CHAPTER ELEVEN

General Discussion and Conclusions

This final chapter begins with a synthetic account of red-necked wallaby social organisation, and a comparison of reproductive strategies and variances in reproductive success in the two sexes. I then present a brief comparative review of ecology and group size in macropods, which yields some evidence for the importance of feeding style in limiting group size. This is followed by some wider comparisons and arguments on sex-differences in dispersal and philopatry in mammals; on the role of home range overlap among females in shaping some fundamental characteristics of male reproductive behaviour; and on the influence of home range overlap among females on the consequences of competition for resources between them.

11.1 Synthesis : social organisation of the red-necked wallaby

Although red-necked wallabies in my study area have rather small home ranges (median=15.2 ha), the high density at which they live (on average, 48 wallabies per km ^{2}) ensures that their home ranges overlap extensively. A simple calculation - population density multiplied by home range size, to give Damuth's (1981) S - shows that the average point on the ground at Wallaby Creek is covered by the home ranges of just over seven wallabies, or, equivalently, just over seven wallabies live in an area the size of the average wallaby's home range. However, these seven-plus wallabies almost never gather together in one group. Groups of more than two or three wallabies form very rarely, and adults drift apart frequently, so that even small groups tend to be short-lived. For all their ability to adapt to a range of climates, and their generalist's approach to habitat choice (as shown by, amongst other things, the climatic breadth of their distribution in Australia, and their success as an introduced species elsewhere), red-necked wallabies reach uniformly low levels of gregariousness in all of the areas where they have been observed, and remain nearly solitary even when living at high densities. Relatively large groups form more regularly during winter at Wallaby Creek than during summer, but these winter-time groups are loosely coordinated and unstable; they probably result from the concentration of the wallabies on shrinking patches of preferred feeding habitat.

The strongest relationship within wallaby society is that between mothers and their pouch young. Young in the pouch are absolutely dependent on their mothers, and when they leave the pouch for short periods their mothers remain watchful, prevent them from following strange females, and facilitate (and often induce) their return to the pouch. This relationship changes its character when the mother excludes her young from the pouch, and the responsibility for the maintenance of contact between the two shifts towards the young-at-foot. The mother still plays a very important role in sustaining the relationship, especially during the first month or two after the infant leaves her pouch, when she seeks it out after the two have separated in one way or another, and regularly grooms and sniffs it. However, young-at-foot are more likely to follow their mothers than their mothers are to follow them, and differences between male and female infants in the persistence with which they follow their mothers correlate with the amounts of time they spend with their mothers : males follow more closely, and associate more often at this stage.

The difference between male and female infants in the frequency with which they associate with their mothers is accentuated in subadulthood, when young males are seen in groups with their mothers up to four times as often as young females. The relationship between a male subadult and his mother diminishes in strength as the mother's next infant leaves the pouch, and is severed completely when the male disperses, at two years of age. Dispersal by males takes them several home range widths away from their mothers. Males are not obviously driven out of their mothers' home ranges by any other wallabies, but appear to leave of their own volition.

Having dispersed, males settle in small home ranges. They associate most often with other small males; most of their interactions with these other males result in fights, although small males rarely fight as intensely or as bitterly as large males. To begin with, they are subordinate to almost all other males, but as they continue to grow they become able to dominate some other males, and they establish clear dominance relationships with males similar to themselves in size as well as with dissimilar males. Dominance-subordinance relationships between closely-matched males may at times be reversed, and males interact more frequently and become more likely to initiate interactions with other males close to their own rank as they ascend the scale of body size and dominance status. Very large males who hold dominions - non-exclusive, discrete areas of absolute dominance - rarely confront one another, but selectively interact with and assert their dominance over males just below their own rank, and thereby create a ceiling of aggression over the rest of the male population. When one of these dominant males disappears, the male immediately below him in rank may be able to step into his place. As they grow in social and physical stature, males extend their home ranges : this may also enhance their prospects for moving up into the first rank. Although dominion-holding males have large, overlapping home ranges, their dominions are relatively small, and discrete.

Males are strongly attracted to each female during the seven days before she permits any of them to mate, and during this period she is followed by a group of up to seven males. Males follow the female more closely and in larger numbers as the day of her mating approaches, and the long period of her heightened sexual attractiveness practically guarantees that a very dominant male will be closest to her when she becomes ready to mate. This dominant male tolerates the presence of much smaller males, provided they stay at least ten metres from the oestrous female, but, particularly during the first few days of the female's oestrus, he tries to keep males nearer to his own rank at least 40 metres from the female. Adult males are therefore placed into three broad classes : dominion-holding ('dominional') males, who, for the most part, face no serious threats to their ability to retain sexual access to oestrous females within their dominions; 'bachelor' males, who are forced by dominional males out of groups containing oestrous females; and 'secondary consorts' whose presence in groups with oestrous females is tolerated, although they are not permitted to interact with these females. This structuring of the male population, which emerges only around oestrous females, is enforced by the behaviour of the most dominant males.

Although female subadults spend less time with their mothers than do male subadults, they settle within their mothers' home ranges, and the association between mothers and daughters is maintained into the daughter's adult life. Groups of wallabies frequently disintegrate and re-form in varying combinations, but this does not happen randomly or chaotically. Females usually associate regularly with only one or two companions, who are likely to be close relatives, while avoiding other females who also use home ranges overlapping their own. Pairs of females who associate preferentially are more likely to give birth within two or three months of one another than are pairs of females who have overlapping home ranges but exercise no preference for each other's company; they also stay closer together when in the same groups.

Although the reproductive fortunes of females vary with the types of habitat in which they live, the most important determinant of a female's breeding success appears to be the strength and number of her social relationships with other females and with subadults. The infants of social females have much lower survival rates than the infants of solitary females, regardless of local density, and females who are still being accompanied by subadult offspring, sons in particular, are the least likely to produce surviving infants.

These contrasts between the social organisations of females and males are matched by differences in the numbers of offspring that members of the two sexes are potentially able to parent in a lifetime. Given that very few wallabies of either sex live to 12 years of age (see Appendix I), females can hope for a reproducitve life of, at most, ten years, during which they might give birth to 12 offspring, of whom only 40% (on average) will survive to adulthood - most females who reach adulthood probably produce no more than three or four surviving offspring. I have good information on the durations of four males' terms as holders of dominions; using information on the numbers of females who lived within each dominion during those periods, I estimate that these males could have sired lifetime totals of 5, 19, 28 and 36 offspring each. These numbers should be devalued by the 40% juvenile survival rate to estimate the numbers of these males' offspring to reach adulthood. The similar numbers of wallabies of both sexes who die in infancy or subadulthood make no contribution to the next generation, but because males do not become reproductively active until they are at least five years older than females giving birth for the first time and, as judged by the sex ratios of adults (Appendix I) are more likely than females to die during those years, it seems clear that more males than females die before reaching their reproducitve years. In addition to this, competition between males can be so severe that it may be possible that some males live to old age and yet have little opportunity to mate. All things considered, variance in lifetime reproductive success must be clearly higher for males than for females.

The social and sexual strategies of males and females may interact in a number of ways. Perhaps the most important such interaction in red-necked wallabies is the way in which sexual advertisement by females intensifies competition between males for mates, and may even have shaped its character. The long period before mating during which females are unusually attractive to males makes it practically impossible for a subordinate male who finds a female in the early stages of oestrus to remain at her side until she becomes ready to mate. Her state is noticed by other males, who, day by day, gather around her as the most dominant male among them sustains his defence of her until he is displaced by a more dominant male or until she becomes fully receptive to mating. I think it is likely that the long periods of sexual attractiveness which females undergo have two evolutionary effects on the reproductive behaviour of males. Firstly, because they discount the advantage any male gains by being the first to locate an oestrous female, they make a hypothetical strategy of devoted, solitary searching for untended females unprofitable as an alternative to fighting with other males for rights of sexual access to females, and , secondly, by inciting conflict among males, they stimulate the evolution of large body size and prowess in fighting among males, as these attributes become absolutely essential to success in reproduction.

11.2 Ecological determinants of group size

The loose coordination and small size of red-necked wallaby groups can plausibly be accounted for as a consequence either of the tactics they use to avoid being killed by predators, or of their feeding ecology.

Red-necked wallabies will flee over long distances if closely pursued by dingoes, but they try to evade sustained pursuit by getting out of sight as quickly as possible when alarmed. To this end, they stay close to cover, even when feeding in the open, so that they need never travel far to conceal themselves in dense vegetation or down gullies. Perhaps the maintenance of groups is incompatible with this kind of flight behaviour : a wallaby may be reluctant to stay in a group if the other members move to an uncomfortable distance from her own familiar routes of flight into cover, she might also find it easier to flee inconspicuously and hide silently when alone (even mothers and young-at-foot separate when fleeing into cover). Of course, these kinds of costs must still be set against the potential benefits, such as early warning of approaching predators, which may follow from grouping.

Alternatively (or additionally), the effects of the species' feeding style on the rates of movement of feeding individuals and the inter-individual spacing they maintain may make the coordination of groups difficult and expensive. As Jarman (1974) has pointed out, animals who feed selectively on discrete, widely-spaced food items face this problem, whereas those feeding on uniformly abundant foods (grass leaves in dense swards, for example) are free of it. Although the red-necked wallaby's diet is known only in its broad outlines (see Ch. 1) they do seem to be more selective and to take less grass than some other species of *Macropus*. The relatively high rates of movement of wallabies feeding in groups is oblique evidence of significant feeding interference between wallabies in groups.

I do not have enough information on red-necked wallabies to allow me to say which of these two hypothetical pressures has had the greater influence on their grouping behaviour, but a comparison with black-striped wallabies at Wallaby Creek is of some help. During the first two years of my study, I spent several days and nights in every month following black-striped wallabies and exploring their habitat, and I caught and marked ten individuals. Black-striped wallabies feed in the open at night, moving up to 200 metres, sometimes more, from the forest edge (individuals habitually feed in the same areas), but during the day they retreat as far as 600 metres back into forest, and rest in scrubby gullies. They are very nervous when feeding on open pastures, and, like red-necked wallabies, they flee back into their forest when disturbed. Unlike red-necked wallabies, however, they are usually seen in groups of up to ten individuals each, and these groups remain well-coordinated even when the members have been disturbed. A group of alarmed black-striped wallabies makes its way slowly back into cover, as each individual hesitates, listens for its companions, and stays close to them. Groups of relaxed black-striped wallabies are much more compact and stable than are gatherings of red-necked wallabies. Black-striped wallabies are grazers (Tierney, pers. comm.; Ch. 1) and the comparison between them and red-necked wallabies suggests that diet composition has been more important than flight behaviour in shaping sociality in these two species.

If this view is correct, then diet composition and average group size should be strongly correlated across other species of macropods; in particular, because grasses often grow in dense, even swards and may require little searching and selection of the grazing herbivore, the proportion of the diet made up of grasses should predict average group size. I have plotted this information for nine species in Fig. 11.1; where possible, I plotted average group sizes against diet compositions measured from the same populations. The proportion of the diet composed of grass explains 61% of the variation of average group size in these nine species ($l_n y=0.01x + 0.15$; $r=0.78$; $P<0.02$). Mean group size increases exponentially with proportion of diet composed of grass.

The relationship of Fig. 11.1 should be viewed with the circumspection it deserves ; there may be species (the hare-wallabies for example) which feed very selectively on certain parts of grass plants, and for them a stand of grass may yield only a small number of

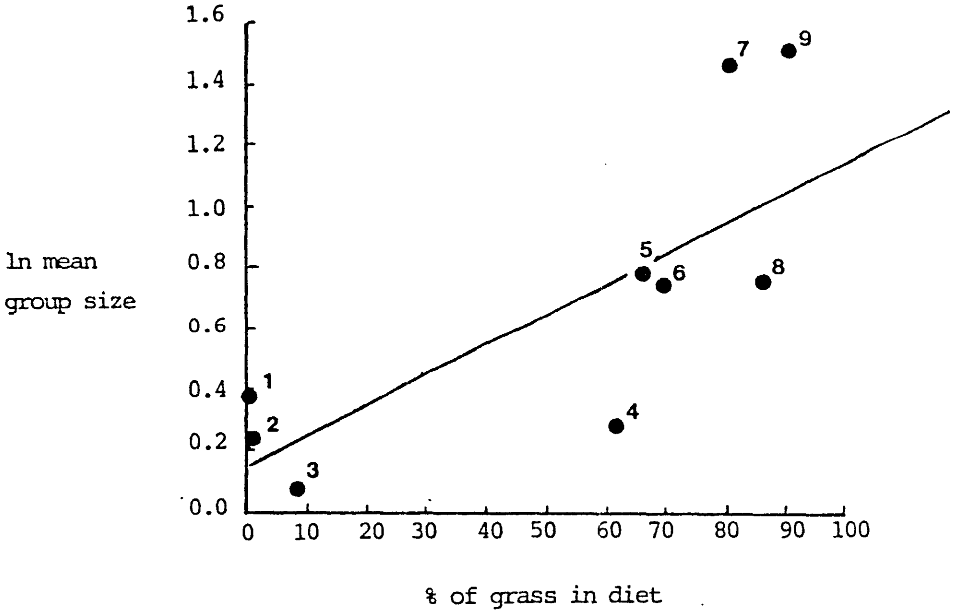

Fig. 11.1 Relationship between diet composition and sociality in some macropods ($y = 0.01x + 0.15$; $r=0.78$, $P<0.02$). Species can be identified from their numbers (see Table 11.1).

discrete and widely-spaced food items, which they may therefore be obliged to exploit solitarily. The analysis does suggest, however, that many solitary species of macropods would live in groups were it not for the restraints imposed on grouping by their feeding styles.

11.3 Philopatry and dispersal

Behavioural and ecological differentiation between male and female red-necked wallabies begins in the pouch, when the durations of the pouch lives of males vary seasonally while those of females do not, and becomes profound at two years of age, when males disperse to establish new home ranges away from their mothers', while females remain and begin breeding within their mothers' home ranges.

Selection for the dispersal of at least some offspring is likely to come from more than one direction. By dispersing, individuals avoid the deleterious effects of inbreeding, effects which have now been demonstrated in the wild (Greenwood et al. 1978, Packer 1979a) as well as in captive animals (see Ballou and Ralls 1982) : offspring of incest are generally less likely to survive than are outbred offspring. Dispersers go and live among unrelated strangers, and thereby avoid inbreeding, while those animals who do not disperse can choose newcomers for mates (see Duncan et al 1984). Dispersal of juveniles is clearly advantageous in patchy and capricious environments, but Hamilton and May (1979) have shown that some dispesal should be expected even in stable, uniform environments. They argue that where parents need only produce a small number of offspring to ensure their own replacement, surplus offspring can be entered, through their dispersal, into competition for other living spaces.

Dispersal is always likely to be difficult and risky, but these strong pressures for the dispersal of at least some members of each generation should encourage and maintain the dispersal of those classes of young least prey to its dangers, while the rest remain philopatric. In some species of mammals, male and female juveniles are equally philopatric (eg pikas *Ochotona princeps* Smith and Ivins 1983) or equally likely to disperse (eg mountain zebras *Equus zebra*, Penzhorn 1984), but sex biases in dispersal and philopatry are common, and in mammals males are usually the dispersing sex, while females are the more philopatric (Greenwood 1980, Waser and Jones 1983, Packer 1979a, Dobson 1982). Juveniles are usually much more likely to disperse than adults. Red-necked wallabies fit this general pattern. Exceptions to this generalisation are few : female dispersal is known to be associated with male philopatry only in African wild dogs (Frame et al. 1979), white-lined bats *Saccopteryx bilineata* (Bradbury and Vehrencamp 1976), red colobus monkeys *Colobus badius* (Strushaker and Leyland 1979, Marsh 1979), hamadryas baboons *Papio hamadryas* (Sigg et al. 1982, Kummer 1984) chimpanzees *Pan troglodytes* (Pusey 1979, Nishida 1979) and humans.

Two hypotheses have been offered to account for the observation that male mammals are usually more likely than females to disperse. Greenwood (1980) contrasted male dispersal in mammals with the greater prevalence of female dispersal in birds. He argued that the philopatry of male birds of many species has arisen as a result of their territorial behaviour - males should be better able to establish and defend territories on familiar ground, close to male relatives, than among strangers in unfamiliar country - while males should be more ready to disperse in species of mammals where they defend females and adjust their own movements to match the distribution of females, instead of influencing the distribution of females by partitioning resources among themselves. If this hypothesis is correct, then philopatry and territoriality of males should be associated in mammals as well as in birds. However, as Waser and Jones (1983) have pointed out, there is a sufficient number of species of mammals in which male dispersal and territorial defence are associated to justify rejection of this hypothesis (see also Murray's 1981, 1982a and 1982b detailed account of male dispersal, male territoriality and philopatry of females in impala).

The second hypothesis, which has several variants, links male-biased dispersal to polygyny (Clutton-Brock and Harvey 1976, Packer 1979, Dobson 1982). As Packer put it :

> "In any polygamous species, differential availability of sexually receptive mates would be more likely to result in male migration than in female migration. This is because the

> increase in the reproductive success of a male from gaining access to large numbers of receptive females would usually be greater than the increase to a receptive female from gaining access to a larger number of males...This asymmetry may have resulted in the greater numbers of mammalian species in which males rather than females commonly transfer between groups, both from the natal group and subsequently".

But males might also make great gains in reproductive success by waiting patiently in the home area, ready to seize opportunities for increasing their social status and usurping dominant males. And females face competition of one kind or another, they too might sometimes gain by dispersing and seeking better conditions elsewhere. Any path that a male of a polygynous species takes is likely to lead him to a more extreme outcome than a female might expect, but this fact in itself should not necessarily result in a general predisposition towards dispersal among polygynous males. In fact, one could argue that, since dispersing males of polygynous species are likely to face very rigorous competition from other males wherever they go, any males who do not undergo the costs of dispesal may thereby retain a competitive advantage and perform better than dispersers, while females, if they compete less potently than males, might find it easier to settle after dispersing, and therefore be more predisposed to move.

The 'polygyny' hypothesis is supported by the observation that polygyny and male-biased dispersal are often associated in mammals (Dobson 1982), but is weakened by its inapplicability to birds (Greenwood 1980) and by the observation that those species of non-human primates in which males are more philopatric than females are actually more polygynous, as judged by sexual dimorphism and socionomic sex ratios (see Clutton-Brock et al. 1977), than most species of primates.

An alternative approach to the problem is to consider how the immediate costs to males and females of dispersing might regularly and predictably differ. Dispersing juveniles must pass through unfamiliar terrain, and perhaps spend some time in suboptimal habitats, before establishing a stable home range or territory in appropriate habitat.

During these travels and sojourns, dispersers might be more than usually vulnerable to predators, or become weakened and subsequently die. Dispersal by males is associated with their differential mortality in a number of species of mammals (Palls et al. 1980) while high mortality accompanies dispersal by female acorn woodpeckers *Melanerpes formicivorous* (Koenig et al. 1983). Holekamp (1984) showed that although juvenile male Belding's ground squirrels *Spermophilus beldingi* who disperse are significantly heavier when they leave than males of the same age who do not disperse, their body weights drop below those of the non-dispersing males over the ensuing five weeks. She suggested that the shift "...may reflect the large energetic demands of emigration itself, or difficulties experienced by newly-dispersed individuals in finding or storing energy in the relatively unfamiliar habitat of immigration areas". Because males and females are generally more similar in morphology and behaviour as juveniles than they are as adults, the effects of dispersal on survival probably differ little between the sexes. However, if dispersal is survived, the energetic stresses it imposes and the time lost in suboptimal habitats should have a quite different significance for female and male juveniles, if the sexes typically start breeding at different ages. In polygynous species of mammals, females usually begin breeding as soon as they reach maturity, while in males reproduction is often delayed, sometimes for many years, because of the control that old, dominant males exert over opportunities for mating. Fig. 11.2 compares generalised fecundity schedules for male and female mammals of polygynous species, and shows how they differ in shape and position (fecundity schedules have been compiled for the females of several species of mammals, but they are rarely constructed with precision for males; the male fecundity schedule in Fig. 11.2 is derived from numerous accounts of changes in reproductive behaviour with age of males).

This means that if juvenile dispersal takes up a significant portion of a female's time and causes her to lose condition it will necessarily result in a delay in the age at which she first produces a surviving offspring of her own, while for males, this does not follow with the same inevitability. In red-necked wallabies at Wallaby

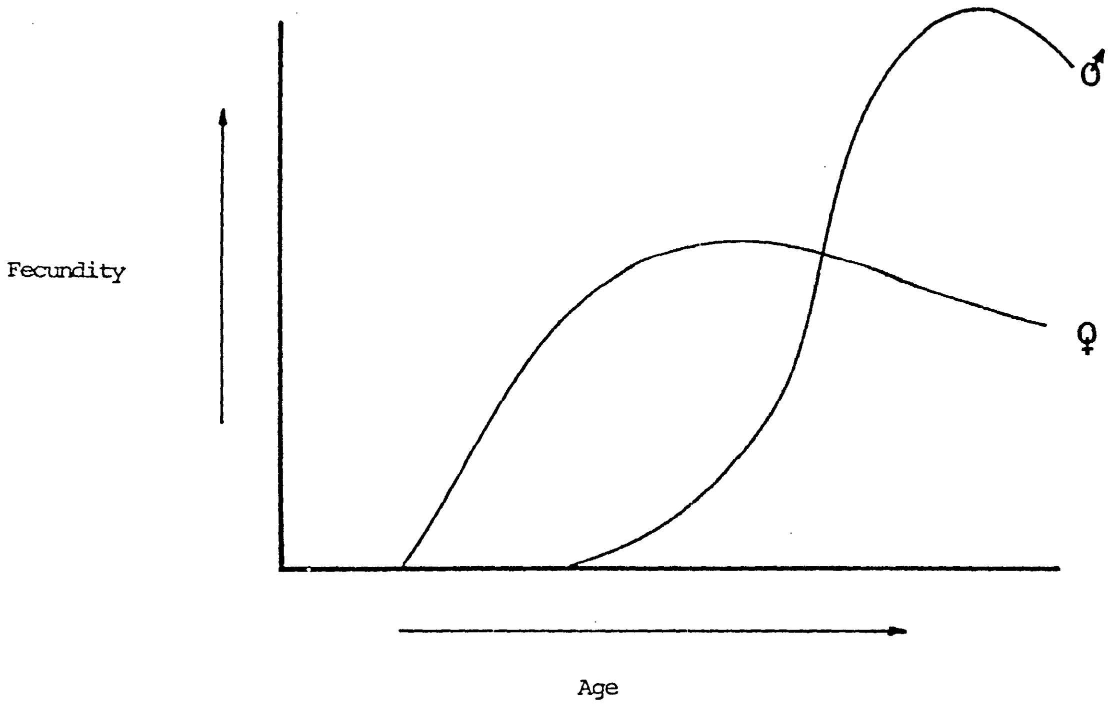

Fig. 11.2 Generalised fecundity schedules for male and female mammals (see Sherman and Morton 1984, Caughley 1976 and Clutton-Brock, Guinness and Albon 1982).

Creek, for example, males disperse at 24 months of age, but females may give birth at 18 months of age. If females rather than males dispersed, it is unlikely that they could start breeding so young. Males are forced to wait five years or more before being able to mate, and although it is quite conceivable that the costs of dispersal could cause this delay to be extended, the effect should not be so immediate or so unalterable for them as it must be for females.

This point assumes greater weight if one considers that the age at which an individual produces its first surviving offspring has a particular evolutionary significance, distinct from the significance of the total number of offspring produced in a lifetime. With its first offspring, an animal replaces itself, genetically speaking (although it does not do so completely if it reproduces sexually), and the earlier it can do this, the more rapidly will its lineage increase (see Horn 1978 : recall also that the rate of increase of a population is more strongly influenced by mean generation length than by total number of young produced by each female, Southwood (1976)).

I therefore offer the hypothesis that the sex for which dispersal is most likely to cause a delay in age at first reproduction will be most predisposed to philopatry, and, given the selection pressures for the dispersal of some proportion of each generation, the other sex will disperse.

This is not the same as saying that the sex which starts breeding youngest will therefore be philopatric, for members of the other sex might be obliged to begin preparations for breeding while younger still, and their preparations might be very vulnerable to disruption by dispersal (if, for example, the males of a species enter a dominance hierarchy as juveniles, and the age at which they enter the hierarchy correlates directly with the age at which they acquire sufficient social status to begin mating, dispersal will have a predictable, explicit effect on their age at first reproduction). Generally speaking, however, the delay in onset of breeding by males which usually accompanies polygyny should diminish the effects of dispersal on age at first reproduction of males, and males should therefore be less predisposed to philopatry than females.

This hypothesis predicts a general correlation between male

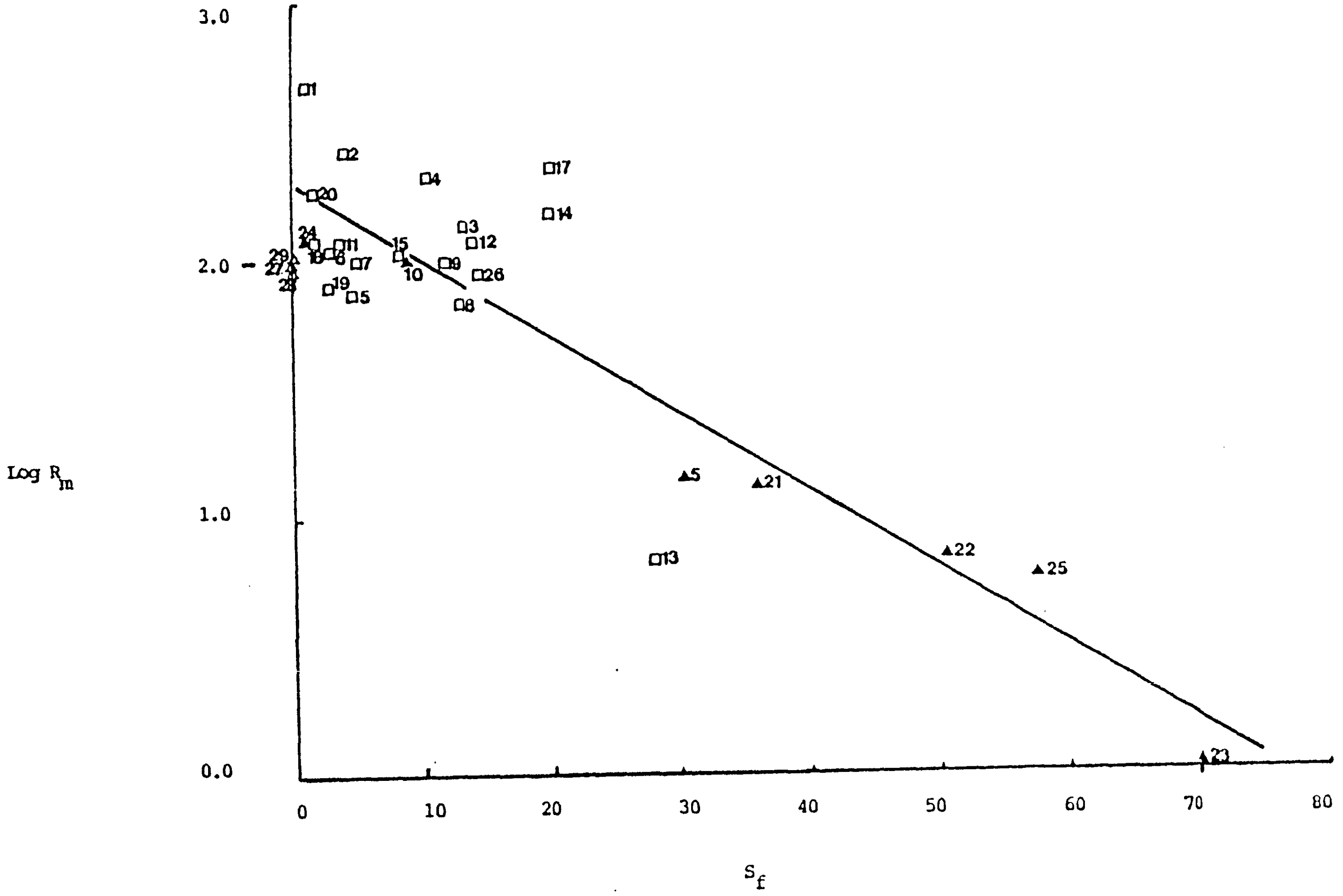

Fig. 11.3 Relationship between home range overlap among females (S_f) and sex differences in ranging behaviour (R_m) in ungulates and macropods. Species can be identified from Table 11.2.

dispersal and polygyny, but because factors other than the type of mating system may induce differences between the sexes in their vulnerability to the effects of dispersal on the commencement of reproduction, male philopatry may sometimes be expected to arise even in polygynous systems. In polygynous species where female competition for resources is so intense that it forces females to delay first reproduction well beyond sexual maturity, or where males are able to use behavioural tactics to consistently begin their reproductive careers while still young, even though older males might still dominate most mating, the balance of selective pressures could shift far enough to cause females rather than males to disperse, and males to be philopatric. Most of the well-documented cases of male philopatry occur in primates; in some species of primates reproductive competition between females may be very potent (eg yellow baboon *Papio cynocephalus*, Wasser 1983) and males may begin mating while still of relatively low status, by forming coalitions with other young males (eg olive baboons *Papio anubis*, Packer 1977; chimpanzees, Bygott 1979), or by founding small harems on the peripheries of the larger harems of older males (hamadryas baboons, Sigg et al. 1982, Kummer 1984). The existence of these kinds of behaviours is consistent with the (apparently) relatively common occurrence of male-biased philopatry in primates, but because the effects of a sex bias in dispersal and philopatry are so ramified, and so fundamental to the development of many types of social behaviour, the social behaviours themselves can usually not be invoked to explain why, in a particular species, one sex or the other is philopatric : the dangers of falling into circular argument are too great. For example, dominance is much more closely correlated with mating success of males in olive baboons (Packer 1979b) than in chimpanzees (Bygott 1979). Young chimpanzee males therefore have better chances of mating than do young olive baboon males, and male chimps are philopatric, while male olive baboons disperse. This correlation is congenial with the hypothesis I have advanced, but the reduction in competition between male chimps could be due to the fact that they live in stable communities of patrilineally related individuals (Goddall 1983, Wrangham 1979), which they are able to do because they are philopatric. Male olive baboons, on the other hand, regularly compete with unrelated males (Packer 1979a, b), and may compete the more bitterly for that reason, because they disperse as juveniles.

This kind of difficulty is unfortunate because it makes the hypothesis I have offered very resistant to rigorous testing; it is a problem which besets all arguments which postulate effects, direct or indirect, of social behaviour on the evolution of sex differences in dispersal and philopatry. Tests of this hypothesis could be devised for species in which diffferences in the ages at which males and females begin reproducing arise for reasons unconnected with social behaviour.

It is probably worth noting in passing that consideration of the effects of dispersal on the progress of a reproductive life can be used to account for the prevalence of juvenile (rather than adult) dispersal in mammals as well as for the dispersal of young males rather than young females. If dispersal is likely to delay the beginning of reproduction for a young animal, it should also, and for the same reasons, interrupt reproduction by an adult. Because adults usually breed without pause dispersal by them will have an unavoidable, immediate effect on reproduction, so young individuals who are, by dint of their immaturity, non-reproductive, should be more likely than adults to disperse.

11.4 Female dispersion, and male ranging and reproductive behaviour

The overlapping of the home ranges of neighbouring female red-necked wallabies represents what Emlen and Oring (1977) have called an "environmental potential for polygyny". In other words, it allows each male's home range to easily encompass the home ranges of several females, and encourages dominant males to claim and defend exclusive mating rights over those females. Male red-necked wallabies respond to this potential by using home ranges which are much larger than the average for females, and which therefore encompass the home ranges of many females; and try to retain absolute dominance within sections of their home ranges. These sections, the males' dominions, are still as large, or larger than, the home range of the average female. This strategy is obviously advantageous : males who successfully practice it account for the great majority of matings. However, other approaches can be imagined. In many species of African antelopes, dominant males do all of their mating within territories which may be much smaller than the home ranges of females, and the boundaries of which are deferded against other males and often marked with scent or piles of dung (Jarman 1974, Owen-Smith 1977). Why do red-necked wallaby males, and the males of other species of macropods, not do the same?

One possible answer to this question is that, although home ranges of female red-necked wallabies overlap extensively, the number of females living in an area the size of the average female's home range (S_f, Damuth's S calculated for females only) is still quite small (S_f=4.0). Any male who maintained a dominion or territory smaller than the average female's home range would find that, on average, very few females would be in this dominion. (Imagining how many females might live in an area smaller than the average female's home range demonstrates the partly abstract quality of S : its value can be the sum of fractional females. It really tells us the average number of females who will be in the area at any time). We should expect dominant males to use small mating areas (territories, dominions, or whatever) only where S_f is high enough that many individual females pass through them, in spite of their small size.

Fig. 11.3 shows how S_f and the relative size of the area over which the average dominant male mates (R_m), are correlated for macropods and ungulates. The species included in this comparison can be identified from Table 11.3, which also cites data sources. I have used data from ungulates as well as from macropods because the two groups occupy similar ecological niches and have radiated in similar fashions, and should therefore be directly comparable. R_m is defined precisely as the average size of the areas within which individual dominant males mate with females, expressed as a percentage of the size of the average female's annual home range. Where dominant males defend territories, their mating areas correspond to their territories. In non-territorial species, I have assumed that dominant males mate throughout their home ranges - even though this is not so for red-necked wallabies - because in most of these species it has not been explicitly shown whether or not mating activity is restricted to certain parts of the home range. (The range of values of R_m used in Fig. 11.3 is so wide that it makes little difference to the correlation whether one uses dominion size or home range size in calculating R_m for the red-necked wallaby : in both cases R_m is greater than 100). Where R_m is less than 100, dominant males have restricted their movements to some extent; where it is greater than 100, dominant males move widely in search of females. When mating occurs only at certain times of the year, I have tried to use data on the movements of breeding males only at those times of the year while retaining the females' annual home ranges as the standard of comparison. I have only considered species where all of the data necessary to calculate S_f and R_m have been collected from the same population.

Where females live in separate, non-overlapping home ranges (S_f=1.0), males usually do not extend their own home ranges to encompass the complete home ranges of several females; instead, they defend territories which coincide with the home ranges or territories of single females (eg blue duiker, dikdik, klipspringer). These species are distinguished in Fig. 11.3 If they are excluded from analysis, S_f and R_m are related through the function

$$\text{Log } R_m=2.302-0.030S_f \text{ ; } r=-0.89451 \text{ } P<0.01.$$

Therefore, where S_f is low (but greater than 1.0) males usually range more widely than females. However, the relationship is altered only slightly if species in which females are territorial are included. It becomes

$$\text{Log } R_m=2.254-0.029S_f\text{; } r=-0.8852\text{; } P<0.01.$$

Thus, as expected, males use relatively small mating areas only where the home ranges of many females overlap, but where home range overlap among females is low, dominant males tend to range widely.

This relationship is not simply incidental to effects of body size (as Fig. 11.4 shows, body sizes distributions are similar for species

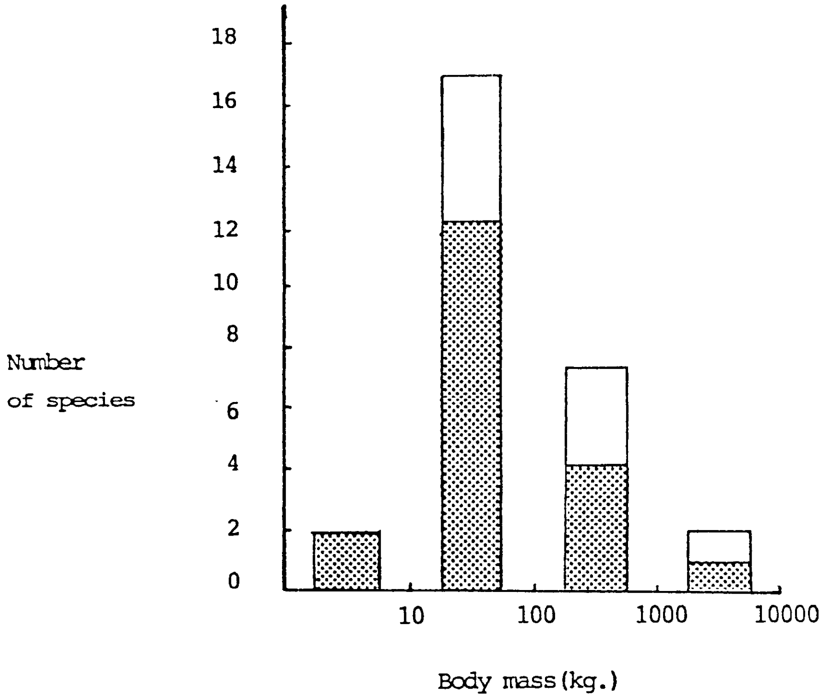

Fig. 11.4 Body size distributions for high (>30) S_f species (open bars) and low (< 30) S_f species (stipled bars).

where measured S_f values are low (<30), and high (>30)), or to seasonality of breeding (61.5% and 54.5% of species in low and high S_f ranges respectively, are seasonal breeders).

The negative exponential shape of the relationship of Fig. 11.3 means that the mating areas used by males of species in which the home ranges of many females overlap contain fewer females, on the average, than the mating areas of species whose females are more dispersed. This may be because males in the former category of species place their territories in areas especially heavily used by females, where a greater than average number of females will pass through them. This kind of fine adjustment of territorial location has been observed in male impala (Jarman 1979; see also Kitchen 1974 on pronghorns, *Antilocapra americana*).

The relationship between S_f and R_m is interesting because it seems to be a general trend underlying the evolution of territorial defence by males. When S_f is high, males are not compelled to range widely in search of females : they may remain within small areas and still contact many females. Because S_f is not strongly correlated with body mass ($S_f = 3.17\ W^{0.45}$; $r^2=0.189$) but the relative sizes of the ranges of dominant males become smaller as S_f increases, males of species with high S_f values mate within areas that actually have much shorter boundaries relative to their user's body size than do males at the other end of the continuum : therefore these males' mating areas should be much more easily defended against intrusion by other males. In Fig. 11.5, I have plotted male body mass against average size of breeding range for the species of Table 11.1 (excluding the three species whose females are territorial). The dashed line on the graph indicates a hypothetical direct linear relationship between the two variables. The majority (78% n=9) of territorial species fall below this line, while most non-territorial species lie above it (only 12.5% are below it); these proportions differ significantly ($x^2=10.64$, $P<0.01$). The important point is that the species which lie below the line - that is, those whose males travel little to mate with females - can do so because of their high S_f values (from Fig. 11.3). Territorial defence has the advantage that it guaranteees uninterrupted consortship by the territory-holder with females, for as

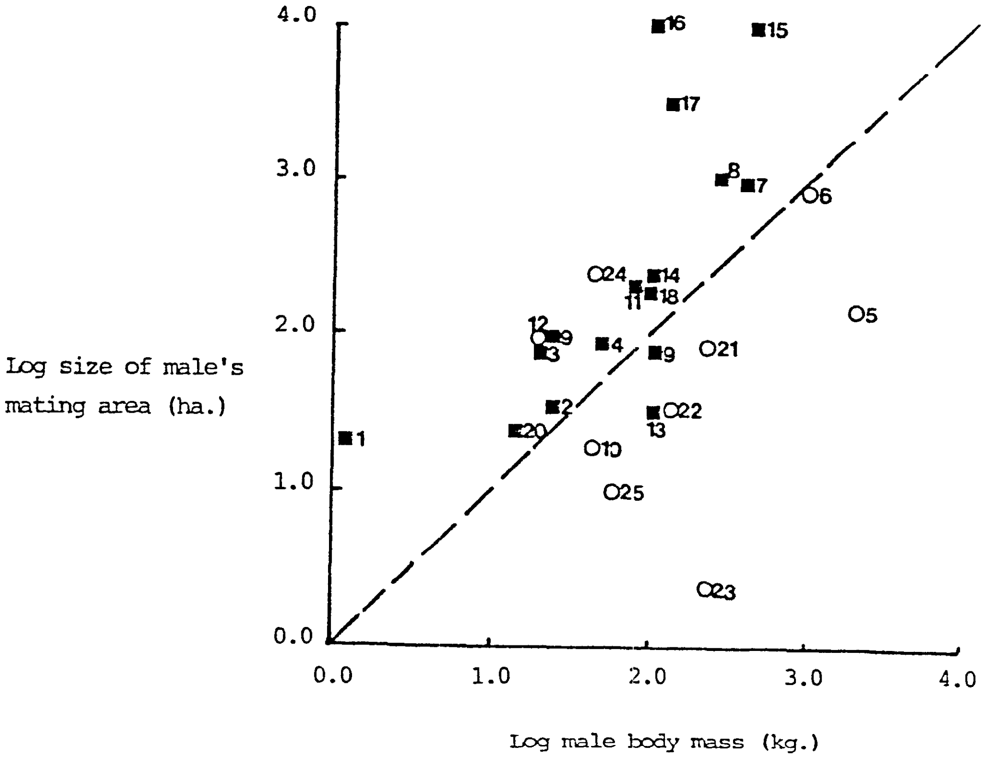

Fig. 11.5 Relationship between body size and mean size of mating range for male ungulates and macropods of species in which males are territorial (o), or non-territorial (●).

long as those females remain within the territory. I suggest that males can grasp this advantage if they stay within defendable areas, which they can afford to do only if S_f is high.

This argument can account for the broad trend of the ecological distribution of territoriality, but it leaves unexplained the occurrence of the defence of large (female home range size, or slightly larger) territories by males of some species where S_f is low, but greater than 1.0 (in this sample, gerenuk and roe deer fit this description) while in ecologically similar species (lesser kudu, for example) males do not defend territories. Perhaps, however, the differences between these species are not as great on a categorisation of some as "territorial" and others as "non-territorial" would suggest. The dominionality of red-necked wallabies is akin to territoriality : other species with low S_f values may have similar spatial organisations of dominance, which could, perhaps due to fine differences in ecology, be expressed in several ways. If there is only one point worth making from this analysis, it is that a fundamental attribute of the reproductive behaviour of males (breadth of movement in search of mates) varies continuously along a fundamental ecological gradient (low to high S). It seems that this trend produces (or facilitates) other variations in reproductive tactics : classification of species according to these tactics should be a secondary focus of analysis.

Values of S_f far outside the one-to-70 range considered here (which includes most species of ungulates and macropods) have been recorded for several large, very mobile species of ungulates. These species, for all of which S_f in the studied populations equals or exceeds 200, are eland *Taurotragus oryx* (Hillman 1979), African elephant (Leuthold and Sale 1973) plains zebra (Klingel 1967) and African buffalo (Sinclair 1977). In these species, males use home ranges equal in size to, or smaller than, the home ranges used by females.

So far, I have been arguing from the degree of home range overlap among females to the movement patterns of males. However, it is clear that if the home ranges of males were not modified by their reproductive strategies, then their home range overlap (S_m, would correlate very closely with S_f. One could therfore argue that males use smaller home ranges where S_f is high in order to avoid encountering, and being drawn into conflict with, large numbers of other males, as they would do if S_m remained similar to S_f. This argument might be sound, but it cannot easily be extended to account for the wide movements of males at the other end of the continuum. I therefore conclude that the general characteristics of the reproductive strategies of male red-necked wallabies are determined by the dispersions of their females, and that territoriality, in the classical antelope mould, has not arisen in macropods because in no species does the number of females living in an area the size of the average female's home range become sufficiently large.

11.5 Reproductive success and social behaviour of females

Differences in infant survival contribute most to variability in reproductive success amongst female red-necked wallabies, and the survival of a female's infants correlates most strongly with her frequency of association with other wallabies. Association with her own subadult offspring suppresses an adult female's reproducitve succes most strongly; association with other adult members of her social group has a less profound influence; while association with members of other social groups is immaterial. Females feed close to their subadult offspring when in groups with them; they rarely stand close to other adult group members, but are more likely to feed near members of their own than near members of other social groups. Any female's closest neighbours, those whose home ranges overlap her own most completely, are usually members of her own social group. In the light of these correlates, and in the absence of observations of direct reproductive interference (infanticide, or such-like) between female wallabies, I suggest that the decline in reproductive success with sociality is due to competition for resources (probably food) between matrilineal relatives (see also Clutton-Brock, Albon and Guinness 1982; Van Schaick 1983).

That females tolerate this competition at such serious costs to themselves is presumably due to kin selection (Hamilton 1964) : their own losses in reproductive success must be passed on as benefits to the relatives who are permitted to share the resources of their home ranges. These benefits to relatives could exert a pressure for the evolution of cohesive kin-groups. As MacDonald (1983) put it;

> "It is axiomatic that groups may be expected to develop when the costs to the resident's fitness of evicting an interloper exceed those of tolerating it...However, to an extent which depends on their degree of relationship, the net costs of tolerance to the occupier's fitness is diminished in proportion to the benefits accruing to the interloper..."

Although competition between relatives can be invoked to account for the variations in reproductive success between female wallabies, competition itself is a very difficult interaction to observe and measure - especially if it is mediated indirectly, through overlapping use of resources - and it is therefore difficult to confirm that it is as important as I have supposed. However, the verity of this interpretation can be tested by examining specific hypotheses that it suggests. Two such hypotheses are :

a) The reproductive success of individual females should decline most steeply with matirlineal group size in species where each female's home range is overlapped by a small number of others, and most gently in species where many females use common home ranges. (Imagine a species with a social organisation based on small groups of very closely related females occupying discrete territories. Each territory therefore contains a set of resources used only by closely-related group-members, and, provided density is limited by food availability, the addition of a new female to a group directly reduces the resources available to other group members, and lowers their reproductive success. However, if these groups were to use overlapping home ranges, the quantity of resources available to each individual would be determined not only by the size of its group, but by the number and size of other groups in the area. Under such circumstances, the effects of group size on reproductive success of group members should be light).

b) If reproductive success declines with group size because of tolerance of competition between relatives, we should not find a similar effect when females live in groups of unrelated individuals. Where females live in groups of non-kin, additional members should only be tolerated when their presence has negligible effects on the reproductive success of other members.

I evaluated the first hypothesis by looking for a relationship across species between S_f (see above) and the rate of decline in reproductive success with increases in size of matrilineal groups. Seven species were included in the analysis (see Table 11.3); in each of these species females have been shown to live in matrilineal groups, and for each of them data on home range overlap among females, numbers of females in groups and per capita reproductive success of group members have all been collected from the same population at the same time. Where groups of females were territorial, S_f was the average group size; where their home ranges overlapped, S_f was calculated as the product of the average home range size of females and their density (Damuth 1981). An index of the effect of increases in group size on reproductive success of members was calculated for each population from the regression of numbers of infants per female on numbers of females per group. The calculation of the index began with a group of median size, added another female for each original female member, and expressed the resulting change in numbers of infants per female as a percentage of the (projected) numbers of infants per female for lone females. This index was chosen because of its independence of average group size; it can therefore confidently be plotted agianst S_f. This plot is shown in Fig. 11.6. As predicted, where few females live within the average female's home range, the addition of females to matrilineal groups has a severe effect on the reproductive success of the original members (declines of up to 60%) but where the home ranges of many females overlap, the effect is slight. This result is consistent with the view that competition for (or sharing of) resources within matrilineal groups contributes importantly to variations in reproductive success with group size.

In all of the matrilineal species of Fig. 11.6, reproductive success of group members declined to some extent with group size. The only precise, comparable data I can find for groups of unrelated

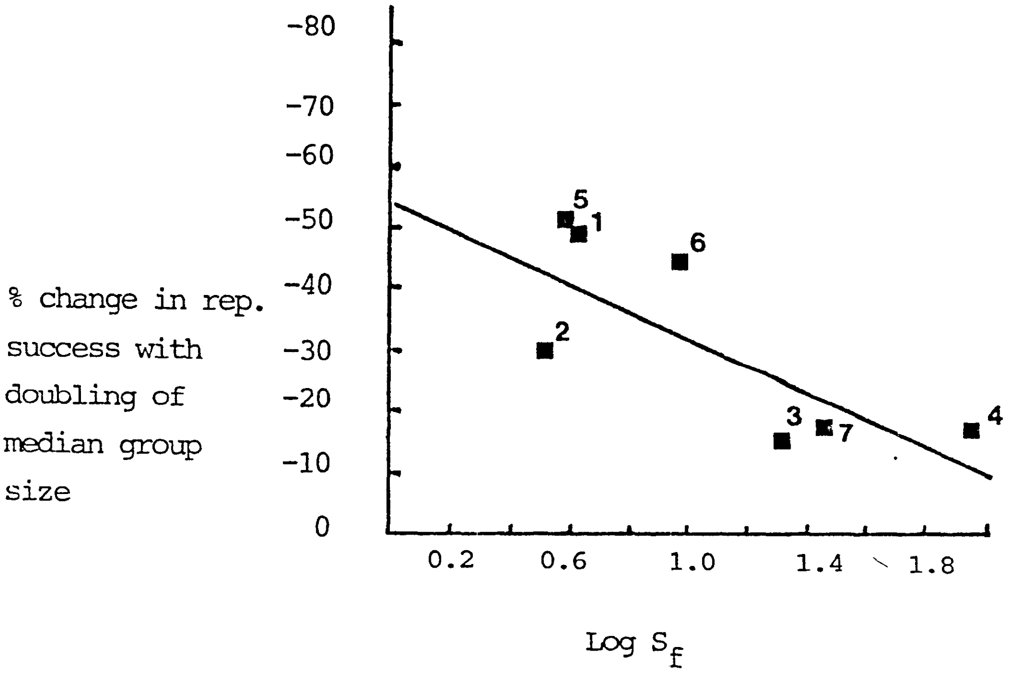

Fig. 11.6 Relationship between home range overlap among females (S_f) and the strength of the effect that females in matrilineal groups have on one another's reproductive success ($y = 53.0 - 21.92 \text{ Log } S_f$; $r = -0.78$, $P < 0.05$).

females are Schaller's (1963) on the mountain gorilla *Gorilla gorilla*. Most gorillas, male and female, disperse from their natal groups, and live out their adult lives in groups of non-kin (Harcourt et al. 1981). The numbers of infants per female increases slightly with numbers of females per group ($y=0.64-0.14x$, $r=0.28$, 8 d.f.). The effect of a doubling of the median group size of females is to increase the number of infants per female by 12.5%. I calcualte S_f for Schaller's population of gorillas to be 30.5. From Fig. 11.6, if female gorillas lived in matrilineal groups, the same increase in group size should have caused a 22% reduction in per capita reproductive success. Gorillas tend to confirm the second prediction.

These two tests give support to the view that declines in reproductive success with group size in matrilineal species are caused by the tolerance of competition between relatives, although this interpretation still requires information on the effects of this postulated nepotism on young females. If such tolerance really does have its strongest effects where S_f is low, then matrilineal groups should be most likely to evolve under that circumstance.

Pressure for the evolution of matrilineal groups probably comes from several directions, so that such groups might still evolve in species which have high S_f values. For example, in long-lived, intelligent, wide-ranging species, such as elephants, traditional knowledge on the locations of certain resources (perennial water-holes, perhaps) may be critical to the reproduction and survival of individuals, and females may form life-long relationships with their daughters in order to pass on such knowledge, even though groups of female relatives may not retain exclusive access to any of the resources they use. Cases like this aside, however, we should expect that where S_f if low (but greater than 1.0) females will often live in cohesive matrilineal groups within which competition is tolerated; whereas a lower proportion of high S_f species should have matrilineal social organisations, and in such species dominance status and reproductive success should often be clearly and steeply correlated among females.

TABLE 11.1: Species included in Figure 11.1

Species	Authority
1. Red-legged pademelon	Redenbach (1982, personal observation
2. Rufous bettong	Schlager (1982), Southgate (1980)
3. Swamp wallaby	Harrington (1976), Kaufmann (1974b)
4. Parma wallaby	Redenbach (1982), Maynes (1977)
5. Red kangaroo	Ellis *et al.* (1977), Croft (1981a)
6. Euro	Ellis *et al.* (1977), Croft (1981b)
7. Black-striped wallaby	Tierney (pers. comm.), personal observation
8. Eastern wallaroo	Taylor (1982a), Taylor (1983)
9. Eastern grey kangaroo	Taylor (1982a), Taylor (1983)

TABLE 11.2: Species included in Figures 11.3 and 11.5

	Species	Authority
1.	Potoroo, *Potorous tridactylus*	Kitchener (1973)
2.	Red-necked wallaby	This study
3.	Whiptail wallaby	Kaufmann (1974a)
4.	Eastern grey kangaroo	Jarman, Southwell and Stuart-Dick (pers. comm.)
5.	White rhinoceros	Owen-Smith (1975)
6.	Black rhinoceros, *Diceros bicornis*	Goddard (1967)
7.	Horse	Salter and Hudson (1982)
8.	Ass, *Equus asinus*	Seegmiller and Ohmart (1981)
9.	Collared peccary, *Dicotyles tajuca*	Sowls (1974), Ellisor and Harwell (1969), Schweinsburg (1971)
10.	Vicuna	Franklin (1974)
11.	Warthog, *Phasochoerus aetiopicus*	Cumming (1975)
12.	Roe deer	Bramley (1970)
13.	Red deer	Lowe (1966), Lincoln and Guiness (1973)
14.	White-tailed deer	Michael (1965)
15.	Moose	Hauge and Keith (1981)
16.	Caribou, *Rangifer tarandus*	Fuller and Keith (1981)
17.	Bighorn sheep	Leslie and Douglas (1979)
18.	Lesser kudu, *Tragelaphus imberbis*	Leuthold (1974)
19.	Nyalla, *T. angasi*	Anderson (1980)
20.	Cheurotain, *Hyemoschus aquaticus*	Dubost (1975)
21.	Waterbuck, *Kobus defassa*	Spinage (1969)
22.	Hartebeest, *Alcelaphus buselaphus*	Gosling (1974)
23.	Wildebeest	Estes (1969)
24.	Gerenuk, *Litocranins walleri*	Leuthold (1978a,b)
25.	Impala	Murray (1981, 1982a,b)
26.	Giraffe, *Giraffe camelopardalis*	Leuthold and Leuthold (1978)
27.	Blue duiker, *Cephalophus monticola*	Dubost (1980)
28.	Klipspringer, *Oretrogus oreotragus*	Dunbar and Dunbar (1974)
29.	Dikdik, *Madoqua kirki*	Hendrichs (1975)

TABLE 11.3: Species included in Figure 11.6

Species	Authority
1. Red-necked wallaby	This study
2. Black-tailed prairie dog	Hoogland (1981)
3. Red deer	Clutton-Brock, Guinness and Albon (1982)
4. African elephant	Douglas-Hamilton (1972)
5. Black-and-white colobus	Marler (1969), Oates (1977)
6. Hanuman langur, *Presbytis entellus*	Sugiyama (1967), Hrdy (1977)
7. Yellow baboon, *Papio cynocephalus*	Altmann and Altmann (1970), Altmann (1980)

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APPENDIX I

Aspects of Survival and Mortality

Introduction

I was not able to collect sufficient volumes of information to enable me to construct complete and accurate survivorship and fecundity schedules for the red-necked wallaby population of my study area; the critical data are still being accumulated, and a complete analysis of the dynamics of this population will soon be possible. I do have moderately extensive sets of data on the survival of young wallabies, and on sex ratios. I will briefly describe and discuss this information here because of its relevance to other parts of the thesis, and also offer some comments on the probable patterns of adult mortality.

Survival of young

Fig. I.1 shows lx (survivorship) and qx (mortality rate) schedules for wallabies from the age at which they first became visible to me as a bulge in an adult female's pouch (four months of age) up until their twentieth month of life (at which age females reach or approach sexual maturity). All wallabies who disappeared within this age interval are assumed to have died. Other data (Ch. 7), show that males begin to disperse after their twentieth month of life : it is thereafter impossible to decide whether males who disappeared were dead, or had moved out of the study area. Information on 78 young wallabies, collected from mid-1981 to mid-1984, were used to construct the schedules shown in Fig. I.1. The analysis shows that mortality rates were low during most of pouch life, but increased abruptly during the eleventh month of life, when most young had just left the pouch. The

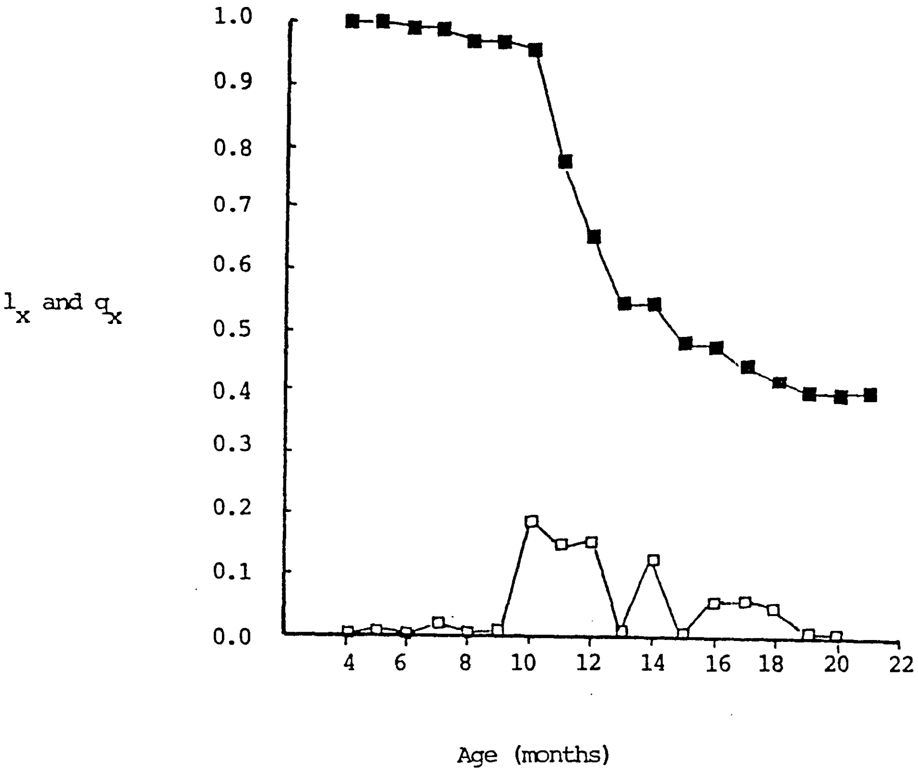


Fig. I.1 Survivorship (l_x) (■) and mortality (q_x) (□) schedules for young wallabies.

mortality rate declined over the succeeding three months, during which period the infant is still dependent on its mother and spends much of its time following her as a young-at-foot, and increased again during month fifteen, when most young are weaned (see Ch. 6). Mortality rates then returned to low levels over the succeeding months. Approximately 50% of all wallabies born die before they reach weaning age, and only 40% survive to give birth, or disperse.

It was impossible to directly estimate mortality rates during the first four months of pouch life, when I could never be certain that a female had anybody in her pouch. However, the low incidence of delayed or interrupted reproductive cycles of females, which would have resulted from the loss and replacement of very small pouch young (see Ch. 5), suggests that the mortality rate during the first months of life is low, probably less than five per cent.

Fig. I.2 shows how infant survival rates varied through the study period. Each point on the graph represents the percentage of infants leaving the pouch during each four-month period, who subsequently survived to weaning age. These data show no obvious effect of weather on infant survival : survival was low during the dry winter of 1981, high during the dry winter of 1982, and high during the summer of 1982 (cf. Fig. 2.2). Infant mortality rates were weakly correlated with the number of dingoes seen in the study area during each four-month period (r=0.47, n=8, n.s.). The measured index of dingo activity may account for some of the deaths, but the majority remain unexplained. In chapter 10, I showed that infant mortality rates were strongly related to the mothers' frequency of association with other wallabies, especially offspring of previous years. Therefore, a period of high infant survival and consequent high recruitment of subadults into social groups, should result in a subsequent fall in infant survival rates. The data in Fig. I.2 are consistent with this expectation : the high infant survival rates of 1982 were followed by low survival in 1983, and preceeded by low survival in 1981. Data from the first part of 1984 suggest another increase in infant survival, perhaps in response to low recruitment the year before. More data will be needed to show whether such a negative feedback mechanism exists, but if it does it could have some interesting consequences for the regulation of

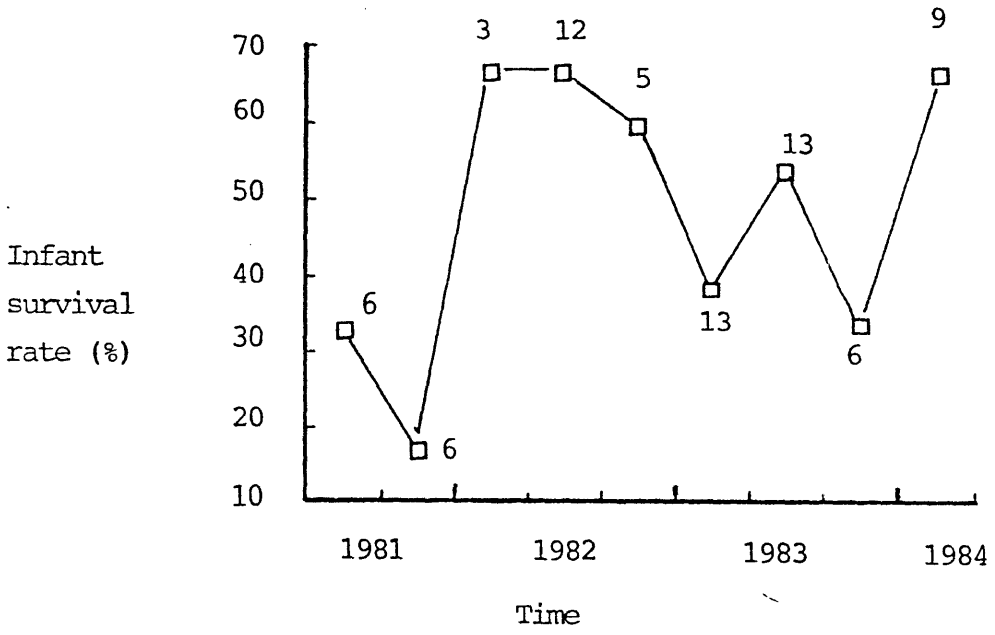


Fig. I.2 Variation in infant survival rates through the study period (sample sizes are numbers of infants leaving the pouch during each period).

the growth of the population.

Mortality of adults

A total of 35 adults disappeared during the study. As adults very rarely shift their home ranges (see Ch. 3, and Ch. 7), I assume that these disappearances were predominantly due to deaths.

Adults disappeared according to a clear seasonal pattern : most went during the winter months, very few went in mid-summer (see Fig. I.3; the frequencies differ significantly from a uniform distribution : $x^2=14.21$, 5 d.f., $P<0.05$). As Fig. I.3 also shows, dingo activity, as judged by the numbers of dingoes seen in the study area, was highest when the rate of disappearance of adult wallabies was lowest. This observation suggests that dingoes were not imposing this seasonal pattern of disappearance, and were a relatively unimportant agent of mortality. Adults began disappearing in autumn, and were steadily lost through the winter. This pattern suggests that declining food quality and abundance precipitated the deaths of at least some of these adults. Although the evidence is weak, and it is not possible to exclude other possible agents of population regulation, it does seem more likely that the population is regulated by food supply than by predation.

A total of 41 skulls of red-necked wallabies were picked up at Wallaby Creek, and aged by molar progression (Kirkpatrick 1965). The age distribution of this skull collection is shown in Table I.1. Skulls of young (< 2 years old) wallabies were clearly underrepresented, probably because they break down more rapidly in the field than do the skulls of adults. Survival rates up to almost two years of age have been measured directly (Fig. I.1) and it is possible to use the skull collection to complete a q_x schedule for adults as well, using the method of Sinclair (1977). This has been done and the results entered into Table A.1, although the sample sizes are so small that the results should be regarded as, at best, a very crude preliminary approximation of the true pattern of mortality. Mortality rates seem to remain low for several years after maturity has been reached and then increase in late adulthood, according to the pattern commonly found in large mammals (see Caughley 1966, Hutchinson 1978).

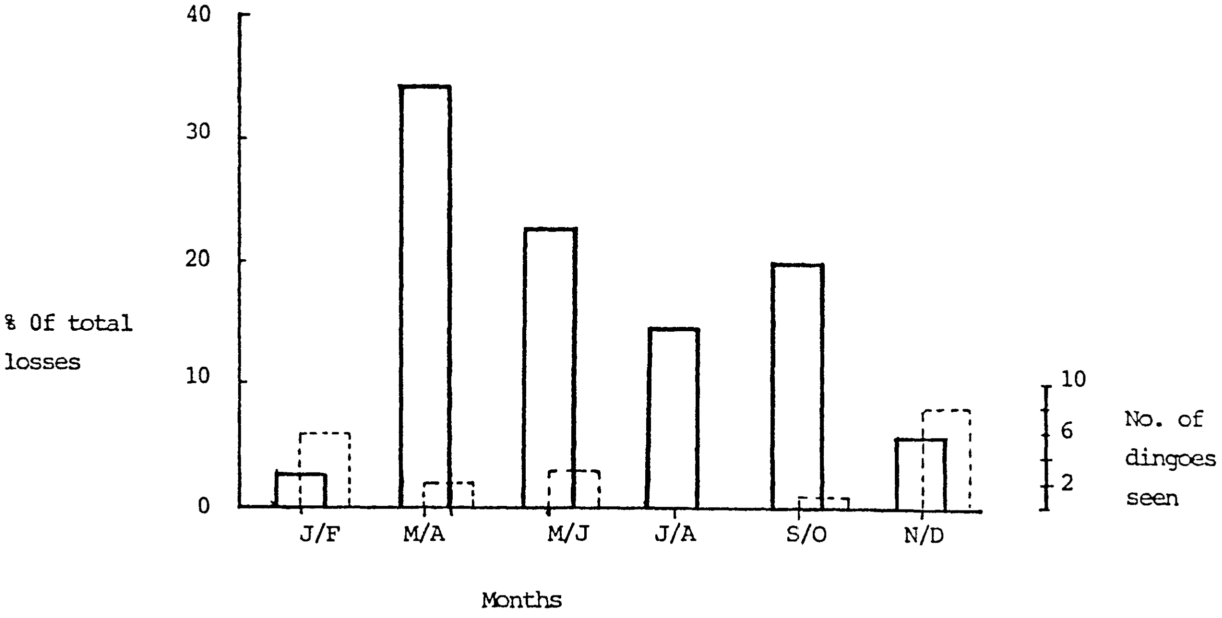


Fig. I.3 Seasonal variation in numbers of adult wallabies disappearing, compared with an index of dingo activity in the study area.

Sex ratios

Table I.2 records sex ratios of young-at-foot, subadult and adult red-necked wallabies in the Wallaby Creek study area. The data for adults are the numbers of males and females in the standing population at the end of 1983, data for younger age classes include all males and females recorded during the three years of study. The table also shows a sex ratio of pouch young recorded from near Bonalbo (about 30 km south of Wallaby Creek), by J.C. Merchant (pers. comm.).

Sex ratios of pouch young, young-at-foot and subadults were all close to parity, indicating that males and females die at similar rates up to the age at which males disperse. However, the adult population was composed of significantly more females than males. This excess of adult females in the study population could have been due either to a higher rate of death of young adult males, or to a differential loss of males through emigration. In the second case, the deficit of males in the study area should have been balanced by an excess of males in neighbouring areas of suitable habitat. I tested this possibility in August of 1982 by searching for and sexing wallabies to the east and south of my study area. I searched as far as 600 metres to the east and 600 metres to the south, and did not retrace my steps while searching, so that each individual should only have been counted once. I counted a total of 47 adults, 10 of whom could not be sexed. Nine of the sexed adults were males, and 28 were females, a significant deviation from parity ($x^2=9.76$, $P<0.01$). The deviation remains significant if half of the unsexed wallabies are assumed to be male, and the other half female ($x^2=6.89$, $P<0.01$). This result suggests strongly that the female-biased sex ratio in my study area was not due to a differential loss of young males through dispersal. If that had been the case I should have detected at least the beginnings of a swing to a male-biased sex ratio to the east or south of the study area, given the short distances over which males are known to disperse (see Ch. 7); instead, the sex ratio of adults outside the study area was even more heavily biased towards females. It seems clear, therefore, that a differential mortality of males sets in at, or some time after, the age at which males disperse.

TABLE I.1: Ages at death of red-necked wallabies of Wallaby Creek (q_x values for the first two age-classes have been taken from Figure I.1)

	A G E (years)												
	0	1	2	3	4	5	6	7	8	9	10	11	12
Number of skulls found	0	1	3	7	7	2	7	3	6	2	1	2	1
q_x	*0.45*	*0.25*	0.07	0.18	0.22	0.08	0.32	0.20	0.50	0.33	0.25	0.67	1.00

TABLE I.2: Sex ratios of red-necked wallabies at Wallaby Creek (except for pouch young, from Bonalbo, J.C. Merchant, pers. comm.)

	Age class			
	Pouch young	Young-at-foot	Subadult	Adult
Number of males	41	28	18	34
Number of females	41	30	19	56
Males per 100 females	100	93.3	94.7	60.7
Significance of deviation from parity	n.s.	n.s.	n.s.	$\chi^2 = 4.90$, $P < 0.05$

APPENDIX TWO

Geographical Variation in the Sex Ratios of Infants

The arguments of Fisher (1930) and MacArthur (1965), now widely accepted, predict that sexually reproducing organisms should distribute their parental investment in equal quantities to male and female offspring. However, parental investment may take many forms (Trivers 1982), and animals may be selected to dispense different kinds of investment at different rates to their sons and daughters (Maynard Smith 1980). In Chapter ten, for example, I presented data which suggested that female red-necked wallabies make a life-long investment in their daughters, through tolerance of ecological competition from them, while they stop investing in their sons at the time that those sons disperse. The interspecific comparisons drawn in that chapter also suggested that this prolonged maternal investment in philopatric daughters can be balanced by several kinds of early investment in dispersing sons : in galagos, more males than females are born (Clark 1978); in red deer, male calves suckle more than female calves do (Clutton-Brock, Guinness and Albon 1982); while in red-necked wallabies, subadult males spend more time feeding with their mothers than do subadult females.

The patterning of investment in sons and daughters may vary within as well as between species. There is evidence of some such inter-population variation in kangaroos : sex ratios of pouch young of eastern grey kangaroos and red kangaroos tend to be biased in favour of males in the drier parts of those species' ranges (Johnson and Jarman 1983). Trends of this kind suggest that investment in individual females may be heavier in dry than in mild regions. In this appendix, I report on a cline in the sex ratios of infant red-necked wallabies; suggest how this might reflect a shift from one form of early investment in males to another; and point out the data that should be collected to allow us to either dismiss or favour the hypothesis.

Table 11.1 gives estimates of the sex ratios of pouch young from five populations of red-necked wallabies, and a sex ratio of young-at-foot from a further population, together with climatic data for each site. All of the sampled populations from Australia and New Zealand are unconfined and, apart from some unselective removal of animals in some populations, unmanaged. The English wallabies are free-ranging in a large enclosure, and are lightly provisioned during winter. Averages of temperature and precipitation are long-term means for all months of the year. Seasonality of temperature is measured as the difference between the mean temperatures for the hottest and coldest months, expressed as a percentage of the mean temperature for the hottest month. Sex ratios of pouch young did not vary significantly with rainfall, but were significantly correlated with mean temperature over the whole year ($r=-0.91$, 3 d.f., $P<0.05$); mean temperature for the coldest month ($r=-0.88$, 3 d.f., $P<0.05$); and seasonality of temperature ($r=0.89$, 3 d.f., $P<0.05$). Inclusion of the young-at-foot sex ratio strengthened these conclusions (sex ratio on temperature for the whole year : $r=-0.93$, 4 d.f., $P<0.01$; on temperature for the coldest month : $r=-0.91$, 4 d.f., $P<0.02$; and on seasonality of temperature : $r=0.87$, 4 d.f., $P<0.05$). Fig 11.1 illustrates the relationship between average temperature over the whole year and sex ratio of infant wallabies. Infant sex ratios are strongly biased in favour of males in regions experiencing cold winters (Tasmania, New Zealand, England), but are closer to parity in warmer, less seasonal climates (Warwick, Bonalbo, Wallaby Creek).

I suggest that the costs to young females of dispersal are likely to be so important that daughters will inherit their mothers' home ranges in all populations (see Ch. 11), but that the strong association between mothers and subadult sons - which I observed at Wallaby Creek, and which appears to balance later investment, through continued association, in daughters - could be disrupted in cold, strongly seasonal environments. In Tasmania, New Zealand and England, young wallabies leave the pouch in early summer, and are weaned several months later. If newly-weaned males in cold, seasonal environments associate with their mothers according to the pattern observed at Wallaby Creek, then they must do so through a cold winter,

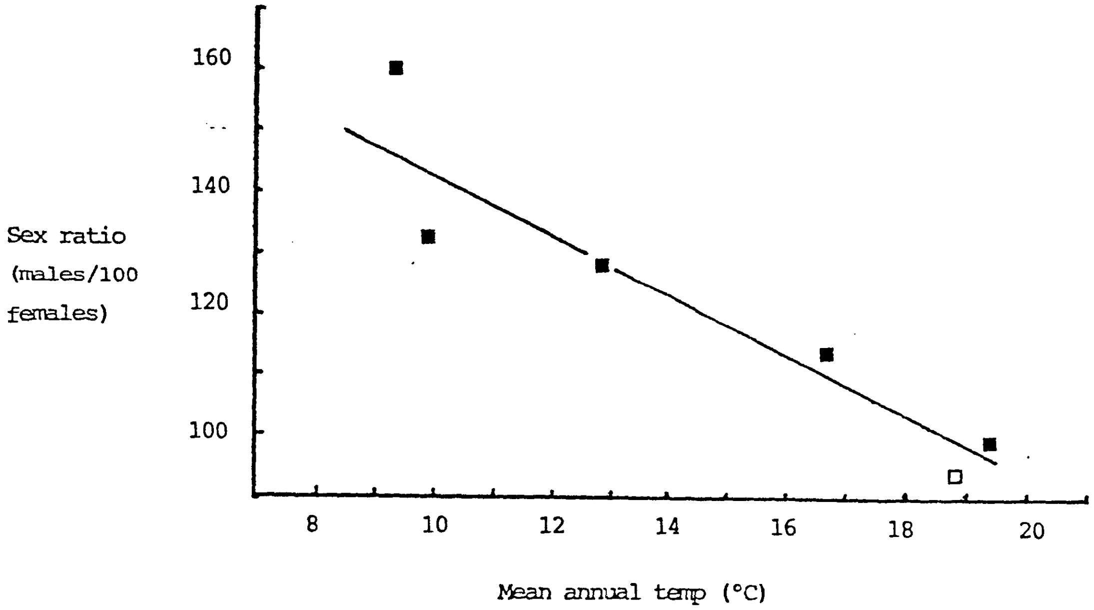


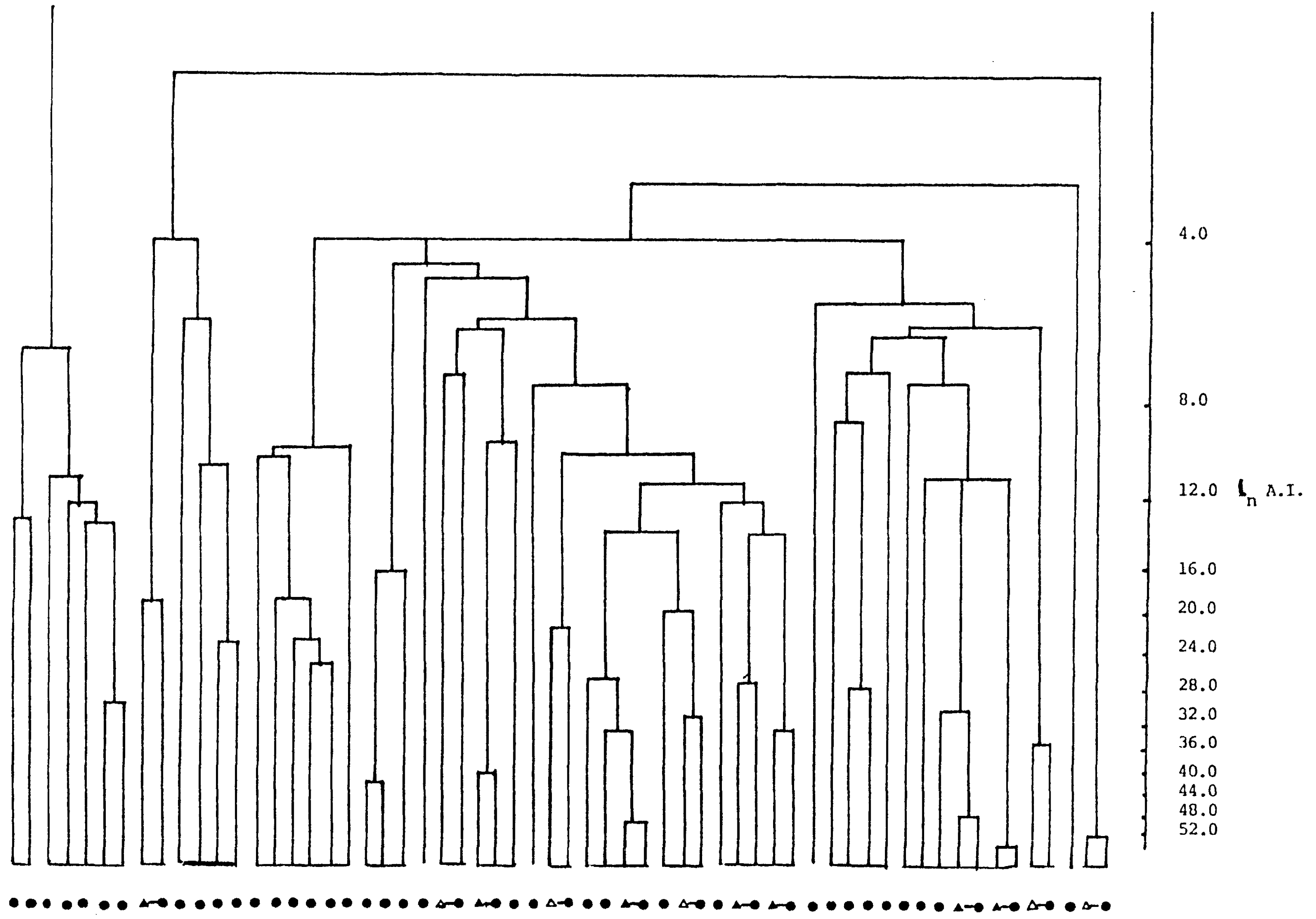
Fig. II.1 Relationship between environmental temperature and the sex ratios of pouch young (■) and young-at-foot (□) red-necked wallabies.

and disperse during or at the beginning of the following summer. The relatively minor deterioration in pasture quality during winter at the temperate Wallaby Creek site results in an increase in the distances separating feeding wallabies, and a decline in the stability of feeding associations (see Ch. 4). If this response to seasonal deterioration of pasture were exaggerated in the severe winters at higher latitudes, it is plausible that a strong association between mothers and subadult sons would not develop in populations at high latitudes, and mothers might instead equalise investment in male and female offspring by producing males in greater numbers. In other words, geographical patterns in the sex ratios of infant red-necked wallabies might be generated by the inevitability of life-long investment by mothers in their daughters, and variation in the appropriateness of alternative forms of early investment in sons.

This hypothesis would be substantiated if it could be shown that the strong association between mothers and their newly-weaned sons which is seen in temperate regions did not occur in populations of wallabies experiencing cold, severe winters, and would be disproved were it shown that the patterns of association between mothers and their sons and daughters did not vary with climate. Analysis of this geographical pattern should also consider the possibility that male-biased sex ratios of pouch young in cold regions arise in response to a differential mortality of infant or subadult males in such climates (see Fisher 1930). At Wallaby Creek, the sexes die at similar rates up to the age at which males disperse (see Appendix I).

TABLE II.1 Sex ratios of infant red-necked wallabies according to locality and climate (sources: (1) J.C.Merchant, pers.comm.; (2) T.H.Kirkpatrick, pers. comm. and M.Walker, pers. comm.; (3) Catt 1977; (4) Fleming et.al. 1983 (5) This study)

	Locality	Sex Ratio	Mean annual ppt. (mm)	Mean annual temp. (°C)	Seasonality of temp (%)	
(1)	Bonalbo 28° 45' S. 152° 37' E.	100 (n=82)	1103	19.4	50.0	
(2)	Warwick 28° 12' S. 152° 6' E.	114 (n=250)	644	16.7	60.8	
(1)	Gladstone 40° 57' S. 148° 1' E.	128 (n=123)	1167	11.8	60.7	(pouch young)
(3)	Hunters Hills 44° 30' S. 170° 30' E.	133 (n=56)	729	9.9	77.8	
(4)	Whipsnade Park 51°52' N. 0° 33' W.	160 (n=104)	636	9.4	78.9	
(5)	Wallaby Ck. 28°28' S. 152° 33' E.	93 (n=58)	1018	18.9	56.3	(young-at-foot)



Appendix III. Dendrogram for associations among adult females (●), subadult females (△) and subadult males (▲) in 1983. Symbols joined by lines are mother-subadult pairs. A.I. = association index. Horizontal lines at the base of the dendrogram join individuals assigned to the same social groups according to the criterion given in the text (see Ch. 7.4.1.).