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Enhancement of reproductive success through mate choice in a social rock-wallaby, *Petrogale assimilis* (Macropodidae) as revealed by microsatellite markers

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Abstract The reason why a female who is socially paired to one particular male seeks extra-pair copulations (EPCs) with others has important implications in life history models and to the study of behaviour. The Allied rock-wallaby, *Petrogale assimilis*, lives in spatially isolated colonies in tropical north Queensland, Australia. Extensive observations of a colony at Black Rock showed that intense behavioural bonding occurs between pairs of adult males and females; about two-thirds of males paired with one female, the remainder paired with two females simultaneously. Single-locus microsatellite profiling determined the paternity of 63 offspring from 21 females for which long-term behavioural data were available. One-third of the young were fathered by males which were not paired socially with the mother. The mating system was heterogeneous: (1) all offspring of 11 females were fathered by the mother's partner, (2) all young of 5 females were fathered by extra-pair males, and (3) only some of the young of 5 females were fathered by their regular consort. Analysis of individual longitudinal demographic records showed that females whose young were always fathered by their consort had higher reproductive success than those whose young were always fathered as a result of (EPCs). However, females with some offspring fathered by their regular consort and others via EPCs had the highest probability of raising young to independence. These females were significantly more likely to have an offspring fathered as a result of an EPC if their previous young had failed to survive to pouch emergence. These results are consistent with the hypothesis that females choose mates for their genetic quality. Comparison of the males with which these females sought EPCs and the regular consorts suggested that arm length rather than body weight or testes size was used as the index of genetic quality. Results from a second colony of rock-wallabies in which the reproductive rate was accelerated were also consistent with the genetic-quality hypothesis. These results imply that by choosing better-quality fathers irrespective of social pairing, females are able to maximise their overall lifetime reproductive success, and presumably, those of their offspring.

Key words Monogamy · Sexual selection · Marsupial · *Petrogale assimilis* · Microsatellite

Introduction

Long-term preferential associations between particular males and females (pair-bonding sensu Wickler 1976), are a component of the definition used to describe "monogamy" (Kleiman 1977, 1981; Wickler and Seibt 1983). Monogamy apparently develops when the members of one sex (usually males) can neither monopolise essential resources sufficiently to attract several females nor defend a group of females in a localised area (Emlen and Oring 1977; Kleiman 1981; Ribble 1992). Two constrained forms of mating have been identified in the relatively few mammal species found to be monogamous (Kleiman 1977; but see Zeveloff and Boyce 1980): (1) facultative monogamy, where ecological constraints do not allow monopolisation by males due to limiting resources, for example where there is limited food availability or high competition for shelter sites and (2)

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obligate monogamy, in which male mammals are precluded from being polygynous because a female cannot successfully rear young without the direct aid of an attending male (e.g. Brotherton et al. 1997; Kleiman 1977, 1981). Although mates may engage in extra-pair copulations (or EPCs), sexual exclusivity is *not* a requirement of monogamy (Kleiman 1977; Carter and Getz, 1993).

Until recently, kinship and mate choice were inferred primarily from behavioural observations. Males and females which associated closely were assumed to have been mating, and any resultant young were presumed to be their descendants. However, a combination of genetic and behavioural data are becoming increasingly relevant in these studies (e.g. Goossens et al. 1996; Brotherton et al. 1997; Hogg and Forbes 1997). Molecular techniques such as DNA fingerprinting (Jeffreys et al. 1985) and more recently microsatellite markers (Ellegren 1992; Westneat and Webster 1994) have demonstrated that behavioural observations alone do not provide a reliable understanding of mating systems (Birkhead et al. 1990). A significant proportion of the offspring of many species which were assumed to mate exclusively with their consorts result from EPCs (e.g. Saino et al. 1997; Slagsvold and Lifjeld 1997). Females of many species mate with males with whom they are not paired and then raise their young with the assistance of their consorts, raising an important distinction between genetic and social partners.

The functional significance of these EPCs remains uncertain, particularly when there is no direct paternal investment in the young, suggesting that mating strategies, particularly in monogamous species, are more complex than previously thought (Mock and Fujioki 1990). The extent of mate fidelity is highly variable, indicating that the apparent uniformity existing in *social* mating systems masks a diverse range of *genetic* mating systems (Kleiman 1977, 1981; Gowaty and Karlin 1984; Yezerinac et al. 1995).

Genetic benefits are the most widely accepted explanation for EPCs (Birkhead and Møller 1992; Kempenaers et al. 1992; Kirkpatrick 1996). Females may enhance their fitness either by diversifying the genotypes of their offspring (“genetic-diversity hypothesis”), or by choosing better-quality mates (“genetic-quality hypothesis”). The genetic-diversity hypothesis suggests that females aim to increase their reproductive success by producing offspring sired by many different males (Williams 1975). The genetic-quality hypothesis predicts that females mate with genetically “superior” males. This assumes that females can reliably estimate the genetic quality of potential mates.

Birkhead and Møller (1992) suggested two ways in which the genetic-diversity and genetic-quality hypotheses could be tested. A “sexual ornament” such as tail length in birds can be manipulated and copulatory preferences recorded. If females mated with males with a range of tail lengths, this would provide support for the genetic-diversity hypothesis. Alternatively, if females mated preferentially with males with longer tails, this would support the genetic-quality hypothesis. However in species with multiple young per brood, Birkhead and Møller (1992) point out that by mating with a number of long-tailed males, “females could increase their genetic diversity of their offspring and get better quality genes by seeking higher quality mates”. Thus, manipulating an ornament will only distinguish between the two hypotheses if females are shown to mate with males showing a range of ornament types.

The second, more testable method of distinguishing between the two hypotheses “involves an examination of the extra-pair copulation activity of females of species that lay single egg clutches, such as long-lived seabirds, with long-term pair bonds. Females paired to relatively poor quality males, and in search of genetic quality, would be expected to engage in EPCs each year. In contrast, females in search of genetic diversity, because they lay only a single egg per year and cannot increase the diversity of their “brood” within years, should mate outside the pair bond only in some years” (Birkhead and Møller 1992).

Continuously breeding marsupials that give birth to a single young per breeding cycle and form long-term social pairs are ideal study animals for experiments to distinguish between the genetic-diversity and genetic-quality hypotheses (sensu Andersson 1994). Marsupial young spend long periods attached to a teat in their mother’s pouch allowing them to be sampled at a time when their maternity is unambiguous. In addition, the birth rate can be accelerated by removal of pouch young soon after birth, a common practice in studies of the reproductive physiology of marsupials (e.g. Tyndale-Biscoe and Renfree 1987).

Most macropodid marsupials (kangaroos and wallabies) are polyoestrus and monovular, producing only one young per oestrus cycle (see Fig. 1). Both male and female Allied rock-wallabies, *Petrogale assimilis*, breed continuously (Delaney 1993). Behavioural studies of an isolated colony of Allied rock-wallabies at Black Rock in tropical north Queensland suggest that female *P. assimilis* remain in close contact with their consort partners and exclude other males (Horsup 1996). Pair members were faithful to small shared (and highly overlapping) territories on the rock, which were defended against other rock-wallabies. The simultaneous trap captures of pairs, night observations and radio-tracking data suggest that pair members also forage together at night (Horsup 1994). Mate fidelity was fostered by female aggression towards other females and non-paired males and by intense male-male aggression, both in the presence and absence of their partners. Females showed little aggression towards their consorts (Horsup 1996). The behaviour of socially paired wallabies was highly coordinated and a female in oestrus was typically accompanied by her partner, who presumably would actively intervene to prevent EPCs. Pair-bonds may persist for periods of up to at least 4 years (Horsup 1996), which is much longer than the length of the oestrus cycle (30 days; Johnson 1979). Females have

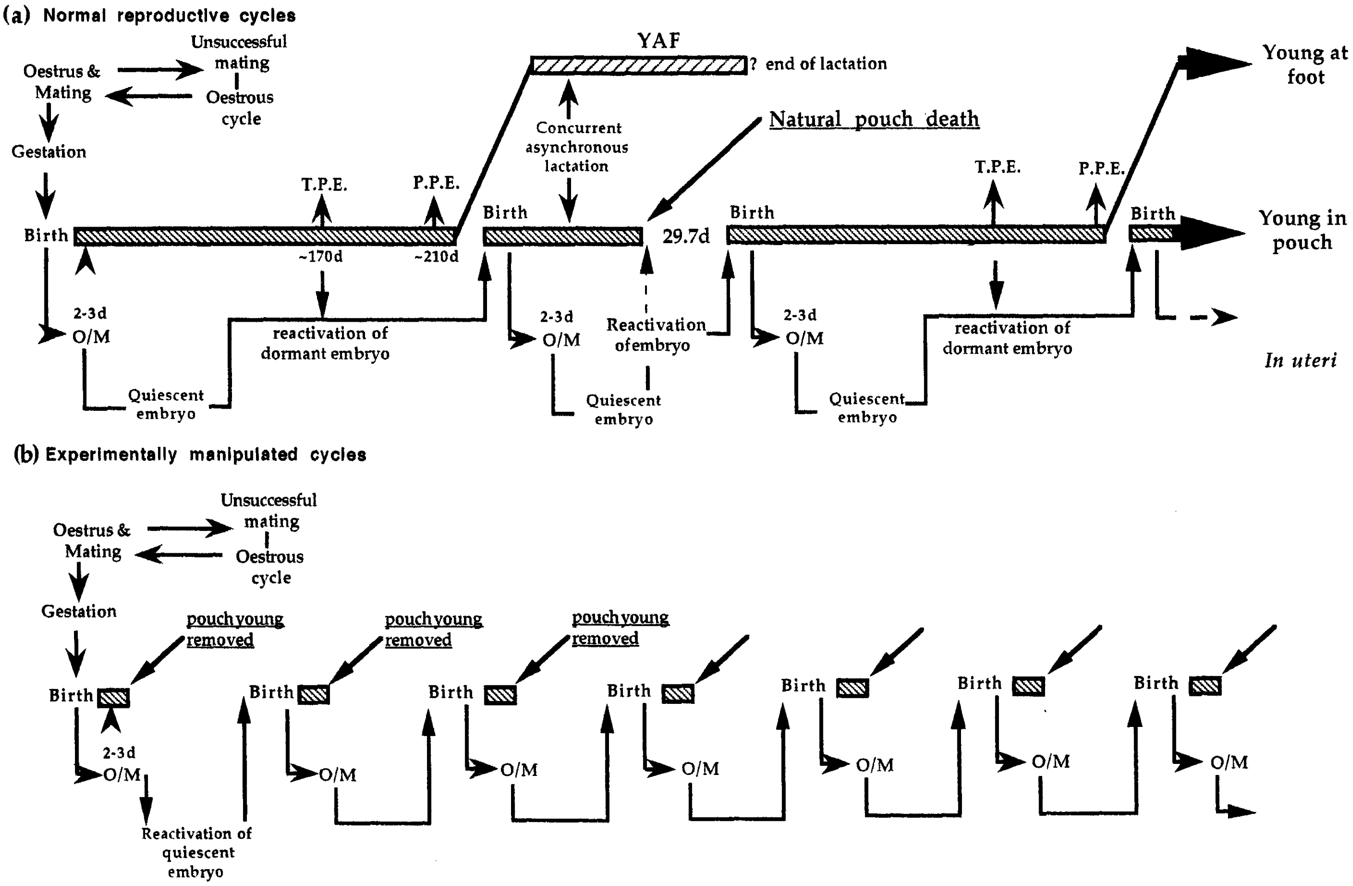

Fig. 1a, b The reproductive cycle of *Petrogale assimilis* (and most macropods; sensu Tyndale-Biscoe and Renfree 1987). **a** A cycle in which a pouch young is born, and the female re-enters oestrus and mates (*O/M*). The pouch young continues to grow in the pouch and exits the pouch temporarily (*T.P.E*) at about 170 days and permanently at 200 days (permanent pouch emergence; *P.P.E*). Alternatively, it may die from natural attrition during pouch development (*YAF* young at foot). **b** The reproductive cycle is experimentally manipulated to accelerate the rate of pouch young production at Mt. Stuart

a post-partum oestrus and the resultant young remains suspended as a blastula (in an embryonic diapause) until the resident pouch young either dies or exits the pouch and becomes independent (see Fig. 1). Females probably remain sexually receptive to their partners for only a short period of time, probably less than 12 h (see *Macropus eugenii*, Tyndale-Biscoe and Renfree 1987). Therefore, the opportunity for females to copulate with multiple males during this brief period appears limited, particularly as female aggression towards non-partner males is high and social bonding intense (Horsup 1996). Females receive no resources or assistance in parenting from males, except perhaps some assistance in defending themselves and their shelter sites (Horsup 1996).

In this paper, we describe the *genetic* mating strategies of the Allied rock-wallaby at two colonies: Black Rock, the site of the behavioural observations described above, and Mt Stuart 250 km to the east, where we experimentally accelerated the reproductive rate of three females by removing pouch young soon after birth. Using five polymorphic PCR-microsatellite markers, we confirm that similar to findings from many studies of "socially monogamous" species (e.g. birds and mammals; Andersson 1994), the Allied rock-wallaby seek EPCs in addition to those from their social mates. Based on these findings, we are able to use long-term demographic and behavioural data to distinguish between the hypotheses that females seek these EPCs to increase either (1) the genetic quality or (2) the genetic diversity of their progeny.

Methods

Black Rock

Field studies were carried out at Black Rock (19°04′S, 144°27′E), Australia, between June 1986 and December 1993. Rock-wallabies were caught in up to 53 wire cage traps baited with a mixture of peanut butter, rolled oats and honey. Animals were cleared from the traps before midnight (2200 hours) and again at dawn (approx. 0700 hours), and taken to a field camp where they were examined, measured and a small blood sample was taken (~ 1.0 ml). Individuals were released at (or near) their site of capture as soon as possible after examination. The behavioural ecology of *P. assimilis* at Black Rock was studied during separate monthly field trips between March 1986 and January 1990 (Horsup 1996). Scan sampling (Altmann 1974; undertaken for 2 h at dawn and dusk for 7 days in each month) and radio-tracking were used to collect detailed behavioural data on individual wallabies. Adults were classified as paired if they were: (1) recorded within 5 m of each other during at least six scan samples taken on monthly trips and (2) observed mutually allogrooming in at least every 2nd month recorded together. Pairing was also inferred if a male and (non-oestrus) female were caught in the same trap.

The date(s) of oestrus was estimated from the age of the pouch young using techniques developed by Delaney and De'ath (1990). It was logistically difficult to sample all young from this study. Because sampling occurred approximately monthly, not all females were captured on each field trip and there was a high mortality of pouch young (Delaney and Marsh 1995). Consequently, our conclusions are based only on those pouch young and juveniles which were DNA profiled.

Mt. Stuart

An experimental manipulation was performed at a colony of *P. assimilis* at Mt. Stuart (19°20′S, 146°46′E), near Townsville in north Queensland (described in Barker 1990) between July 1992 and May 1994. Field sampling was carried out at intervals of approximately 40 days [i.e. the gestation period of *P. assimilis*, 30 days (Johnson 1979) plus 10 days – to allow for individual variation in the gestation length].

Animals were trapped and sampled using the same techniques as at Black Rock. Two adult females (2MS002; 2MS006) were captured repeatedly; a third (2MS004) was caught on the first two trips but not subsequently. Neonatal pouch young (estimated age 8–10 days post-partum; sensu Delaney and De'ath 1990) were removed from these three females (see Fig. 1b), euthanitised with 0.5 ml kg^{-1} of Lethobarb, immediately preserved in 70% EtOH and stored at −20 °C. Behavioural observations at Mt. Stuart were opportunistic. The animals are human habituated and feed only metres from dwellings and barbecue areas.

Laboratory techniques

Five highly polymorphic microsatellite loci (Spencer et al. 1995, 1997) were amplified using the polymerase chain reaction (PCR) and used to confirm maternity and identify paternity in *P. assimilis*. Each single-locus microsatellite (profile) was amplified on at least two separate occasions, and the products resolved on gels (6% polyacrylamide) independently of known relationships to minimise both cross-contamination of samples and bias in assigning parentage.

Microsatellite products were visualised by autoradiography. Each individual produced a characteristic pattern with either one (homozygote) or two (heterozygote) bands at each locus. Allele size was determined by electrophoresis of an accompanying (M13mp8) standard. No evidence was obtained for linkage between any of the loci studied using the computer program GENEPOP (version 1.3; Raymond and Rousset 1995); additionally, maternal alleles showed Mendelian inheritance in all pouch young for which the mother was known. As expected, alleles differed by the number of multiples of the repeat (either di- or tetra-base pairs) size, indicating that all alleles at these loci vary in the number of repeat units.

At Black Rock, we used two methods (based on mate exclusion and relatedness) to estimate parentage amongst individuals (e.g. see Moritz et al. 1997). Firstly, paternity (and maternity) were determined by exclusion using a C++ computer program. The parentage of each animal was determined by identifying each individual allele. The first allele was then compared to both alleles at this locus in every other animal typed. The second allele was then used in the same way. Mothers were identified if they contained (at each of the five loci) at least one allele in common with the offspring. Paternity was assigned by identifying a male with the paternally inherited allele (i.e. the allele not from the mother) at each of the five loci. In addition, parentage was also investigated by comparing the DNA profiles with long-term demographic (e.g. evidence from pouch tenancy) and behavioural data to confirm or exclude potential mates. For example, three cases of ambiguous paternity were detected, but in all cases one of the suspected fathers was not present (or available) in the colony: two were presumed dead and one had not yet reached sexual maturity. Secondly, an index of relatedness (*R*; Queller and Goodnight 1989) was estimated. Pairwise estimates of relatedness (±SE) were calculated using the program KINSHIP (version 1.1.2). The primary hypothesis was fixed to individuals having a relatedness value of $R = 0.5$. A summary of the relatedness between cohorts of different relatives is shown in Fig. 2.

Female reproductive success was defined as the number of young that a mother raised to permanent pouch emergence (PPE; 200 days), as a function of young she could theoretically have raised in successive 200-day periods during the time she was trapped. For example, if a female raised every young to age 200 days, then the probability would equal 1.00. Logistic regression analysis was carried out on the proportions of matings with the paired male and extra-pair matings (using the measure of reproductive success as a covariate) to determine if reproductive success was significantly different in those females choosing to mate with their consort partner or an extra-pair mate. Models were weighted for the number of young actually DNA-typed from individual females with more than three young. The SPSS computer program was used for all statistical analyses. All values are given as mean ± SE.

Results

Black Rock

Over the 8-year trapping period, 131 (69 females, 62 males) adult rock-wallabies were captured at Black Rock over some 15,000 trap nights. Single-locus microsatellite profiles were obtained for 94 (71.8%) of these animals. During the same period, a total of 306 births were recorded from 69 females in the colony. The genotypes for five microsatellite loci were determined for 124 of these young (i.e. 40.5% of births). The high heterozygosity estimates (between 81.4% and 89.7%; Table 1) allow high confidence to be placed in assigning paternity to individual pouch young if the parents were sampled and DNA-typed.

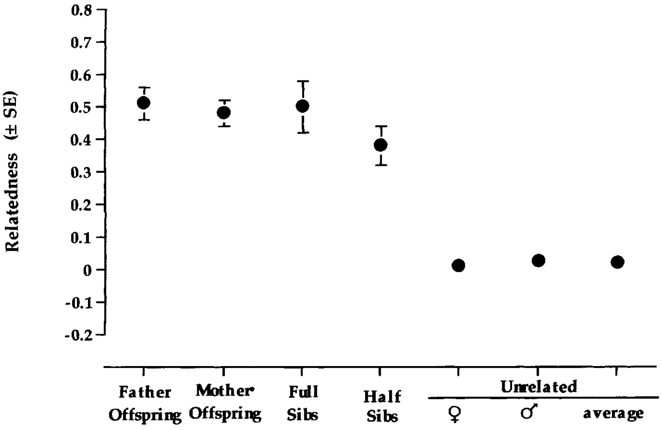

Fig. 2 Estimated values of relatedness (*R* ± SE) between cohorts of different relatives (father-offspring, mother-offspring, full and half sibs) and for unrelated rock-wallabies (females, males and average relatedness) at the Black Rock colony

Table 1 Heterozygosity and the exclusion probability of 128 adult individuals at each of the five microsatellite loci in the Black Rock colony [*Unbiased heterozygosity* is based on Nei's (1978) estimate; *Expected exclusion probability* sensu Double et al. (1997)]

Parameter	Locus				
	p*Pas*385	p*Pas*593	p*Pas*595	p*Pas*297	p*Pas*59
Sample size (*n*)	127	108	123	128	127
Number of alleles	9	12	15	15	19
Unbiased heterozygosity (%)	81.4	83.0	88.1	85.3	89.7
Expected exclusion probability	0.9620	0.9732	0.9907	0.9831	0.9914

We were unable to assign complete parentage to a surprisingly high proportion (49%) of the 124 young rock-wallabies (both pouch and independent young). For 18 of these 61 young, the mother was identified but the father was unknown. Null alleles were not obvious at any of the five loci and heterozygote deficiencies were not found (see Spencer et al. 1997). By eliminating the maternally inherited alleles, the microsatellite data from paternally heritable alleles indicate that these 16 young were fathered by a minimum of five different (unknown) adult males. Log-linear regression showed that (1) the proportion of young for which paternity could not be assigned did not change over the 8 years of the study (likelihood ratio test; $\chi^2 = 3.61$, $df = 6$, $P = 0.73$) and (2) the proportion of young for which paternity could not be assigned did not decrease with year (Mantel-Haenzel test for linear association; $\chi^2 = 0.64$, $df = 1$, $P = 0.43$; Fig. 3).

Single-locus microsatellite profiling data were available for 63 offspring of 21 females for which pair-bonds were established using the behavioural criteria outlined above. This represented between 10% and 86% of the young born to each of these females (Table 2). Over the study period, 21 of the 63 DNA-typed young were fathered by males who were not paired socially with their mothers. Eleven of the 21 females remained faithful to their consorts for all pouch young typed. Five females were recorded as mating only with extra-pair males. The remaining 5 females mated both with their paired consort and males extraneous to the pairing (Table 2).

The probability that a female had young fathered by her behavioural consort covaried with her reproductive success (log-linear regression model; $\chi^2 = 42.89$, $df = 20$, $P = 0.0001$). Females with all young fathered by their pair-bonded partner had a significantly higher probability of reproductive success than females who sought exclusive EPP. The females with poor reproductive success were more likely to have all their young fathered by extra-pair males. The group of females who had some young fathered by within-pair males and others by extra-pair males had the highest level of reproductive success (Fig. 4). On all occasions ($n = 11$ young), these females were significantly more likely to have young fathered by EPCs when the previous young failed to survive to PPE. If this pouch young survived to 200 days, these females then mated successfully with

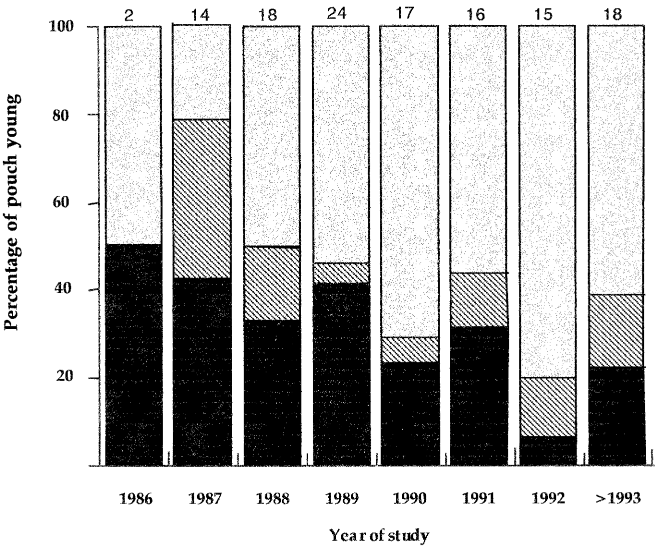

Fig. 3 The proportion of young in which both parents were identified (*filled*), only the mother was identified (*hatched*) and in which neither parent was known (*stippled*) for each year of the study. *Sample sizes* are given at the top of each bar

Table 2 Summary of the single-locus DNA-profiling information for the pouch young studied from each female rock-wallaby sampled at Black Rock. Note that the number of young DNA-typed may not add up to the number of young in which paternity could be identified, because at times the consort mate was not known, and pairing was not inferred and therefore not included. Actual births are recorded from field records

Female ID number	Number of young fathered by		Number of young		
	Paired male	Extra-pair male	DNA typed	Actual births recorded	Percentage typed
001	4	5	9	17	53
008	1	0	1	7	14
010	0	2	2	7	29
013	0	1	1	9	11
014	1	0	1	9	11
032	1	1	2	9	22
037	1	0	1	10	10
046	0	1	1	6	17
054	2	0	3	13	23
"1E"	4	0	4	6	67
061	3	0	4	10	40
076	4	0	5	14	36
082	2	0	3	11	27
097	0	2	2	7	29
107	0	3	3	8	38
111	8	0	7	19	37
"4E"	2	2	4	7	57
133	1	0	1	7	14
225	2	0	2	3	67
159	3	2	5	11	45
226	3	2	6	7	86
Total	42 (67%)	21 (33%)			

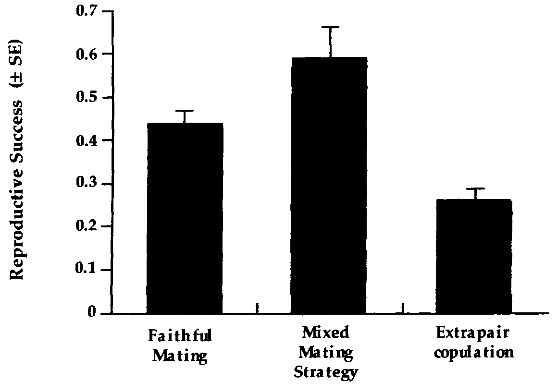

Fig. 4 Females remaining faithful to their socially paired males had a significantly higher probability of reproductive success than those seeking only extra-pair copulations. However, a female utilising a combination of mating strategies (i.e. a 'mixed mating strategy') had the highest probability of raising a young

their behavioural consort. There was no behavioural evidence to suggest that females were attempting to make a permanent switch in partner (*sensu* Cezilly and Nager 1995), and after EPCs, all females carried pouch young that were subsequently fertilised by their consort mates. This result suggests that females engage in EPCs when they have been unsuccessful in raising their previous young to independence, presumably mating with different males in order to increase their probability of reproductive success.

How are females able to gauge the genetic quality of their mates? We investigated this by comparing the extra-pair mates of the females which adopted a mixed mating strategy with their regular consorts. We found no significant difference with respect to testes size ($t = 0.28$; $df = 10$; $P = 0.78$) or body weights ($t = 0.33$; $df = 10$; $P = 0.75$) of their consorts or extra-pair males. However, the extra-pair males had significantly longer arms than the long-term partners ($t = 2.23$; $df = 10$; $P = 0.03$). However, the size effect is small (~ 4%), and the relationship (if any) between arm length and "upper-body musculature" is an index of fighting ability used in intrasexual competition amongst some male macropod species (discussed below).

Mt. Stuart

Over 22 months, 20 (12 female, 8 male) adult rock-wallabies were captured. Single-locus microsatellite profiles were obtained for 17 adult animals. A total of 21 neonatal pouch young were sacrificed from three females in the colony. The genotypes for five microsatellite loci were determined for all these young. The expected exclusion probability was estimated to be >0.999 for all five loci pooled. Paternity analysis revealed that two (2MS002; 2MS004) of the three females studied remained faithful to their consorts (Fig. 5a), whereas the third (2MS006) did not (Fig. 5b). The male (4MS001) who fathered all 12 offspring of 2MS002, had a mean weight of 5,174 g (SE = 41.8), 43% heavier than any of the other five males caught at Mt. Stuart (mean weight = 3618 g, SE = 106.9; $t = 13.55$; $df = 21$; $P < 0.001$).

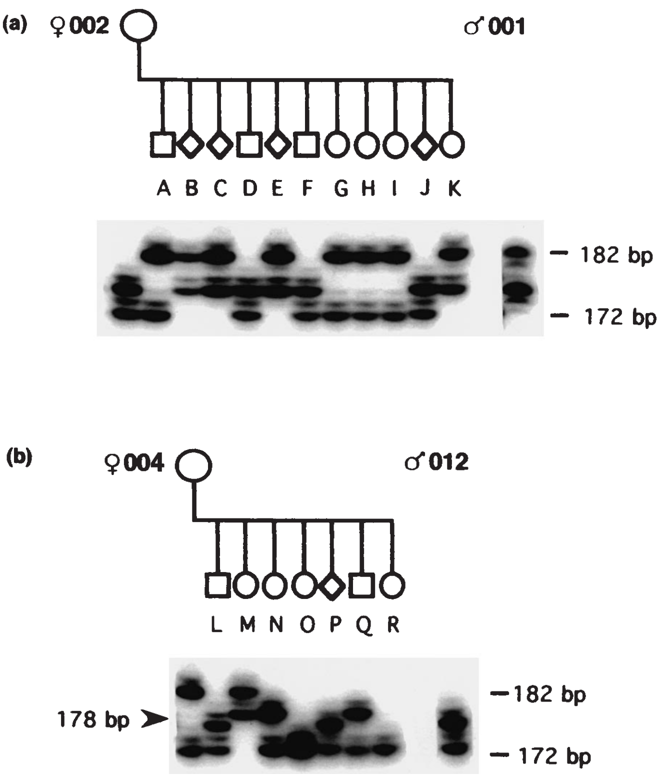

Fig. 5a, b Illustration of the use of the polymorphic microsatellite locus p*Pas*385. A series of pouch young are shown for two different pairs of wallabies from Mt Stuart, with the mother and her socially paired mate. **a** The young (*A–K*) from female 2MS002 were all fathered by the socially paired male (4MS001; profile on far right side of the picture). **b** However, three pouch young (*M*, *N*, *Q*) from mother 2MS004 were not fathered by her socially paired mate (4MS012; profile on lower right side of picture). The *arrowhead* indicates non-matching paternal alleles (at 178 bp). Fragment sizes (in base pairs) are given on the far right

Discussion

Our genetic data indicate that, on average, only 66% of the young of *P. assimilis* at Black Rock were fathered by a female's socially paired mate. Our investigations were limited to animals for which social pairing was identified, and this estimate of mate fidelity may be upwardly biased. Nonetheless, this study indicates that pair fidelity is not as obvious at the genetic level as it is behaviourally, a result similar to findings in other studies of socially monogamous species (Burke and Bruford 1987; Birkhead and Møller 1992). However, as mating exclusivity is not a prerequisite for monogamy (Kleiman 1977; Carter and Getz 1993), our results do not negate the conclusions that *P. assimilis* forms long-term stable relationships (Barker 1990) and that it is best described as a facultatively monogamous rock-wallaby (Horsup 1996).

Despite a high trapping effort, we could not identify one or both parents of nearly half the young rock-wallabies profiled from the Black Rock colony, a result similar to that of Yezerinac et al. (1995) in the yellow warbler (*Dendroica petechia*). These data suggest that there may be: (1) a large number of untrappable rock-wallabies resident at Black Rock, a result which is not supported by the behavioural observations and which we have not considered further (Horsup 1996), (2) a significant number of transient individuals and (3) demonstrates the difficulty of studying wild populations, with incomplete sampling of all potential parents. Additionally, many of the young were from early in the study period when the population was undersampled, and therefore we may not have sampled a number of the putative fathers or mothers. These "floater" males and females (sensu Smith and Arcese 1989) were apparently responsible for a disproportionate number of EPCs and included at least five males which had a high level of reproductive success. Parentage may have also been misassigned if null alleles were present, as reported in several studies (Callen et al. 1993; Pemberton et al. 1995; Jones and Avise 1997).

Our paternity data suggest that some females at Black Rock and Mt. Stuart are more likely to have young fathered by EPCs than are other females. There must presumably be a benefit from accepting or seeking extra-pair paternity (EPP) in situations where lower breeding success and production of young appear to be associated with females switching partners and mating with another male (e.g. Coulson and Thomas 1983). EPP in the Allied rock-wallaby at Black Rock could have occurred in one of three ways: forced EPC, solicited EPC and rapid mate switching (Cezilly and Nager 1995). EPC as a result of rapid mate switching appears the least likely explanation, as females continued to accompany their socially paired mates after accepting or seeking EPCs. The low number of copulations observed in the field by Horsup (1996) precludes distinction between the other two explanations of EPCs. However, studies have shown that females may actively accept or encourage EPC attempts by some males, whilst rejecting others (Lifjeld and Robertson 1992; Kempenaers et al. 1995), suggesting that female choice (Birkhead and Møller 1993) may be important in any outcome (Smith 1988; Kempenaers et al. 1992; Graves et al. 1993). The data from this study suggest that females with a lower probability of raising young to independence were more likely to have young fathered as a result of EPCs than females with a history of raising young to independence. Under these circumstances, it might be advantageous for a female to mate with another male solely to obtain "good" genes, as non-paired males do not offer any effective paternal assistance (e.g. Westneat et al. 1990).

In the Allied rock-wallaby, females who have some young fathered by extra-pair males are choosing or accepting to mate with males with slightly longer arms than those of their long-term partners. Although the difference is small (4%), it is likely that arm length is an index of fighting capacity. In other macropods, the forearms and upper-body musculature are used as weapons for intrasexual competition and are equated to functional ornaments, such as the antlers in deer (Jarman 1989). For example Batchelor (1980) found in the Brush-tailed rock-wallaby (*P. penicillata*), that individuals with larger arm circumferences were likely to be dominant. Delaney (1993) found that arm length in *P. assimilis* was the most heteromorphic feature of the species, with arm length in males, 12% greater than in females. This may be an important difference between different males, as the forelimbs in *P. assimilis* are used in displays during aggressive interactions between males (Barker 1990; Horsup 1996).

The most apparent cost to females which engage in EPCs seems to be that paired males might reduce their parental care (Trivers 1972; Møller 1988). However, as male rock-wallabies provide no direct paternal care to their young (Horsup 1996), we conclude that female rock-wallabies incur little or no cost from seeking EPCs. We are unable to determine why the offspring failed to survive (in this field study), but the current offspring, sired by the new extra-pair male, had a significantly higher probability of reaching independence.

This raises the question as to why females do not "divorce" (sensu Cezilly and Nager 1995) their mates and pair with higher-quality males. We are unable to answer this question, as our long-term data are as yet insufficient to follow females which are paired with poor-quality males over their lifetime. The data suggest that females are "making the best of a bad job" (Koprowski 1993) and are unable to obtain a divorce over medium periods of time (3–4 years). An average adult *P. assimilis* lives for about 7 years (Delaney and Marsh 1995), and we have records of individuals surviving for 16 years (S. Delean, unpublished data). Shortage of suitable shelter sites in the rock outcrop may force rock-wallabies into any available territory where they have few choices of mate. Once established, they may then have to move to obtain better-quality mates. Only two of 21 females achieved EPP with the mates of females whose young were always fathered by their consort. This result suggests that these may not be premium males, or that high levels of female:female aggression prevent EPCs with the consorts of these females (Horsup 1996).

Analysis of the longitudinal demographic records of individual females at Black Rock showed that females whose young were always fathered by their regular consort had higher reproductive success than those whose young were always fathered as a result of EPCs. However, females with some offspring fathered by their regular consort and others via EPCs had the highest probability of raising young to independence. These females were significantly more likely to have a young fathered as a result of an EPC if their previous young had failed to survive to pouch emergence. These data demonstrate a significant correlation between the proportion of potential offspring successfully raised to independence (that were within pair) and the proportion of EPPs. Based on this relationship, females that engaged in EPCs was a result of a tremendous cost, as their previous young tended to die before reaching independence.

However, one of the disadvantages of using longitudinal demographic records to test between the genetic-quality and genetic-variability hypotheses is that it takes several generations to do so. We were able to formally test this hypothesis in *P. assimilis* by artificially accelerating pouch young production by removing young from three females at Mt. Stuart (see Fig. 1b). If females seek mates for their genetic diversity, then at least some of their young maybe a consequence of EPP – regardless of who they are socially paired with; however, if females seek males for their genetic quality, then females paired with "good-quality" males should only have young fathered by their social mate, and therefore none from EPCs. Conversely, females paired with "poor-quality" males should seek some EPCs, in order to increase the genetic quality of (at least some of) their young. At Mt. Stuart, all offspring of two females (2MS002 and 2MS006) were fathered by their social partners whereas the third female (2MS004), had pouch young fertilised by a male(s) other than her socially paired partner. Unfortunately, we have no comparative data from the Mt. Stuart colony on arm lengths of rock-wallabies, the apparent index of male "genetic quality" for wallabies at Black Rock. The data from the two colonies are consistent with the hypothesis that Allied rock-wallabies seek EPCs to increase the genetic quality of their offspring, the most widely accepted explanation of EPCs (see Kempenaers et al. 1992; Andersson 1994).

In mammals, data are scarce supporting the hypothesis that females choose males for their genetic quality and the results presented here are the first for a marsupial, whereas birds have been the subject of many studies of mate fidelity (Burke and Bruford 1987) because most species are apparently monogamous. In addition, birds tend to be easier than mammals to manipulate in the field. We, however, demonstrate that despite being socially monogamous, Allied rock-wallabies obtain EPCs, a result that is fascinating precisely because it was similar to the results (and levels) of EPCs observed in many studies of birds (Birkhead and Møller 1992; Andersson 1994; Kirkpatrick 1996; Saino et al. 1997 and references therein). Their mating system is therefore heterogeneous with all, none or some of a female's offspring fathered by her regular consort to maximise the probability of raising young to independence. Therefore, females that successfully reared offspring produced a significant proportion of those young with their social mate and females that had low reproductive success tended to seek more extra-pair fertilisations. A number of questions from this study remain unanswered (due to both small samples sizes and insufficient long-term data), including the reasons why (and how) offspring failed to reach independence. Nonetheless, this study provides a preliminary and unique insight into the genetic mating system and reproductive ecology of a marsupial, the Allied rock-wallaby. Due to their unique reproductive ecology (e.g. a suspended blastula and neonate young), this work also demonstrates the tremendous opportunities that marsupials offer for studies of sexual selection and experimental/manipulative research.

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