records from early ( $\blacktriangle$ ) and late ( $\circ$ ) oestrous.

'secondary' respectively). Fig. 9.2, which plots the average size ranks of males in their order of proximity to the oestrous female, demonstrates this clearly and also shows how the pattern changed from early to late oestrus : males of intermediate size were generally absent from consorting groups during early oestrus, but began to appear regularly on the peripheries of these groups during late oestrus. The dominant male spent most of his time within four metres of the oestrous female, while the secondary males were usually between 10 and 16 metres from her (Fig. 9.3). In terms both of size, and distance from the female, the distinction between the dominant and the secondary males was much clearer than were any orderings among the secondary males.

Unless the dominant male among a group of consorting males was also the most dominant male in the area, he was always vulnerable to a takeover by a higher-ranking individual. The frequency with which the coveted position beside an oestrous female passed from one male to another increased during the first few days of oestrus. Usually however, by the time day four or five had been reached, a very high-ranking male had found the female and taken his place beside her; thereafter the average frequency of takeovers dropped (Fig. 9.4). As a result of this process of successive takeovers of oestrous females by progressively larger and more dominant males, females tended to be courted by larger males late in oestrus than they had been early in oestrus. The observed size distribution of males closest to females in late oestrus differed significantly from the frequency distribution expected had there been no change from early oestrus (see Fig. 9.5;  $\chi^2=10.08$ , 4 d.f.,  $P<0.05$ ). The dominant males also tended to spend significantly more of their time very close to females when those females were in late oestrus. Fig. 9.6 shows that dominant males spent very little of their time at distances of more than nine metres from females in late oestrus, whereas they had been willing to move further from their females during early oestrus ( $\chi^2=12.03$ , 5 d.f.,  $P<0.05$ ; test performed as for Fig. 9.5).

### 9.5 Movements of oestrous females

Some females moved widely while in oestrus. Females normally

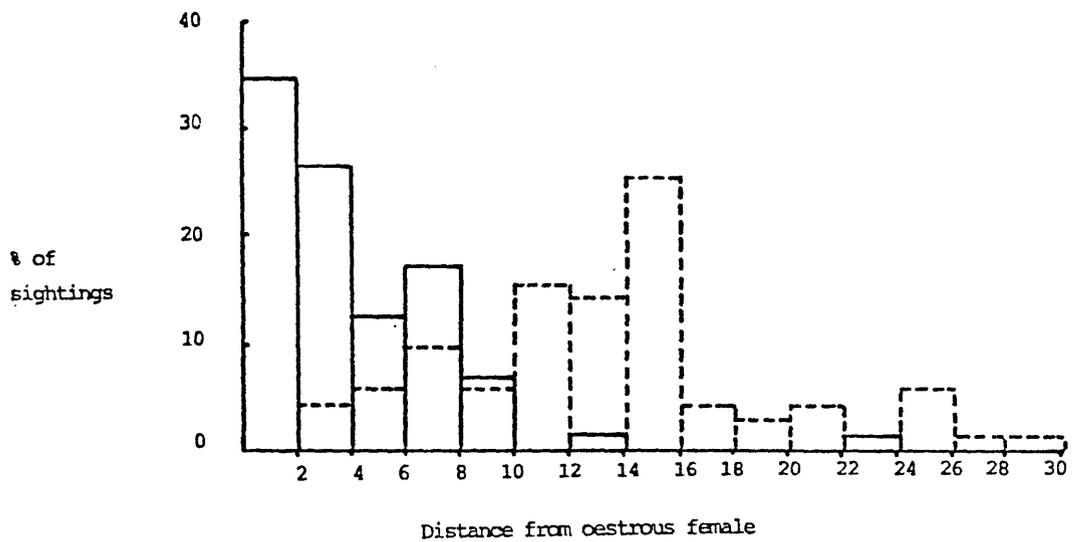


Fig. 9.3 Closeness of association of dominant (solid lines) and secondary males (dashed lines) to oestrous females ( n=72 and 71 respectively).

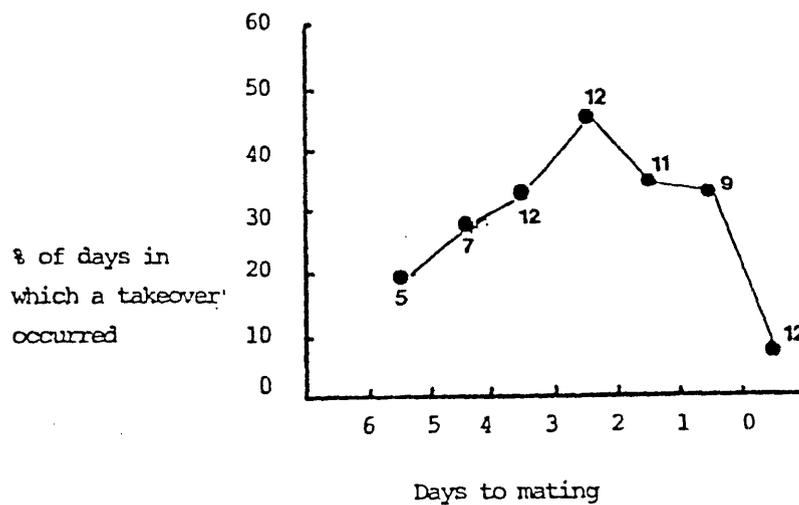


Fig. 9.4 Relationship between day of oestrous and probability of occurrence of a takeover of the dominant position (sample sizes are numbers of female.days of observation).

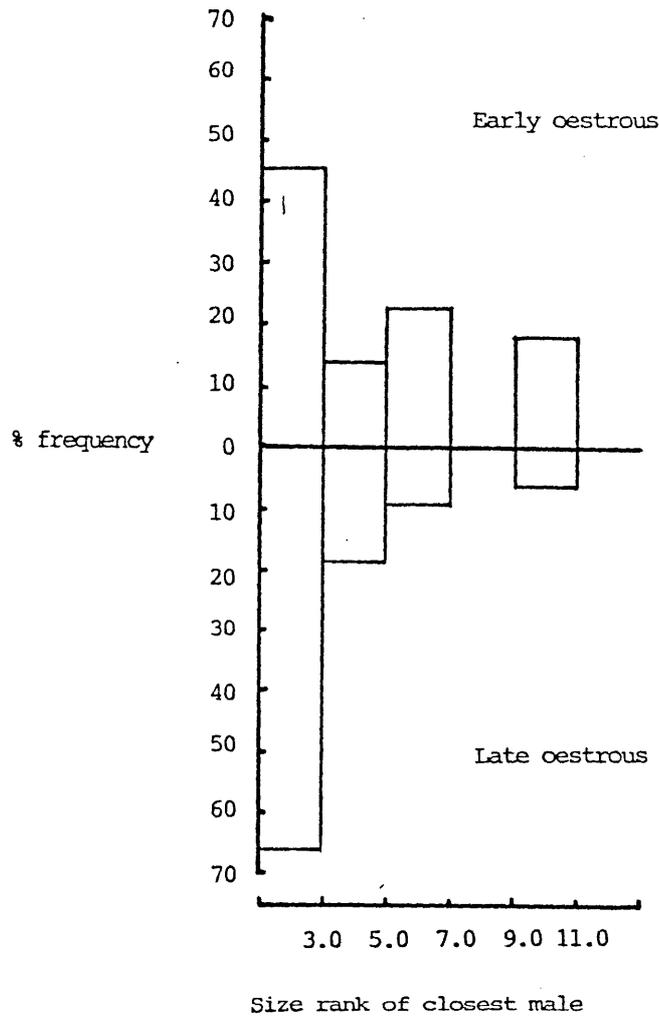


Fig. 9.5 Frequency distributions of size ranks of males closest to oestrous females in early (n=35 sightings) and late (n=32 sightings) oestrous.

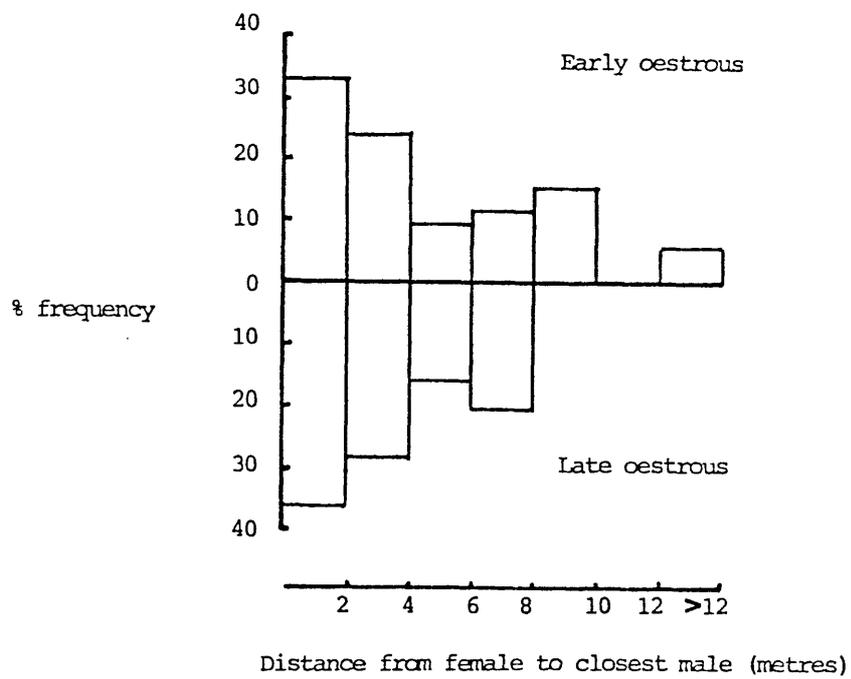


Fig. 9.6 Closeness of dominant males to females in early and late oestrous.

spend most of their time within a central portion, the core area, of their home ranges (see Ch. 3). To determine whether or not females were more likely to move out of their core areas while in oestrous than at other times I found, for each of the twelve females in the intensive sample, the proportions of their sightings while in oestrous which fell within that central portion of their home ranges which enclosed 90% of the sightings I made of them through the rest of the year. Nine of these twelve females spent less than 90% of their time within these core areas while in oestrus. These nine females ranged into peripheral parts of their home ranges, which they rarely visited at other times. One female, who was located 16 times while she was in one of her oestrus periods, was in her 90% core area for only 37% of these sightings. The number of females included in this analysis is too small to permit a meaningful statistical analysis of the results, so the observation must remain suggestive rather than conclusive.

During the last day or two of oestrus, females sometimes fled from their following males, and in so doing led them on chases. Such courtship chases could last for several minutes and continue over several hundred metres, with the female moving through little-used parts of her home range, or even leaving it altogether for brief periods. It was not clear to me whether courtship chases began because the females actually became frightened or upset by some actions of the males, or whether females started them for reasons unconnected with the immediate behaviour of the males. The pace maintained by females in courtship chases varied considerably : one female simply hopped slowly over a meandering path, not moving more than fifty metres from her starting point; while another fled at nearly top speed and was over 300 metres from her point of departure when she settled down. Courtship chases usually ended when the female voluntarily stopped moving away from her pursuing males, although I did see one male arrest the full flight of a female by catching and mounting her.

#### **9.6 Interactions among consorting males**

Most of the interactions between consorting males involved the dominant male and one or other of the secondary males, and began with

attempts by the secondary males to interact with the female. Secondary males spent much of their time carefully watching the dominant male and his female, and if that male's attention wandered from the female, would move towards her. This sometimes happened, for example, if the dominant male lay down to rest and the female moved more than a few metres away from him to feed, or if he became involved in interactions with other males, or if the group was temporarily split up by some disturbance. If an opportunity like this arose, a secondary male would hop quickly up to the female, sniff her pouch and cloaca, and perhaps try to mount her. As soon as a dominant male realised that something like this was going on, he quickly displaced the secondary male, forcing him back to a distance of ten metres or more from the female. Secondary males sometimes edged towards a female even while the dominant was alert and standing beside her : in such cases it was necessary only for the dominant to stare at the incoming male, or step towards him, to send him back. I saw no overt cooperation among secondary males, but it sometimes happened that if a dominant male became distracted by one secondary male, another would take advantage of this and approach the female. However, provided the dominant male remained beside the female, the other males had little chance of interacting with her.

If another large male approached the female the dominant male would displace him continuously until he had forced him completely out of the group, provided, of course, that he was dominant to that male, otherwise he himself would be displaced. This kind of interaction between large males was often accompanied by frequent grass-pulling by the dominant of the two, and usually forced the lower-ranking male to 40 metres or more from the female and the other males, whereupon the dominant male returned to the female and the other either left the area entirely, or tried to follow the group from the distance to which he had been relegated. These interactions provided excellent opportunities for secondary males to gain temporary access to oestrous females, and probably for this reason dominant males became less likely to move away from their females as oestrus progressed and mating became imminent (see Fig. 9.6); therefore, other large males were more often able to remain in consorting groups, albeit usually on

the edges of them, during late rather than early oestrus (see Fig. 9.3; the other large males were probably also more strongly attracted to the female as the likelihood that she would be ready to mate increased).

Most of the kinds of interactions described above were conducted with little overt aggression - subordinate males usually gave way with little resistance. However, interactions between males could become very bitter and direct when the female led them on courtship chases, and when she finally permitted mating. During courtship chases each male tried to stay as close behind the female as possible, so as to be the closest male to her when she stopped. Because the female was usually nearly or actually ready to mate when she became involved in courtship chases, this competition between the pursuing males was often intense. Several times I saw males charging headlong at one another as they chased a female, apparently attempting to throw one another from her path. Males sometimes also delivered swift kicks or jabbed and cuffed one another with their forearms as they chased females. As at other times, subordinate males were only able to be close to the female for very short periods; when she stopped fleeing, the dominant male quickly took his place beside her. It was, therefore, the dominant male who mated with the female, but other males, particularly the larger secondary males in the consorting group, might try to interrupt his mating. The following incident, as recorded in my field notes, is the best example I saw of this:

1710: 4 wallabies, Sarsparella, Henslowe, Max, Hubert.

Sarsparella apparently giving birth, Henslowe staying very close to her, with penis erect, walking around her and watching the other males (who also have erections). Two other large males (Jack and Geebung are also within 50 m of Sarsparella).

1715-1730: Max and Hubert approached Sarsparella several times, each time Henslowe sent them away by staring at them or moving towards them.

1730: Hubert moves up to Henslowe/Sarsparella quite quickly, Henslowe lunges at him, pushing him and raking him across the back with his forepaws, Hubert darts away.

Same incident repeated with Max.

1735: Henslowe mounts Sarsparella, but moves off her when he hears one of the males coming up behind him, he turns the male away with a look, and remains standing beside Sarsparella. Both Max and Hubert are watching Henslowe and Sarsparella very intently. Geebung and Jack also seem aware of what is going on, but have not yet approached.

1745: Henslowe mounts Sarsparella again, for approx. 45 seconds. The other two males immediately hop in close and dart round Henslowe/Sarsparella, appearing willing to attack. Henslowe lifts Sarsparella completely off the ground and spins around, trying to keep facing the other males. She struggles and gets free of him, hops away, all the males follow her, I think including Jack and Geebung (it is getting dark). A short chase ensues with some brief but severe encounters between the males. Henslowe delivered at least one good blow with his hind feet and one with his forepaws. Sarsparella stops about 40 m away.

As darkness fell, I caught a last glimpse of Henslowe guarding Sarsparella, again as the other males stood around in a circle. Another incident illustrates the severity with which similarly sized males sometimes competed at mating. On this occasion I saw a female being pursued by two large males, one of whom was much closer to her than the other. She stopped, and the first male mounted her for about 30 seconds, until the other male hopped rapidly up, went round behind the pair, clasped the first male briefly, then jumped up into the air and kicked him hard on the back. The mating pair broke up at this, the female dashed off with both males in hot pursuit, and I lost sight of them all. I was unable to identify any of the participants in this encounter.

All of my observations indicated that, although dominant males might be harassed while mating with females, this caused only momentary lapses in their ability to control access to oestrous females and they retained the strongest chances of siring the female's

offspring.

### 9.7 Discussion

In a number of species of macropods, oestrous females are followed by groups of males within which stable dominance orders determine priority of sexual access to the female (see Kaufmann 1974a, Coulson and Croft 1981 and Jarman 1983). In red-necked wallabies, the long duration of each female's period of heightened attractiveness to males clearly enhances the mating success of high-ranking males. Male wallabies are alert to any signs of oestrus in females, and become particularly inquisitive of females who are being courted or investigated by other males. Therefore, even though an oestrous female might first be located and followed by a small, low-ranking male, her condition quickly becomes obvious to other males, including more dominant individuals, so that the place beside her is taken by progressively larger males over the ensuing seven days, and by the time she is ready to mate it is almost certain that a very dominant male will be at her side. If females did not advertise oestrus over such long periods, larger males would be less likely to find them in time, and females would less regularly be mated by supremely dominant males. Because the females' advertisement of oestrus could plausibly be different to what is observed, and could thereby produce a different distribution of mating success among males, it constitutes 'mate choice' in the sense that Maynard Smith (1978) has defined the term.

There may be some costs to females of their long periods of sexual attractiveness to males. One consequence of the competition among several males for a single female was that, especially when one male was mating and the others were attempting to dislodge him, the female might be roughly handled. One female was limping the day after she had been mated; another had a cut, not deep but long, on her back. The chance that a female might be killed by a predator was probably also relatively high while she was being followed by a group of males. Courting groups are unusually large (by red-necked wallaby standards) and the behaviour of the males made them conspicuous to other males, to me, and probably to dingoes as well. The wide movements made by

some females while being followed by males took them through rarely-visited areas and across open terrain, and this, together with the distractions provided by the males, might have reduced their chances of escaping from a predators. Under these circumstances, a female's personal safety would probably be compromised least if, instead of making herself the object of a crowded and competitive courtship, she were to conceal her reproductive condition until ready to mate, then approach a solitary male and lead him silently to a secluded place for a brief mating.

It is at least plausible, therefore, that the long period of sexual attractiveness of female red-necked wallabies has evolved because it leads to intense competition between males for access to them, and guarantees, for each female, a mate who has demonstrated his ability to dominate many others. A long period of courtship may be necessary for this because in a non-gregarious animal like the red-necked wallaby, there should be a considerable delay in the detection of a female's oestrus by all of the local males. Kaufmann's (1974a) discussion of courtship in the more social whiptail wallaby implies that female whiptails are persistently followed and courted by males for shorter periods than are female red-necked wallabies. In many species of ungulates, females are followed closely ('tended') for varying periods of time by males who compete for mating rights. This heightened interest by males in females at and before their time of mating corresponds to 'oestrus' as I have used the term in this chapter, and, as Table 9.1 shows, it tends to be of longer duration in solitary species (e.g. moose) than in very social ones (e.g. American bison). Although it may be dangerous to make direct comparisons of courtship behaviour across species differing so widely in gregariousness, the trend is consistent with the suggestion that an extended period of sexual attractiveness has evolved in the females of solitary species to ensure that they will be found and competed for by a broad array of males before they become receptive to mating. Note that Table 9.1 does not include species in which males pre-empt direct competition for females by defending territories or gathering harems.

In some species of mammals, females show clear preferences, while in oestrus, for contact with dominant males (e.g. brown lemmings

*Lemmus trimucronatus* Huck and Banks 1982, feral goats *Capra hircus* Shank 1972 and African elephants Moss 1983), and in other species, some aspects of the behaviour of oestrous females incite competition among males and thereby lead to the suppression of mating by low-ranking males. The best-known example of this is the tendency of female elephant seals *Mirounga angustirostris* to protest loudly when males attempt to mate with them, thereby drawing the attention of other males who may intervene if they are of sufficiently high status (Cox and Le Boeuf 1977). Oestrous female lions *Panthera leo* initiate competitive interactions between males by moving towards one male while being followed by another (Packer and Pusey 1982) and female toque monkeys, when in oestrus, move to the edges of their troops so that they attract males from other troops as well as from their own (Dittus 1977).

In a species such as the red-necked wallaby, the attention of several males at the same time has no immediate benefit for the female, and may actually be damaging or dangerous. Therefore, if we are to regard the extended period of attractiveness as a true adaptation, we must conclude that it evolved because females who are mated by males who have attained large size and high social rank will leave offspring who are more likely to also possess these traits than would otherwise be the case. The difficulty with this argument is that the heritability of traits directly correlated with Darwinian fitness should be very low (Williams 1975, see also Borgia 1981). However, as Maynard Smith (1978) Searcy (1982) and Partridge (1983) have pointed out, because the heritability of fitness, though low, will usually not be zero, choice for males of high genotypic quality may still be discernible in species, such as red-necked wallabies, whose females have no other grounds for mate choice.

TABLE 9.1: Duration of close following of females by males in the courtship of several species of ungulates

Species	Duration of following (days)	Source
Moose, <i>Alces alces</i>	7-12	Almann (1959)
African elephant	2- 6	Moss (1983)
Bighorn sheep and Dall's sheep	2- 3	Geist (1971)
African buffalo, <i>Syncerus caffer</i>	2- 3	Sinclair (1974)
Sheep	1- 3	Grubb (1974b)
American bison	1- 2	Lott (1981)
Greater Kudu, <i>Tragelaphus strepsiceros</i>	1- 2	Owen-Smith (1984)

## CHAPTER TEN

### Social Organisation and Reproductive Success of Females

#### 10.1 Introduction

The tendency for the females of many species of mammals to spend their lives close to the places where they were born, while their brothers disperse, often results in the sharing of home ranges among female relatives, who may therefore compete with one another for the same resources. Given that tolerance by mothers of ecological competition from their daughters (and other relatives) represents a form of investment in them, it follows that in matrilineal species, maternal investment may be much more prolonged in daughters than it is in sons (see Hamilton 1967, Clark 1978, Dittus 1979, Bulmer and Taylor 1980, Clutton-Brock, Albon and Guinness 1982). These inferences are supported by two series of observations.

Firstly, the reproductive success of individual females declines with group size in a number of species (e.g. yellow-bellied marmots *Marmota flaviventris*, Downhower and Armitage 1971; hoary marmots *M. caligata*, Wasser and Barash 1983; Black-tailed prairie dogs *Cynomys ludovicianus*, Hoogland 1981; red deer, Clutton-Brock, Albon and Guinness 1982; elephants, Douglas-Hamilton 1972; most studied primates, Van Schaick 1983). Per capita production of young may increase with group size in some species with well-developed systems of cooperative breeding, such as black-backed jackals *Canis mesomelas* (Moehlmann 1979), but as shown by data on wolves, *C. lupus* (Harrington et al. 1983) and African wild dogs (Malcom and Marten 1982), this is by no means always the case. These results imply that mothers will, in general, find it costly, in terms of their own future reproduction, to enter long-term associations with their daughters.

Secondly, and as Fisher (1930) would have predicted, the inferred prolonged maternal investment in daughters appears to be balanced by

other forms of early investment in sons. Male red deer calves suckle more than female calves (Clutton-Brock, Guinness and Albon 1982), and female galagos *Galago crassicaudata*, who probably compete with their daughters at high quality food patches, give birth to more sons than daughters (Clark 1978).

In this chapter, I measure the reproductive costs to female red-necked wallabies of associating with their subadult offspring, and compare the short-term costs of producing male and female offspring. I then analyse the effects of a female's association with other members of her social group on her reproductive success, and compare this with the effects of association with the members of other social groups.

## 10.2 Reproductive success and association with subadult offspring

The proportion of her time that a female wallaby spent with her subadult offspring during the six months following its weaning seemed to have a strong influence on the probability that her subsequent infant would survive to weaning age (see Fig. 10.1). Females who produced two surviving infants in succession had spent a median of 5.6% (n=9) of their time with the first young during the six months between its weaning and the emergence of the next young from the pouch, while females whose second young died in infancy had spent 37.9% (n=7) of their time with the first young; a significant difference (U=9.0, P<0.05).

Mothers spent significantly more time with their subadult sons than with daughters of the same age (see Ch. 7), and surviving subadult males were less likely to be succeeded by surviving infants than were surviving subadult females (only 30% (n=10) of subadult males were succeeded by an infant who also survived, whereas 90% (n=10) of subadult females were succeeded by surviving infants;  $\chi^2=5.20$ , P<0.05). The relationship between association with subadults and survival of succeeding infants was repeated within each sex of subadult, although the data are too scant to demonstrate the statistical significance of the trends within each sex.

Infants who died had had pouch lives only slightly shorter (median of 9.0 months, n=16) than those who survived (9.5 months, n=18), and

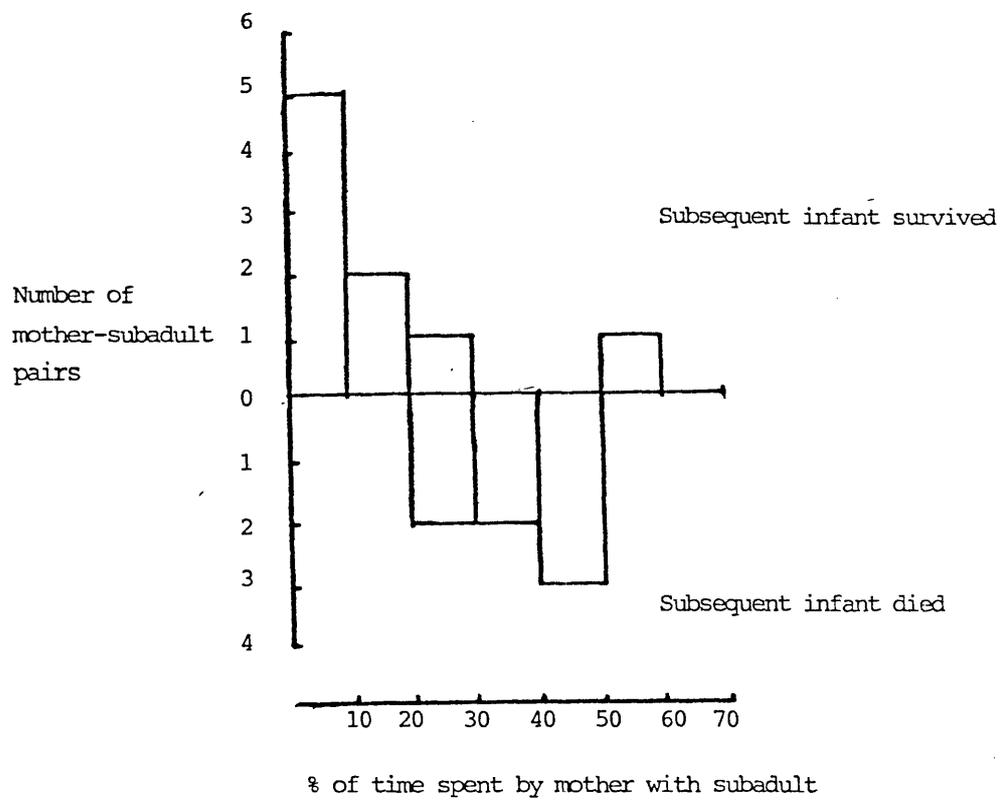


Fig. 10.1 Frequency of association by mothers with their subadult offspring, in relation to the survival of the subsequent infant.

the length of a young wallaby's pouch life did not vary according to the fate of the preceding infant (medians of 9.25 months in both cases). This result, together with the observation that very few females ceased breeding altogether during this study (see Ch. 5), demonstrates that females whose infants were dying were not compensating for the loss through increased fecundity, and that consistent differences in reproductive success between adult females were due almost entirely to variations in the survival of their infants.

### 10.3 Reproductive success and sociality

To discover whether there were costs to females of associating with wallabies other than their own subadult offspring, I calculated indices of each female's sociality during the six month period prior to the emergence of each of her infants from the pouch (i.e. during the latter two thirds of those infants' pouch lives), and compared these indices for successful (infant survived to weaning) versus failed (infant died before weaning) reproductive attempts. The sociality index was calculated by expressing the number of times the female was seen with other wallabies during the period of interest as a percentage of the total number of times she was seen over that period, and multiplying this percentage by the mean number of companions with her on the occasions when she was not alone. This index is a good standard measure of a female's degree of sociality, because it is not distorted by the tendency of mothers to isolate themselves from other adults while being accompanied by a young-at-foot (see Ch. 7). Several different indices, each measuring her degree of sociality with the members of a different category of the population, were calculated for each female, and females who had no yearling offspring were singled out for special attention.

The results in Table 10.1 show that those females whose infants died had been significantly more social (with other adult females, and subadults of both sexes) during that infant's mid to late pouch life, than females whose infants subsequently survived ( $U=270$ ,  $Z=-2.637$ ,  $P<0.01$ ). This effect was due entirely to associations within social groups : association with members of social groups other than her own

had no influence on a female's reproductive success. This relationship between sociality and reproductive success was evident for females who had no subadult offspring (either because their most recent offspring had not survived, or because they were breeding for the first time). Again, the effect was due entirely to the correlation between sociality with other members of the same social group and reproductive success (see Table 10.1).

These data can be treated in a different way. Records of 38 females were included in the above samples; of these 38, data had been collected on the outcomes of, and sociality at, more than one reproductive attempt for 17 females, and 11 of these females had produced both surviving and non-surviving infants at different times. These last females showed a significant tendency to have been more social (within social groups) prior to their failed reproductive attempts than they were before their successful attempts (by Wilcoxon Matched pairs signed-ranks test,  $T=13$ ,  $P<0.05$ , one-tailed. A one-tailed significance level was accepted because other analyses had justified a firm prediction of the direction of the result).

Table 11.2 presents data on the survival rates of infants born into social groups of various sizes. Survival rates were very much lower in medium-sized than in small groups, and lower still in large groups; the observed frequencies of infants surviving differ significantly from the numbers expected had survival been uniform across groups ( $\chi^2=6.76$ ,  $P<0.05$ ). Survival rates in small and medium-sized groups differed significantly ( $\chi^2=3.87$ ,  $P<0.05$ ). This pattern of infant survival declining as social group size increased was also apparent for other indices of survival. For example, rates of survival to 20 months of age were 43.5% ( $n=23$ ) from small, and 18.2% ( $n=11$ ) from medium-sized social groups; the sample sizes and range of group sizes available for this analysis are small and the difference does not reach significance ( $\chi^2=2.36$ ).

Durations of inter-birth intervals did not vary with social group size. Plainly, then, females living in small social groups enjoyed higher reproductive success, at least in the short term, than their counterparts in large groups.

#### 10.4 Reproductive success and experienced density

Experienced densities were measured for each female as the number of other wallabies whose centres of activity were within 200 metres of her own. Two hundred metres is approximately the mean plus one standard deviation of the distances of all of the average female's sightings from her centre of activity. Therefore, any two females whose centres of activity were within 200 m of each other should have experienced substantial home range overlap. Table 11.4 compares the densities of several categories of wallabies, experienced by females who reproduced successfully and unsuccessfully (success is again defined by infant survival). These data were collected in 1983, by which time the study area had been extended to include a sufficiently large area to allow densities to be accurately measured for a large number of females. Successful females tended to experience slightly higher densities than unsuccessful females, although this tendency reached significance only for the numbers of males and females of other social groups overlapping each female's home range. The relationship between experienced density and reproductive success was, on the whole, rather feeble, and opposite in direction to the relationship between sociality and reproductive success.

#### 10.5 Other variables

The inverse relationship between sociality of mother and infant survival indicated above could be spurious if any other variable acting on the population were to cause increased sociality while at the same time reducing infant survival rates, or vice versa; other variables might also modify the relationship between sociality and reproductive success in interesting ways. The effects of two possible confounding factors - spatial variation in habitat quality, and seasonal variation in plant growth - can be investigated here.

The study area can be divided into two quite different portions : the fertile creek flats and adjacent forest (hereafter referred to as the 'flats') where wallaby densities are high (see Ch. 3), and the rest of the valley (the 'slopes') where wallaby densities are relatively low. When the analysis of sociality with other social group members against subsequent infant mortality was repeated within

each area, the effect was substantial in the slopes sub-sample (socialisation indices averaged 33% (n=21) for females whose infants died, versus 11.1% (n=27) for females whose infants survived;  $Z=-1.73$ ,  $P<0.05$ , one-tailed), and non-significant, but still in the expected direction, on the flats (46.4% versus 33.3%,  $n_1=7$ ,  $n_2=7$ ,  $U=12.5$ ,  $F>0.05$ ;  $<0.10$ ).

The sample of reproductive attempts was divided into two seasonal sub-samples : a winter sub-sample including only reproductive attempts in which the infant left the pouch during the winter months (May to October) and for which at least half of the period of reference for the sociality index also fell within the winter months; and a similarly constructed summer (November to April) sub-sample. The application of these criteria considerably diminished the sample sizes; however the effects of sociality on infant mortality were of the expected direction and magnitude, and were significant, within each sub-sample. (In summer, sociality indices for successful and unsuccessful females were 10.2% (n=6) and 44.1% (n=6) respectively,  $U=8.0$ ,  $P<0.05$ ; in winter the values were 8.3% (n=8) and 36.7% (n=11),  $Z=-1.64$ ,  $P<0.05$ ; both tests one-tailed).

## 10.6 Discussion

All adult female red-necked wallabies produce infants at similar rates, but the infants of social mothers are less likely to survive to weaning age than are infants of non-social mothers. This depression of the reproductive success of social females is evidently due not only to association with recently-weaned offspring, but also to association with other members of the social group.

Red-necked wallabies are a good species for studying relationships of this kind, for two reasons. Firstly, social groups use overlapping home ranges, so that it is possible to compare the effects on a female's reproductive success of the presence in her home range of varying numbers of members of her own, and of other social groups. Secondly, red-necked wallabies are only partly social, and individuals vary in the frequency with which they associate with others. Therefore, one can look at her frequency of association with other wallabies as a second possible predictor of a female's reproductive

performance.

The results discussed here show that females in large social groups produce fewer surviving offspring than those in small groups, but that a female's reproductive success is not depressed by members of other social groups who also share parts of her home range. In fact, the mothers of surviving infants tended to be at rather higher densities than the mothers of infants who died. Moreover, the frequency with which a female associates with other females, and with subadult males, while she is carrying a pouch young is evidently important in determining the subsequent survival of that young. This is a useful result, as it parallels the trend of infant survival against group size, but is independent of any definition of what constitutes a social group. However, if one partitions associations into those within and those between social groups, it becomes clear that a female's frequency of association outside her own group has no effect on her reproductive success, whereas association within social groups is evidently of critical importance. In this way, female red-necked wallabies resemble red deer hinds, who reproduce less well if surrounded by relatives, regardless of the number of non-relatives who share their home ranges (Clutton-Brock, Albon and Guinness 1982).

It is difficult to be unequivocal about the mechanics of this reproductive depression of social female red-necked wallabies, but for a number of reasons I suspect that it is due to the sharing of resources among the members of social groups, rather than to some form of direct reproductive interference between them, such as infanticide or some consequence of social stress experienced by low-status females. (Correlations between reproductive success and dominance status of females, and even reproductive despotism within female groups, are being reported for a growing number of species - see Wasser 1983 and Wasser and Barash 1983 for examples - and should often have the effect of reducing the average performance of females in large groups). Most interactions between female wallabies are rather low-key displacements of one animal by another; and association with a previous offspring reduces a female's reproductive performance, in spite of the fact that dominance status among female wallabies seems to be correlated with age.

One must hypothesise, then, that female wallabies are able, in some subtle fashion, to retain access to certain critical resources against members of social groups other than their own, but share these with members of their own social groups, particularly their own recent offspring. The resources in question could plausibly be either patches of high quality food, or the patches of dense tussocks in which mothers leave their hiding infants immediately after they vacate the pouch. Subadult sons do not compete with their mothers for access to young-at-foot hiding places, but are still very costly for their mothers to associate with. In the light of this, it seems more probable that the cost is incurred through common use of food resources, which in turn is indicated by frequency and closeness of association. I showed in chapter seven that females not only spend a relatively large proportion of their time with their subadult offspring, they also tend to stay close to them when in their company, while they spend less time and associate less closely with other individuals of their own social groups, and associate still more rarely and distantly with other, strange wallabies. In a patchy environment, this tolerance by adult females of close association from their close relatives could result in the sharing of resource patches by related individuals, and the consistent displacement of young or subordinate individuals, with no relatives of high status, from the same patches.

Some support for this suggestion comes from the comparison of the effects of sociality on reproductive success on the flats, where it is weak, and on the slopes, where it is powerful. The flats contain large patches, of several hectares each, of uniformly high quality pasture, where it is difficult to imagine that a female's defence of her individual feeding space could influence the access of other wallabies, regardless of their affinities, to parts of the same patch. However, the rest of the study area is characterised by smaller patches of pasture, wholly or partly separated by clusters of inedible tussocks. These patches obviously vary in quality and it is possible that females, by maintaining varying inter-individual spacings with other wallabies, could in the long term influence the degree to which they share high quality patches with other animals. This result could

be arrived at with no display of overt territoriality (which has not been observed in this species). If this is the case, one should expect to find differences in the spatial relationships of, and tolerance between, relatives and non-relatives in the same feeding groups.

Precisely how sharing of food by the mother might lead to reduced infant survival is another moot point. It could be because the infants of females in less-than-desirable condition are ill-prepared to face the rigours of life outside the pouch, or because their mothers do not visit them to suckle with sufficient frequency, or even abandon them altogether, during their first month out of the pouch (during which the infants spend much of their time in hiding, apart from their mothers; see Ch. 6).

Young wallabies could plausibly benefit from association with their mothers not only if it allowed them access to high quality food patches, which might otherwise be denied them, but also if young, subordinate wallabies enjoyed some shielding from feeding interference and harassment by older non-relatives when with their mothers. Bewick's swans *Cygnus columbianus* provide a good example of this kind of benefit. Scott (1980) has shown that young Bewick's swans feed most efficiently when with their parents, because the older birds intervene when their young are threatened, and because the closeness of the parents deters other birds from approaching the young (see also Scott 1984 for similar data on mute swans *C. olor*). I have no data on the short or long-term benefits to wallabies of association with their mothers, but, plainly, such data are required before the significance of the relationship can be properly understood.

The above discussion has necessarily been speculative, but whatever the proximate mechanisms involved, the fact that association with subadult offspring (and other members of the social group) is so costly to females indicates that mothers make some form of post-weaning investment in those relatives. Because mothers associate so much more often and closely with their subadult sons than with their subadult daughters, and thereby incur a greater immediate cost, it also seems clear that this investment is initially heaviest in sons, terminating at the times at which they disperse, but in

daughters it is continued over longer periods (before weaning, sons and daughters spend equal amounts of time suckling - see Ch. 6).

A similar pattern of differential investment in sons and daughters has been inferred for red deer hinds, but the differential is evidently achieved through different pathways in the two species : hinds suckle their sons more often than their daughters, but associate with them less often after weaning (Clutton-Brock, Guinness and Albon 1982). Clutton-Brock and Albon (1982) noted that in a number of species of dimorphic ungulates mothers seem to invest more heavily in individual male infants than in individual females, and suggested that this may be because heavy investment in male infants allowed them to achieve larger size as adults, and hence to be more fecund, than would otherwise be the case. This argument can also be applied to red-necked wallabies : adult male wallabies vary substantially in body size, and males of high status control sexual access to females. If young male red-necked wallabies really do feed more efficiently because of their frequent post-weaning association with their mothers, this could enhance their early growth rates, and their subsequent reproductive success. Other differences between young males and females - in the variability of durations of pouch life (Ch. 5) and following of their mothers as young-at-foot (Ch. 6) - might have the same ultimate function.

TABLE 10.1: Socialization indices of female wallabies in relation to the success of their reproductive attempts (values are medians, sample sizes are number of reproductive attempts)

Sociality with:	Successful breeding attempts (n = 32)	Unsuccessful breeding attempts (n = 28)	
<b>A</b> Indices of socialization, all females:			
All other females and sub- adult males	33.0	53.6	U=270, z=-2.637, P<0.005
Females and subadult males of own group	15.4	37.4	U=273, z=-2.736, P<0.005
Females and subadult males of other groups	17.6	16.2	U=430, z=-0.267 n.s
	(n = 20)	(n = 28)	
<b>B</b> Indices of socialization, females with no subadult offspring:			
All other females and sub- adult males	32.9	46.4	U = 137.5, P < 0.10
Females and subadult males of own group	16.7	30.5	U = 116.0, P < 0.05
Females and subadult males of other groups	16.0	17.9	U = 194.0, n.s.

**TABLE 10.2:** Survival rates of infants born into social groups of various sizes ( $\chi^2 = 6.76, P < 0.05$ )

	Size of social group		
	Small (1-2)	Medium (3-4)	Large (5-7)
Percentage infant survival rate	67.5	28.0	26.7
Sample size (number of infants)	40	25	15

**TABLE 10.3:** Densities experienced by females who bred successfully and unsuccessfully in 1983

Densities of:	Median densities experienced by:		
	Successful females (n = 12)	Unsuccessful females (n = 17)	
Any females and males	12.0	11.0	U = 85.5, n.s.
Any females and subadult males	8.5	7.5	U = 68.0, n.s.
Females and subadult males of other groups, and males	11.5	7.0	U = 50.5, P < 0.05
Females and subadult males of other groups	6.0	3.0	U = 65.5, n.s.