

Body size, age and paternity in common brushtail possums (*Trichosurus vulpecula*)

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Abstract

Sexual selection should produce sexual size dimorphism in species where larger members of one sex obtain disproportionately more matings. Recent theory suggests that the degree of sexual size dimorphism depends on physical and temporal constraints involving the operational sex ratio, the potential reproductive rate and the trade-off between current reproductive effort and residual reproductive value. As part of a large-scale experiment on dispersal, we investigated the mating system of common brushtail possums inhabiting old-growth *Eucalyptus* forest in Australia. Paternity was assigned to 20 of 28 pouch-young (maternity known) genotyped at six microsatellite loci. Male mating success was strongly related to body size and age; male body weight and age being highly correlated. Despite disproportionate mating success favouring larger males, sexual size dimorphism was only apparent among older animals. Trapping and telemetry indicated that the operational sex ratio was effectively 1 : 1 and the potential reproductive rate of males was at most four times that of females. Being larger appeared to entail significant survival costs because males 'died-off' at the age at which sexual size dimorphism became apparent (8–9 years). Male and female home ranges were the same size and males appeared to be as sedentary as females. Moreover, longevity appears to be only slightly less important to male reproductive success than it is to females. It is suggested that a sedentary lifestyle and longevity are the key elements constraining selection for greater sexual size dimorphism in this 'model' medium-sized Australian marsupial herbivore.

Keywords: marsupial, microsatellites, paternity, sexual size, dimorphism

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Introduction

In species where larger members of one sex obtain disproportionately more matings sexual size dimorphism should be apparent, provided body size is heritable. Recent insights regarding sexual selection (Kvarnemo & Ahnesjö 1996; Brooks & Kemp 2001) suggest that the degree of sexual size dimorphism will depend on the operational sex ratio (OSR; the ratio of fertile females to sexually active males), the potential reproductive rate (PRR; offspring production per unit time for each sex), and the trade-off between current

reproductive effort and residual reproductive value (RRV). The intensity of competition for mates will lessen as the OSR or PRR approaches 1 : 1 (Kvarnemo & Ahnesjö 1996; Kraaijeveld-Smit *et al.* 2003). In long-lived species with low reproductive rates sexual size dimorphism may only be apparent in older animals with lower RRV if increasing body size adversely affects survival (Kokko 1997; Brooks & Kemp 2001).

Kangaroos (larger Macropodidae) demonstrate some of the most extreme examples of sexual size dimorphism in mammals and a great deal is known about their mating systems (Jarman 1991). By contrast, relatively little is known about the mating systems of the smaller Macropodidae and other medium-sized (0.1–5.0 kg) Australian marsupial herbivores (Petauridae, Phalangeridae and

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Potoroidae; Strahan 1995). Unlike kangaroos, most medium-sized Australian marsupial herbivores are secretive, solitary and apparently show little sexual size dimorphism (Strahan 1995). The common brushtail possum (*Trichosurus vulpecula*) is the best-studied of these species and its life history is typical of most (How & Kerle 1995). The PRR of females is low as they are incapable of producing more than two young per year, generally produce only one, and often delay breeding until they are 3 years old. Females often live for up to 14 years in the wild (Cowan 1990; How & Kerle 1995; Clinchy *et al.* 2001) and demographic modelling (Clinchy *et al.* 2001) indicates that adult survival is an order of magnitude more important than current reproductive effort in determining the rate at which females replace themselves in the population.

Two recent molecular genetic studies (Sarre *et al.* 2000; Taylor *et al.* 2000) have described aspects of the mating system of possums in New Zealand. Possums were introduced from Australia to New Zealand in the early 19th century and have since become a significant pest (Cowan 1990). Attempts are underway to develop a sexually transmitted biocontrol programme and the Sarre *et al.* (2000) and Taylor *et al.* (2000) studies were conducted in that context. Taylor *et al.* (2000) found modest but significant differences between males in the number of offspring sired per year while Sarre *et al.* (2000) did not. Taylor *et al.* (2000) also reported that breeding males tended to be older and larger than nonbreeders but the differences were not significant. They cited the fact that possums show little sexual size dimorphism (female body weights are on average only 1.4% less than that of males, based on results from nine separate studies; Cowan 1990) to argue that polygyny is unlikely to be extreme in any population. While the Sarre *et al.* (2000) and Taylor *et al.* (2000) studies both provide useful information they were not designed to address questions concerning evolutionary ecology. Both studies were conducted in areas where, because they are an introduced pest, possums are both hunted and poisoned. Moreover, neither study was conducted in association with an in-depth assessment of the ecology of the species.

In this paper we report on a molecular genetic study of the mating system of common brushtail possums inhabiting undisturbed, old-growth *Eucalyptus* forest in their native Australia. We show that male mating success is clearly related to body size and age. Despite this, sexual size dimorphism is not apparent except among older animals. We present evidence regarding the OSR, male PRR, and the trade-off between current reproductive effort and RRV; to explain the constraints on sexual selection that likely limit the degree of sexual size dimorphism. We argue that a sedentary lifestyle and longevity are critical elements in the mating system of this 'model' medium-sized Australian marsupial herbivore.

Materials and methods

Study site

The study was conducted in old-growth *Eucalyptus* forest near the centre (30°06'00" S, 152°10'20" E; elevation 940–1040 m) of the 121 000-ha Guy Fawkes Wilderness Area, in northeastern New South Wales, Australia (Clinchy 1999). This area has remained largely untouched by European disturbance and approximates the condition of the ancestral forests in which possums are thought to have evolved (Green 1984; NPWS 1992).

Chronology, capture and handling

Two 36-ha study grids were established, 2 km apart, in September 1994. Permanent trap locations were established at 100 m intervals. Possums were live-trapped three nights per month from March (beginning of autumn) to September (beginning of spring) in 1995 and 1996. Traps were set at irregular intervals until July 1997. The grids are treated separately in all genetic analyses (e.g. potential fathers are only considered from among the males on the same grid) because there was no inter-grid exchange over 3 years. Density, body weight, age and behaviour data are pooled across grids because these variables did not differ between the grids (Clinchy 1999).

Adults (males with testes ≥ 18.0 mm, females with invaginated pouches) were weighed to the nearest 50 g using a spring scale. Body weights reported are averages over a season. All adults ($n = 187$), and pouch-young of sufficient size ($n = 28$), were ear-tagged. From March 1995 onwards, every resident adult female was fitted with a radio-collar. From October 1995 onwards, tissue samples for genetic analyses were obtained from all individuals. The age, in years, of a subset of adults was determined from cementum annuli (Clout 1982; Clinchy 1999). Birth dates of pouch-young were back calculated from a regression of head length and age (Clinchy 1999; his Appendix 2). Births per week were summed across years (1995–97) because there was no significant interannual variability (Clinchy 1999; his Fig. 5.2). The focus was placed on autumn (mid-March to mid-June) results because this is when most births occur (Fig. 1).

Location data

Possums are active at night and spend the day in a den, which was almost invariably (99.6%, Johnson *et al.* 2001) in the hollow branch of a large, old *Eucalyptus* tree. Radio-collared females were tracked to their dens about once a week. For every radio-collared female both the arithmetic centre of and the maximum distance (length) between, all of the dens used by her in a given season were calculated,

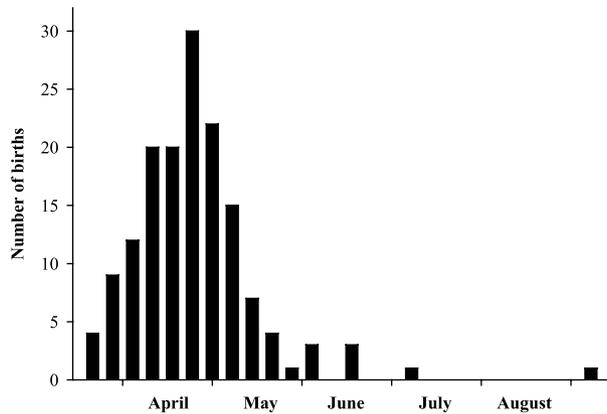


Fig. 1 Number of births per week, summed over 3 years (1995–97).

to describe her 'denning' range. Females used up to six dens in autumn. The descriptive statistics reported regarding den use exclude females that were radio-tracked less than six times.

For each adult, of either sex, both the arithmetic centre of and the maximum distance (length) between all of the locations at which it was trapped in a given season were calculated, to describe its trap-revealed range. The centre of an individual's trap-revealed range was a reasonably accurate indicator (within 44.6 m on average, $n = 65$, range = 3.1–155.9) of the centre of its radio-revealed range. Both males and females were trapped at up to seven different locations in autumn. Descriptive statistics reported regarding trap-revealed ranges exclude individuals trapped less than seven times. To estimate the average proximity between and among male and female home ranges in autumn we calculated the distance between the trap-revealed centre of every individual's range and that of its nearest male and female neighbour.

To gauge the proximity of mothers and putative fathers we calculated the distance between the radio-revealed centre of each adult female's denning range and the trap-revealed centre of each adult male's range. Since males were not radio-collared we assessed their use of the same dens as females by following them after they were released from a trap ($n = 1504$) to see if they remained in the open (35%), ducked into a hollow log (7%), or ran to a tree which was (33%) or was not (25%) a den tree used by one of the radio-collared females.

Statistical analyses of ecological data

Statistical procedures follow Sokal & Rohlf (1995) and Zar (1999). Results are reported as statistically significant based on Bonferroni-corrected α values (Rice 1989). Population estimates were generated using JOLLY-SEBER (Krebs 1999). Deviations from the Poisson distribution

were tested using POISSON (Krebs 1999). All other statistical procedures (including tests of normality) were conducted using STATISTICA (StatSoft Inc. 1995). Descriptive statistics are reported as medians and range if the distribution differed significantly from normality, or means \pm standard error and range, if the distribution was normal. Adult body weights and pouch-young survival differed significantly between years (Clinchy 1999; his Tables 5.4 and 5.12). Since more paternity data were available in 1996, analyses that might be sensitive to interannual differences include data from 1996 only.

DNA extraction and microsatellite analysis

All tissue for genetic analysis was stored in 100% ethanol prior to transport to the laboratory. DNA extractions were performed using the salting-out procedure described in Sunnucks & Hales (1996). Six microsatellite loci (Tv16, Tv19, Tv27, Tv53, Tv58 and Tv64) were scored as described in Taylor & Cooper (1998).

Level and distribution of genetic diversity

Observed (H_O) and expected (H_E) heterozygosities, the likely frequency of null alleles (Nulls), and the average probability of exclusion given one parent is already known (P Exclusion), were calculated for each locus on each study grid separately (Table 1), using CERVUS version 1.0b (Marshall *et al.* 1998). Tests for linkage disequilibrium and deviations from Hardy–Weinberg expected genotypic proportions (HWE P , Table 1) were conducted using GENEPOP version 3.1c (Raymond & Rousset 1995).

Analysis of paternity

All adult males present on the same grid as the mother at any time (i.e. before, during, or after the breeding season in question) were considered potential fathers. We conducted parentage analyses using both KINSHIP version 1.2 (Goodnight & Queller 1999) and CERVUS. Between them (Clinchy 1999; his Appendix 1), these two programs are robust to both: (i) deviations from Hardy–Weinberg equilibrium attributable to nonrandom mating, natural selection and other related causes (KINSHIP; Queller & Goodnight 1989); and (ii) errors attributable to mis-scoring, mutations and null alleles (CERVUS; Marshall *et al.* 1998). KINSHIP assigns a level of confidence to each putative case of paternity by comparing the logarithm of the odds (LOD) score for that case vs. a randomly generated set of LOD scores. CERVUS uses a more conservative approach based on the difference (Δ) in LOD scores between the most likely and next most likely parent in comparison with a randomly generated set of Δ scores. Only if confidence was > 99% did we classify a putative father as having been

Table 1 Genetic variability measures for six microsatellite loci on each of the two study grids

Grid	Locus	No. of alleles	H_O	H_E	HWE P	Nulls	P excl.
West	Tv16	14	0.76	0.89	0.003	0.08	0.78
	Tv19	20	0.89	0.92	0.364	0.02	0.83
	Tv27	13	0.92	0.87	0.573	-0.03	0.73
	Tv53	18	0.91	0.89	0.040	-0.01	0.79
	Tv58	15	0.81	0.87	0.142	0.04	0.74
	Tv64	22	0.89	0.93	0.532	0.02	0.85
East	Tv16	15	0.82	0.91	0.204	0.05	0.80
	Tv19	18	0.95	0.92	0.886	-0.02	0.82
	Tv27	13	0.86	0.89	0.968	0.02	0.77
	Tv53	17	0.97	0.90	0.123	-0.05	0.79
	Tv58	13	0.88	0.88	0.874	0.00	0.75
	Tv64	20	0.95	0.93	0.708	-0.01	0.85

Values reported are observed (H_O) and expected (H_E) heterozygosities, the probability of H_O given H_E (HWE P), the likely frequency of null alleles (Nulls), and the average probability of exclusion given one parent is already known (P excl.).

'identified' by one or both programs. Following Taylor *et al.* (2000) any male mismatching the mother-offspring pair at just one locus that was identified as the most likely parent by CERVUS was included in the set of putative fathers. Males that mismatched at > 1 locus were not considered as putative fathers.

Results

Genetic diversity

The six microsatellites detected a large amount of genetic variation, with an average of 17.0 (± 1.5) alleles per locus on the West grid and 16.0 (± 1.2) on the East grid, and an average H_E of 0.90 (± 0.01) on both grids (Table 1). The average exclusion probability (Chakravarti & Li 1983) over all loci given that one parent was already known was > 0.999 on both grids.

Only one of the 15 pairwise locus combinations (Tv27/Tv53) exhibited significant linkage disequilibrium ($P = 0.029$) prior to correcting α for multiple comparisons ($= 0.003$), and only on one grid ($P = 0.858$ on the other grid). There was also no consistent deviation from Hardy-Weinberg genotypic proportions across both grids (HWE P , Table 1).

Paternity assignment

Paternity analyses were conducted in all 28 cases where genetic samples were available from both mothers and their pouch-young. In 19 cases, the same putative father was identified by both KINSHIP and CERVUS. CERVUS identified one more putative father that mismatched the mother-offspring pair at just one locus. This male was first captured the year after his putative offspring was born, and after the mother had died. Consequently, this male is

not included in any of the statistical tests below because these all involve comparisons within the same year.

In eight cases paternity was unassigned. In all eight cases all of the potential fathers considered demonstrated mismatches with the mother-offspring pair at two or more of the six loci. Using data from all six loci and a typing error rate of 0.01 (around that observed for mother-offspring pairs), CERVUS simulations suggested that if all fathers were sampled only 5% (one of 28) of offspring would fail to have paternity assigned with 99% confidence. The discrepancy between the observed (20/28) and expected (27/28) rates of paternity assignment is most likely the result of incomplete sampling of putative fathers. In six of the eight cases where paternity was unassigned there were ecological reasons (17 males disappeared before the start of tissue sample collecting in October 1995; not all males adjacent to females on the corners of the grids may have been sampled) why the true father may not have been included among the set of potential fathers.

Male reproductive success in relation to body size and age

Putative fathers were consistently larger (> body weight) than other males compared to all males in the population or just those nearest a given mother. The average body weight of putative fathers was significantly greater than that of all other adult males present in autumn (2478.5 ± 42.7 g, range = 2150.0–2650.0, $n = 12$; 2163.9 ± 33.3 g, range = 1750.0–2566.7, $n = 37$, respectively; $t_{47} = 5.04$, $P < 0.001$; data from 1996 only). The putative father's weight was also greater than that of the other three males nearest to a given mother (see below) significantly more often than expected by chance (Fig. 2; $\chi^2_3 = 11.40$, $P = 0.010$). The putative father's weight was not significantly correlated with the mother's ($F_{1,12} = 1.24$, $r^2 = 0.02$, $P = 0.286$).

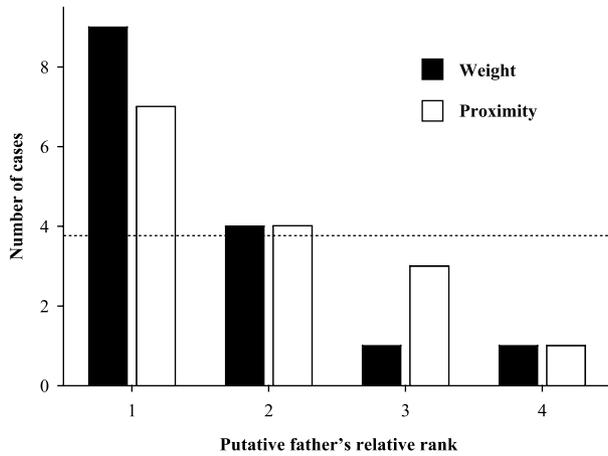


Fig. 2 Putative father's weight and proximity ranked among the four males nearest to each mother. The dashed line shows the distribution expected by chance.

Based on the available sample of known age adult males present at the same time ($n = 7$; autumn 1996 only), in addition to being larger, putative fathers ($n = 3$) were also significantly older (age = 8 years in each case) than other males (median age = 5 years, range = 2–7; Mann–Whitney $U_{3,4} = 0.00$, $P = 0.028$). Adult male body weight in autumn and age were highly correlated ($F_{1,5} = 35.81$, $r^2 = 0.85$, $P = 0.002$; data from 1996 only).

Sexual size dimorphism

In general, adult males and females weighed about the same (Table 2). Males tended to be heavier than females in

summer but females tended to be heavier than males in winter. There was virtually no difference in body weight between the sexes during the autumn breeding season, considering the population as a whole. However, there was evidence of sexual size dimorphism among older animals (Clinchy 1999; his Fig. 5.9). Older (8 + years = age of putative fathers, see above) adult males were significantly heavier in autumn than older adult females (median = 2500.0 g, range = 2450.0–2550.0; median = 2183.3 g, range = 2000.0–2400.0, respectively; Mann–Whitney $U_{3,7} = 0.00$, $P = 0.016$; data from 1996 only).

Proximity of mothers and putative fathers

The mother's and putative father's ranges were immediately adjacent in almost all cases. The median distance (85.3 m, range = 39.6–228.8) between the centres of their ranges was less than one denning range length (94.6 m; see below). In only one case was the distance (228.8 m) greater than the average trap-revealed range length (211.2 ± 9.0 m, both sexes combined; see below). The putative father was often the male nearest the mother, although this was not always so and in one case he was the fourth nearest male (Fig. 2). Based on where he was trapped, the putative father's relative proximity to the mother (whether first, second, third, or fourth nearest male) did not differ significantly from that expected by chance (Fig. 2; $\chi^2_3 = 5.00$, $P = 0.172$). The putative father's behaviour upon release from a trap, however, differed from that of the other three nearest males, insofar as he was more likely to run to one of the mother's dens. Nine mothers had one or more dens that anywhere from one to all four of the nearest males (15 males in total) were observed to run to following

Table 2 Median seasonal body weights (g) of adult males and females over the course of the study

Year	Season	Median body weight (g)		No. individuals		M–W U	P
		Males	Females	Males	Females		
1995	Spring	2200.0	2025.0	15	14	60.5	0.051
	Summer	2250.0	2200.0	31	40	493.0	0.140
	Autumn	2300.0	2233.3	40	51	916.5	0.408
	Winter	2200.0	2275.0	50	65	1433.0	0.278
	Spring	2112.5	2125.0	34	32	529.0	0.847
1996	Summer	2400.0	2175.0	32	31	308.0	0.010
	Autumn	2200.0	2185.4	49	46	988.5	0.302
	Winter	2179.2	2250.0	44	48	843.0	0.096
	Spring	2250.0	2350.0	43	36	678.0	0.344
1997	Summer	2425.0	2250.0	30	25	232.5	0.016
	Autumn	2325.0	2316.7	47	35	729.0	0.380
	Winter	2225.0	2187.5	45	30	601.5	0.426

The Mann–Whitney U (M–W U) test was used to evaluate the probability (P) of significant differences between the sexes.

their release from a trap. By chance alone the putative father would be expected to be one of these males in 3.75 (15 observations/four nearest males) cases. The putative father was in fact observed to run to the mother's dens in all nine cases (binomial $P = 0.004$).

Number of offspring per male

Among the 15 young with assigned paternity born in 1996 there were two cases where two young were sired by the same putative father. This is not significantly different ($\chi^2_1 = 0.75, P = 0.611$) from a random (Poisson) distribution of offspring per male. Only if at least four fathers each sired two young would there be statistically significant evidence of reproductive skew. In those cases where two young were sired by the same putative father the young were born 15 and 24 days apart.

Operational sex ratio

Virtually all adult females were fertile because almost every (98.6%; Clinchy 1999; his Table 5.2) radio-collared adult female that survived the season ($n = 78$) gave birth to a single pouch-young each autumn or winter (Fig. 1). Previous studies (Cowan 1990) have shown that all adult males produce sperm year round and are capable of sexual activity at any time. The absolute ratio of adult males and females can therefore be treated as equivalent to the operational sex ratio (fertile females to sexually active males). Between September 1994 and July 1997 almost the same number of adult males (94) and females (93) were enumerated and the ratio between the average number of adult males (24.0 ± 1.9 , range = 20.5–28.0) and females (25.3 ± 2.0 , range = 19.4–28.0) present in autumn on each grid (Clinchy 1999; his Table 4.5 to 4.8) was very nearly 1 : 1.

Grid-based density estimates may not reflect the operational sex ratio if the sexes differ in their spatial distribution. Female trap-revealed range lengths in autumn (188.5 ± 13.1 m, $n = 13$, range = 116.0–258.3) were double their denning range lengths (median = 94.6 m, $n = 62$, range = 0–324.7; length = 0 if one den, median number of dens = 3, range = 1–6). Male trap-revealed range lengths in autumn (220.1 ± 11.1 m, $n = 33$, range = 50.9–340.9) were not significantly larger ($t_{44} = 1.76, P = 0.086$) than those of females. Nearest neighbour distances between males and females in autumn (median = 58.6 m, range = 2.4–173.4) were significantly smaller than both nearest neighbour distances among males (median = 82.0 m, range = 9.2–174.4; Mann–Whitney $U_{67,68} = 1307, P < 0.001$) and nearest neighbour distances among females (median = 94.6 m, range = 30.0–281.9; Mann–Whitney $U_{75,75} = 1448, P < 0.001$). Nearest neighbour distances among males were not significantly different from those among females (Mann–Whitney $U_{67,75} = 2200, P = 0.202$). Thus, males and females space themselves out to the same

degree with regard to members of the same sex while overlapping the opposite sex.

Body size and longevity

While body size was greater in older males (8 + years = age of putative fathers, see above) longevity was greater in females. Eight of 25 females aged from cementum annuli were > 9 years old whereas none of the 13 males were (two-tailed Fisher's exact test, $P = 0.034$). Males appear to 'die-off' at the age at which sexual size dimorphism becomes apparent, because average adult survival is comparable between the sexes, prior to this point (Clinchy *et al.* 2001).

Discussion

In our study male mating success was clearly related to body size and age. Why then was there not evidence of significant reproductive skew as reported by Taylor *et al.* (2000) and why did Taylor *et al.* not find significant body size and age effects on male mating success? We suggest these apparent differences are methodological in origin and the studies in fact complement one another. Our results show that matings involve adjacent animals. The distribution of matings within a local cluster is therefore the appropriate measure of reproductive skew. Both we and Sarre *et al.* (2000) sampled clusters of one female plus the surrounding males (e.g. Figure 2). Sampling clusters of one male plus the surrounding females is a more direct means of gauging the number of offspring per male. Potential biases associated with partial sampling were not an issue for Taylor *et al.* (2000) because they obtained DNA from every last individual by eradicating their population. Accordingly, Taylor *et al.* (2000) did find significant differences between males in the number of offspring sired. Methodological differences also account for why we found strong evidence that male mating success was related to body size and age while Taylor *et al.* (2000) reported similar, but nonsignificant results. Taylor *et al.* (2000) studied a population subject to intensive hunting and poisoning whereas ours was not. The average age of adult males and females was 2.8 (range = 1–9) and 2.9 (range = 1–8) years, respectively, in the population of Taylor *et al.* (2000), compared to 6.0 ± 0.6 (range = 2–9) and 7.4 ± 0.8 (range = 2–14) in ours (Clinchy *et al.* 2001). In contrast to ours, too few males in the population of Taylor *et al.* (2000) presumably had the 'opportunity' to get old and heavy enough for differences to be measurable.

Since larger males obtain disproportionately more matings (Fig. 2) why is sexual size dimorphism not more apparent (Table 2)? The benefits of reproductive effort in any given year depend on the potential reproductive rate (PRR). As noted in the introduction, the PRR for females

is low. Male PRR will be greater than female PRR if males can obtain significantly more matings per unit time. Our results suggest that in any given year males are constrained to mating with a maximum of just four females. Females exclude unrelated females from their dens (Johnson *et al.* 2001) and their denning ranges rarely overlap those of other females (Clinchy 1999; his Figs 4.4 to 4.15). Males appear to space themselves out to the same extent. Male–male range centres were the same distance apart as female–female range centres (*c.* 100 m) and male range lengths were the same as female range lengths (*c.* 200 m). The distance between male–female home range centres (*c.* 50 m) was roughly half that between members of the same sex (*c.* 100 m). From simple geometry this suggests that each female's home range lies at the centre of the interstitial space between the four surrounding male home ranges and vice versa. Since females mate with only the four surrounding males (Fig. 2) geometry dictates that each male is restricted to mating with just those four females that surround him. Consistent with our results, the data from Taylor *et al.* (2000) regarding reproductive skew documented a maximum of four offspring per male.

Males could attempt to increase their mating success by ranging widely during the breeding season in search of receptive females. Such a strategy would fail if female breeding were highly synchronous or if males were unable to find females. At our study site the mating season lasted well over 10 weeks (Fig. 1). Relative to the 17-day gestation period for possums (Johnson *et al.* 2001) and the 2–3-week interval between multiple matings by the same putative father reported here, there would appear to be ample time for males to search for receptive females. Of course, if females are hard to find, all the time in the world may not suffice. Our results suggest, however, that females are easy to find. Females are not located randomly but instead show a strong preference for denning in trees with larger diameter at breast height (d.b.h.; Johnson *et al.* 2001), and males appear to know exactly which of these larger d.b.h. trees females are denning in given that putative fathers were followed to the mother's den tree significantly more often than expected by chance. Thus, even though males have both the ability and the time to roam about looking for females, they appear to be just as sedentary as females.

Our analysis of the possum mating system was conducted in the context of a large-scale field experiment designed to test the role of dispersal in the population dynamics of a 'model' medium-sized Australian marsupial herbivore. The results of the experiment, together with supplementary evidence (Clinchy 1999; Clinchy *et al.* 2001), clearly demonstrate that dispersal does not play a significant part in the population dynamics or life history, of these species. Almost all daughters settle on or beside their mother's home range (Clinchy 1999) and almost all sons settle only two or three home ranges away from their

mother (Johnson *et al.* 2001; Clinchy unpublished results). The results presented here indicate that this sedentary state continues into adult life.

The benefits of greater reproductive effort early in life must be weighed against the benefits of staying alive to breed in future years (residual reproductive value; RRV). Males presumably remain sedentary during the breeding season because moving about in search of females entails significant survival costs. Being larger also appears to entail significant survival costs because males 'died-off' at the age (8–9 years) at which sexual size dimorphism became apparent. Demographic modelling (Clinchy *et al.* 2001) indicates that longevity is critical to female reproductive success because only females surviving to at least 5 years of age in our population could be assured of producing a single surviving progeny and only females surviving to at least 8 years could be assured of producing more than one. While male PRR may be up to four times female PRR, the fact that sexual size dimorphism is delayed until 8–9 years of age suggests that longevity is only slightly less important to male reproductive success than it is to females.

The pattern of greater male mating success with body size and age together with delayed sexual size dimorphism we have documented is consistent with (Kvarnemo & Ahnesjö 1996; Brooks & Kemp 2001) a mating system involving male–male competition for mates where the operational sex ratio (OSR) and potential reproductive rate (PRR) are roughly equal and reproductive effort is strongly affected by residual reproductive value (RRV). Intriguingly, this same pattern is also consistent with a mating system based on female selection for 'longevity genes' where size is an 'honest' signal of longevity (Kokko 1997; Brooks & Kemp 2001). To discriminate between these mechanisms requires testing for both variation in male mating success with size within an age class (male–male competition) and variation with age within a size class ('longevity genes'). Regardless of whether it is age or competitive ability that determines male mating success, our results suggest a sedentary lifestyle and longevity are the key elements constraining selection for greater sexual size dimorphism.

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Australia's medium-sized marsupial herbivores have suffered more extinctions and declines in the past 200 years than any other mammalian taxon, world-wide. The study reported here was part of a larger, experimental test of the importance of dispersal in the population dynamics of these species. Mike Clinchy collaborated with Liana Zanette and Peter Jarman in conducting the field research. Andrea Taylor carried out the genetic analyses and Charley Krebs assisted with the statistical analyses.
