Female multiple mating behaviour, early reproductive failure and litter size variation in mammals

P. Stockley

Animal Behaviour Group, Faculty of Veterinary Science, University of Liverpool, Leahurst, Chester High Road, Neston CH64 7TE, UK (stockley@liv.ac.uk)

Female promiscuity is widespread among mammals, although its function is poorly understood. Recently, much interest has been generated by the hypothesis that female promiscuity, combined with post-copulatory paternity-biasing mechanisms, may function to reduce the costs of reproductive failure resulting from genetic incompatibility. Here, a comparative approach is used to determine if average rates of reproductive failure differ for polytocous mammal species with contrasting levels of female multiple-mating behaviour. After control for phylogeny, promiscuous species were found to have significantly lower rates of early reproductive failure than monogamous and polygynous species, in which females are relatively monandrous. Monandrous females appear to compensate for higher early reproductive failure with increased ova production, and thus produce comparable average litter sizes to those of more promiscuous females. However, there is significantly more variation around the average litter sizes produced by relatively monandrous females. These findings are broadly consistent with predictions of the genetic incompatibility avoidance hypothesis, although it is emphasized that alternative explanations cannot be ruled out on the basis of the comparative evidence presented. Further studies are needed to explore ecological correlates of multiple-mating behaviour, to investigate potential post-copulatory paternity-biasing mechanisms, and to identify the causes of reproductive failure in natural mammal populations.

Keywords: genetic incompatibility; inbreeding; major histocompatibility complex; meiotic drive; polyandry; post-copulatory sexual selection

1. INTRODUCTION

Explaining the selective advantage of promiscuous female mating behaviour has been a long-standing problem for evolutionary biologists. Although numerous hypotheses have been put forward, in many cases it is still difficult to explain why females should readily solicit copulations with multiple males, despite associated costs (reviews in Reynolds 1996; Jennions & Petrie 2000; Zeh & Zeh 2001; Hosken & Stockley 2002). Recently, much interest has been generated by a hypothesis concerning the role of parental genetic incompatibility in the evolution of polyandry (e.g. Zeh 1997; Birkhead 1998; Stockley 1997, 1999; Newcomer *et al.* 1999; Eady *et al.* 2000; Tregenza & Wedell 1998, 2000; Olsson & Madsen 2001). According to the genetic incompatibility avoidance hypothesis, an important function of polyandry is that it enables females to exploit post-copulatory paternity-biasing mechanisms to minimize the risk and cost of fertilization by genetically incompatible sperm (Zeh & Zeh 1996, 1997; see also Haig & Bergstrom 1995; Olsson *et al.* 1996). Genetic incompatibility can result from a variety of potential sources, including dominance, over-dominance, intra- and intergenomic conflict, foeto-maternal interactions and immune system function (reviewed in Zeh & Zeh 1996, 2001; Tregenza & Wedell 2000). In many cases, parental genetic incompatibility has fatal consequences for developing offspring, such that females incur costs of wasted investment in ova and embryos (Zeh & Zeh 1996). Post-copulatory mechanisms by which promiscuous

females may potentially bias the paternity of their offspring to reduce costs of genetic incompatibility include sperm competition and sperm selection, or post-fertilization selection of embryos (Zeh & Zeh 1997, 2001; see also Wedekind 1994).

Experimental evidence providing support for the genetic incompatibility avoidance hypothesis is currently limited to relatively few, taxonomically diverse species, and the extent to which the hypothesis may have general applicability across various taxa is uncertain (Tregenza & Wedell 2000; Zeh & Zeh 2001). To date, promiscuous mating has been shown to decrease reproductive failure in experimental studies of polyandrous female pseudoscorpions (Zeh 1997; Newcomer *et al.* 1999), crickets (Tregenza & Wedell 1998) and cuis (Keil & Sachser 1998), although other recent studies found no evidence for genetic incompatibility avoidance benefits of polyandry (Eady *et al.* 2000; Simmons 2001). Progress in this field is also limited because post-copulatory selection mechanisms for biasing paternity are notoriously difficult to investigate directly (Birkhead 1998). Current evidence indicates that females of internally fertilizing taxa may be capable of sperm selection on the basis of genetic incompatibility at specific loci (Wedekind *et al.* 1996), or genetic similarity (Olsson *et al.* 1996; Stockley 1999; Tregenza & Wedell 2002; but see Stockley 1997; Cunningham & Cheng 1999).

Although predictions of the genetic incompatibility avoidance hypothesis have not previously been investigated from a comparative perspective, this approach offers the potential to complement current experimental investigations by establishing the likely general applicability of

the hypothesis within a broad taxonomic group such as mammals.

A comparative approach could also provide new insight concerning the likely benefits of polyandry from a life-history perspective (Hosken & Stockley 2002). That is, in addition to potential energetic costs associated with wasted investment in failed ova and embryos, when females typically produce more than one offspring per reproductive attempt, it is possible that genetic incompatibility may also have important consequences for variation in early offspring mortality. This may be important for species such as mammals in which females invest heavily in their offspring, since increased variation in offspring mortality is likely to make it more difficult to control variation in offspring numbers and hence to achieve an optimal litter size. By biasing paternity of their offspring, polyandrous female mammals may thus benefit by reducing variation in reproductive failure caused by genetic incompatibility, in addition to reducing reproductive failure *per se*.

The aim of the present study is to explore predictions relating to the genetic incompatibility avoidance hypothesis, as outlined above, in comparative analyses of mammals. Specifically, comparative analyses are used to investigate if differences in female multiple mating behaviour explain variation in reproductive failure and litter size among polytocous mammals.

2. MATERIAL AND METHODS

Species-specific data on mean numbers of ova released, embryo or foetus numbers (hereafter referred to as embryo numbers) and litter size were collated from Asdell's *patterns of mammalian reproduction* (Asdell 1964; Hayssen *et al.* 1993), for over 70 species of polytocous mammals, including rodents, carnivores, insectivores and lagomorphs (see electronic Appendix A, available on The Royal Society's Publications Web site). In most cases, the mean number of ova released per reproductive attempt was inferred from mean corpora lutea number. One species, *Lagostomus maximus*, was not included in the dataset owing to exceptionally high ovulation rates (200–800 ova per oestrus cycle). Unless otherwise stated, it is assumed that mean species-specific embryo numbers were calculated from samples taken across the full range of development *in utero*. Data on embryo numbers were used in preference to counts of placental scars, mean values of which were often lower than embryo numbers or litter size, even when reported within the same source. Data for mean litter size were only included where sources specified that values were based on the number of young. This is important because some sources combine data on numbers of ova, embryos, placental scars and young when reporting average litter size. Mean numbers of young were also assumed to have been calculated from samples taken at different stages of development before weaning, unless otherwise stated. Mean values based on samples of fewer than eight individuals were not included for any variables in the dataset. It should also be noted that the mean values included are typically based on results of cross-sectional population samples, and do not include cases of females that produced zero numbers of ova, embryos or offspring, respectively.

Data for mean numbers of ova, embryos and young were used to calculate species average values for reproductive failure as follows: (i) early reproductive failure: the average proportion of ova

wasted, either before implantation or because of early embryonic mortality, calculated as (mean number of ova released per oestrus cycle – mean embryo number)/mean number of ova released per oestrus cycle; (ii) late reproductive failure: the average proportion of embryos and/or neonates lost during the later stages of gestation and early postnatal development, respectively, calculated as (mean embryo number – mean offspring number)/mean embryo number. When calculating reproductive failure, mean values of ova, embryos or young were taken from the same source wherever possible, and average values of reproductive failure calculated in cases where this information was available from more than one source. When data were not available from the same source, reproductive failure was instead calculated for each species by using the average of all reported mean values for ova, embryo or offspring numbers, respectively. Negative values of reproductive failure were excluded from the analyses presented, although inclusion of these species as having zero values for reproductive failure does not affect the conclusions of the study.

To calculate variation in litter size, I looked for studies providing information on standard deviations around mean litter size and/or embryo numbers. Where information was available from more than one source, I selected those studies with the largest sample sizes for inclusion in the analyses. Coefficients of variation for litter size or embryo number were then calculated as $V = (s/X) \cdot 100\%$, where s is the standard deviation and X is the mean (Zar 1984).

The species included in the final dataset were those for which data on reproductive failure and published information on female mating behaviour and/or relative testes size were available (see electronic Appendix A). A relatively high incidence of female multiple-mating behaviour was inferred from published reports on the basis of: (i) direct observation of promiscuous female mating behaviour or a promiscuous mating system under natural or semi-natural conditions. A promiscuous mating system is here broadly defined as one in which females typically mate with more than one male within a given oestrus period (Clutton-Brock 1989); (ii) genetic evidence for multiple paternity within litters conceived under natural or semi-natural conditions; and/or (iii) relatively large mean testes size. To determine whether testes were relatively large compared with an average male mammal of the same order and body size, I used the relative testes size (RTS) values calculated by Kenagy & Trombulak (1986), based on regression equations for mean species body and testes mass across a range of mammalian orders. Relative testes size is a useful indicator of probable female promiscuity in the absence of more direct evidence, because it is well established that species with multi-male or promiscuous mating systems typically have relatively large testes for their body size ($RTS > 1$), whereas those with monogamous or polygynous (single male) mating systems typically have relatively small testes ($RTS < 1$) (Kenagy & Trombulak 1986; see also Harcourt *et al.* 1981; Møller 1989). With the possible exception of *Meles meles* (Evans *et al.* 1989), data on relative testes size were broadly consistent with available genetic evidence. Excluding *Meles* from the dataset does not affect the conclusions of the study.

Species were classified as having a relatively low incidence of female multiple-mating behaviour on the basis of: (i) direct observation of a typically monogamous or polygynous mating system under natural or semi-natural conditions. Following Kleiman (1977), the term monogamous is used here to describe a mating system in which each female typically mates exclusively

with a single male for a given reproductive attempt, and may or may not involve paternal care. Polygynous mating systems are here broadly defined as those in which two or more females typically mate exclusively with the same male for any given reproductive attempt (Clutton-Brock 1989); (ii) genetic evidence that there is no, or relatively little, multiple paternity within litters conceived under natural conditions; and/or (iii) the RTS is smaller than expected for an average male mammal of the same body size (Kenagy & Trombulak 1986; see above).

Species cannot be regarded as statistically independent for comparative analyses because closely related taxa are likely to share characteristics of common ancestors (Harvey & Pagel 1991). Analyses performed using species as independent data points were therefore repeated using independent contrasts to control for potential patterns of phylogenetic association within the dataset. The phylogenetic relationships used to identify independent contrasts were inferred from a variety of sources (Avice *et al.* 1979; Anderson 1985; Rogers & Engstrom 1992; Catzefflis *et al.* 1993; Robinson *et al.* 1997; Bininda-Emonds *et al.* 1999; Symonds 1999; Novacek 2001; Madsen *et al.* 2001; Murphy *et al.* 2001), including the mammal taxonomy of Corbet & Hill (1991). Independent contrasts or sister group comparisons (Burt 1989; Purvis & Rambaut 1995) were used to test for the effects of the dichotomous variable, female multiple-mating behaviour (classified as relatively high or low, see above), on a range of continuous variables, including species average number of ova, embryos and offspring, early and late reproductive failure (as defined above), and embryo or litter size coefficient of variation. The independent contrasts were produced by pairing each species in the dataset with its closest relative differing with respect to female multiple-mating behaviour, with the proviso that no species was used more than once, and also ensuring that there was no crossing of lines on the phylogenetic tree linking species or groups of species that were compared. Where alternative contrasts were possible within the dataset, mean values of continuous variables were calculated for closely related species with the same classification with respect to female multiple-mating behaviour. Wilcoxon signed rank tests were used to test results of the paired contrasts, and Mann-Whitney *U*-tests were used for preliminary analyses without control for phylogeny. Probability values given are two-tailed unless otherwise stated.

3. RESULTS

Mean $\pm$ s.e.m. numbers of ova, embryos and young produced by all species in the dataset were 5.68 ± 0.35 ($n = 41$), 5.05 ± 0.21 ($n = 68$) and 4.62 ± 0.20 ($n = 69$), respectively. The average total reproductive failure, calculated as the difference between mean numbers of ova produced by all species in the dataset and mean litter size, is thus *ca.* 20%. This is likely to be an underestimate, for at least two reasons. First, as described above, for methodological reasons, the dataset does not include cases of total reproductive failure, where the entire litter is lost. Second, because information on offspring weaning success is not taken into consideration, total reproductive loss is likely to be considerably higher.

When species are treated as independent data points, there is a significant difference in average early reproductive failure according to levels of female multiple-mating behaviour (figure 1). That is, species with relatively polyandrous females have significantly lower rates of early reproductive failure than do species with relatively monan-

Figure 1. The mean $\pm$ s.e.m. of early and late reproductive failure for polytocous mammal species in which females are polyandrous (high multiple mating; black squares), compared with mean $\pm$ s.e.m. of early and late reproductive failure for species in which females are typically monandrous (low multiple mating; open squares). Polyandrous females have significantly lower early reproductive failure than monandrous females before control for phylogeny (Mann-Whitney *U*-test, $p < 0.005$) but there is no significant difference in late reproductive failure between the two groups (Mann-Whitney *U*-test, $p > 0.50$).

drous females (polyandrous mean $\pm$ s.e.m. = 0.11 ± 0.01 ; monandrous = 0.21 ± 0.03 ; Mann-Whitney $U = 85.5$; $p < 0.005$; figure 1). This difference remains significant after control for phylogeny; species with relatively polyandrous females have lower average early reproductive failure than do species with relatively monandrous females in 10 out of 12 independent contrasts (table 1; Wilcoxon signed ranks test, $Z = -2.67$; $p < 0.01$). By contrast, there is no difference in the late reproductive failure of species with relatively polyandrous versus monandrous females (figure 1), either before or after control for phylogeny. Average late reproductive failure is 0.12 ± 0.02 for relatively polyandrous females, and 0.14 ± 0.02 for relatively monandrous females, respectively (Mann-Whitney $U = 344$; $p > 0.50$), and polyandrous females have lower average late reproductive failure than relatively monandrous females in 7 out of 14 independent contrasts (Wilcoxon signed ranks test, $Z = -0.031$; $p > 0.95$).

Despite the higher early reproductive failure of relatively monandrous females, they do not produce significantly smaller average litters than more polyandrous females. The average litter size for polyandrous females in the dataset is 4.78 ± 0.33 , compared with 4.45 ± 0.20 for relatively monandrous females (Mann-Whitney $U = 589$; $p > 0.95$). Relatively monandrous females have smaller average litter sizes than more polyandrous females in 10 of 17 independent contrasts (Wilcoxon signed ranks test, $Z = -0.17$; $p > 0.85$). To achieve comparable average litter sizes to more polyandrous females, it therefore appears

Table 1. Independent contrasts comparing mean early reproductive failure for paired species or groups of species with contrasting levels of female multiple mating (high versus low). Species with high multiple mating have lower early reproductive failure in 10 out of 12 contrasts (Wilcoxon signed ranks test, $Z = -2.67$; $p < 0.01$).

contrast	high multiple mating	early reproductive failure ^a	low multiple mating	early reproductive failure ^a
1	Soricidae <i>Sorex araneus</i>	0.122	<i>S. minutus</i>	0.08
2	Ursidae <i>Ursus americanus</i>	0.146 ^b	Canidae <i>Canis latrans</i> <i>C. lupus</i> <i>Urocyon cinereoargenteus</i> <i>Vulpes vulpes</i>	0.258 0.029 0.211 0.257 (0.191)
3	Mustelidae <i>Mustela erminea</i>	0.093	<i>Meles meles</i>	0.340
4	Felidae <i>Felis catus</i>	0.058 ^b	<i>F. silvestris</i>	0.180
5	Scuridae <i>Sciurus carolinensis</i> <i>Tamiasciurus hudsonicus</i>	0.083 0.128 (0.106)	<i>Marmota monax</i>	0.167
6	Scuridae <i>Spermophilus columbianus</i> <i>S. richardsonii</i>	0.030 0.154 (0.092)	Heteromyidae <i>Dipodomys ordii</i>	0.048
7	Cricetidae <i>Mesocricetus auratus</i>	0.128	<i>Sigmodon hispidus</i>	0.282
8	<i>Peromyscus boylii</i> <i>P. leucopus</i> <i>P. maniculatus</i>	0.019 0.161 0.075 (0.085)	<i>Oryzomys palustris</i>	0.208
9	<i>Tatera brantsii</i>	0.102	<i>Meriones unguiculatus</i>	0.29
10	Arvicolidae <i>Microtus agrestis</i> <i>M. pennsylvanicus</i> <i>M. montanus</i>	0.175 0.144 0.041 (0.120)	<i>M. californicus</i>	0.583
11	Muridae <i>Apodemus sylvaticus</i> <i>Rattus rattus</i> <i>R. norvegicus</i>	0.211 0.159 0.121 (0.160)	<i>Mus musculus</i>	0.220
12	Leporidae <i>Sylvilagus floridanus</i>	0.121	<i>Oryctolagus cuniculus</i>	0.133

^a Early reproductive failure calculated as (ova number – embryo number)/ova number, except:

^b (ova number – young number)/ova number.

that monandrous females must produce relatively more ova. Relatively monandrous females in the dataset produce an average of 1.37 ± 0.09 ova per offspring compared with 1.22 ± 0.04 ova per offspring produced by more polyandrous females (Mann–Whitney $U = 101.5$; $p > 0.05$, one-tailed). After control for phylogeny, relatively monandrous females produce more ova per offspring than more polyandrous females in 7 out of 10 independent contrasts (Wilcoxon signed ranks test, $Z = -1.94$; $p < 0.03$, one-tailed).

Relatively monandrous females in the dataset also produce more variable litter sizes compared with those of more polyandrous females. The average coefficient of variation around the mean litter sizes produced by typically monandrous females was 33.87 ± 1.72 ($n = 11$ species), compared with 24.91 ± 2.63 for polyandrous females

($n = 17$ species) (Mann–Whitney $U = 38.5$; $p = 0.01$). After control for phylogeny, relatively monandrous females produce more variable numbers of offspring or embryos than more polyandrous females in 7 out of 7 independent contrasts (Wilcoxon signed ranks test, $Z = -2.34$; $p < 0.02$; table 2).

4. DISCUSSION

It appears that at least 20% of the ova produced by polytocous female mammals in this study are wasted between ovulation and early postnatal development. This finding confirms previous reports that female mammals experience high rates of reproductive failure (Brambell 1948; Wasser & Barash 1983). Overall loss may be much higher in many cases, for example, Brambell (1948) esti-

Table 2. Independent contrasts comparing mean offspring or embryo number coefficients of variation for paired species or groups of species with contrasting levels of female multiple mating (high versus low). Species with high multiple mating have lower variation in offspring or embryo numbers in 7 out of 7 contrasts (Wilcoxon signed ranks test, $Z = -2.34$; $p < 0.02$).

contrast	high multiple mating	coefficient of variation (%)	low multiple mating	coefficient of variation (%)
1	Soricidae <i>Suncus murinus</i>	7.5	<i>Crocidura russula</i>	29.5
2	Scuridae <i>Spermophilus beldingi</i> <i>S. tridecemlineatus</i>	31.7 13.1 (22.4)	Heteromyidae <i>Dipodomys ordii</i> <i>D. merriami</i>	19.5 29.3 (24.4)
3	Cricetidae <i>Peromyscus boylii</i>	14.6	<i>P. eremicus</i> <i>P. polionotus</i>	39.3 30.6 (34.9)
4	Arvicolidae <i>Arvicola terrestris</i> <i>Microtus pennsylvanicus</i>	27.4 33.3 (30.4)	Cricetidae <i>Meriones unguiculatus</i>	31.6
5	Muridae <i>Praomys natalensis</i> <i>Rattus exulans</i> <i>R. norvegicus</i>	20.2 5.8 34.7 (20.23)	<i>Mus musculus</i>	37.9
6	<i>Pseudomys desertor</i>	22.0	<i>P. novaehollandiae</i>	25.6
7	Leporidae <i>Sylvilagus floridanus</i>	21.3	<i>Oryctolagus cuniculus</i>	28.0

mated the minimum total wastage of ova produced by wild rabbits to be 43.3%, of which between 10.2 and 13.0% are lost before implantation and most of the remainder before mid-term. In humans, an estimated minimum 30% of all fertilized ova are lost during early pregnancy (Roberts & Lowe 1975). Known causes of reproductive loss include chromosomal anomalies, endocrine disorders and physiological abnormalities, although *ca.* 40% of recurrent human pregnancy failures are unexplained (Hill 1990; Clark 1999).

The association between female mating behaviour and early reproductive failure described appears worthy of further investigation in the context of explaining the genetic benefits of polyandry. Polytocous mammal species in which females are relatively monandrous were found to have higher rates of early reproductive failure than those in which females are more polyandrous. This finding is consistent with predictions of the genetic incompatibility avoidance hypothesis for the evolution of polyandry, and suggests that the hypothesis may be generally applicable to mammals. However, it is important to emphasize that alternative explanations for the higher early reproductive failure of relatively monandrous females cannot be ruled out on the basis of the comparative evidence presented. For example, it is possible that relatively monandrous females may be more likely to adopt an insurance strategy of offspring overproduction and subsequent reduction, according to local resource availability (see Mock & Forbes 1995). This proposal could be investigated further by comparing ecological factors associated with different mating systems. If relatively monandrous females are adopting an insurance strategy of offspring overproduction, we should expect to find evidence that they typi-

cally experience greater variation in resource availability than more promiscuous females.

For the genetic incompatibility avoidance hypothesis to explain the patterns of reproductive failure described here, we must also assume that monandrous females in the dataset may generally have limited opportunities to mate multiply (or that they experience relatively high costs of doing so), otherwise selection would presumably favour increased multiple mating to reduce the costs of reproductive failure associated with genetic incompatibility. Comparative evidence that monogamy evolves most commonly among mammals in which solitary females are easy for males to monopolize is consistent with the idea that multiple-mating behaviour may often be constrained in monandrous females (Komers & Brotherton 1997). However, as for birds, there is also evidence that extra-pair matings often occur in some apparently monogamous mammals (Richardson 1987; Goossens *et al.* 1998). Finally, if the genetic incompatibility avoidance hypothesis is to explain the relatively high levels of early reproductive failure found in monandrous female mammals, further evidence is required to demonstrate the widespread occurrence both of post-copulatory paternity-biasing mechanisms and of genetic incompatibility in natural populations (Zeh & Zeh 1996, 1997; Tregenza & Wedell 2000).

Several potential sources of lethal genetic incompatibility have been suggested to influence the evolution of female multiple mating behaviour in natural populations (Zeh & Zeh 1996, 2001; Tregenza & Wedell 2000). For example, the deleterious fitness consequences of inbreeding are well established, and often include increased reproductive failure due to the unmasking of lethal recessive

alleles in the offspring of closely related individuals (Lacy *et al.* 1993; Lande 1994). There is also growing evidence that females of diverse taxa may be capable of sperm selection on the basis of male genetic similarity or relatedness, an adaptation that could potentially enable polyandrous females to reduce the costs of inbreeding (Olsson *et al.* 1996; Stockley 1999; Kraaijeveld-Smit *et al.* 2002). However, although there is growing evidence that moderate inbreeding may occur in many natural mammal populations, increased selection in such populations may be expected to reduce or purge the genetic load of lethal recessive alleles (Lacy & Ballou 1998; Crnokrak & Roff 1999; Keller & Waller 2002). Regular inbreeding may therefore tend to reduce levels of reproductive failure experienced by monandrous females, the opposite result to that reported here. Conversely, a relatively low risk of inbreeding may be sufficient to maintain selection for polyandry and sperm selection where costs of inbreeding are high (Tregenza & Wedell 2002). Further investigation is thus needed to determine if inbreeding avoidance is a common benefit of polyandry (Stockley *et al.* 1993; Olsson *et al.* 1996; Tregenza & Wedell 2002), and to establish the effectiveness of selection for reducing the genetic load in natural populations (Lacy & Ballou 1998).

As highlighted by Zeh & Zeh (2001), taxa such as mammals, in which development of the embryo takes place within the female, may be particularly susceptible to reproductive failure resulting from genetic incompatibility. Potential sources of genetic incompatibility linked to development of the embryo in mammals include genomically imprinted genes, Y-chromosome genes, foeto-maternal antagonistic genes and immune system foeto-maternal incompatibility (reviewed in Zeh & Zeh 2001). Of these, parental incompatibility at the major histocompatibility complex (MHC) is perhaps the best-studied potential cause of early reproductive failure (review in Tregenza & Wedell 2000). Several studies have found evidence for an increased frequency of shared parental MHC antigens among human couples that have experienced high rates of early foetal loss (Komlos *et al.* 1977; Schacter *et al.* 1984; Ober *et al.* 1998), and similar findings have been reported from studies of captive primates (Knapp *et al.* 1996). There is also evidence that female mammals may be capable of sperm selection on the basis of male MHC haplotypes, suggesting avoidance of MHC incompatibility to be a potential benefit of polyandry (Wedekind *et al.* 1996; Rülcke *et al.* 1998; Zeh & Zeh 2001).

Relatively high early reproductive failure of species with typically monandrous females is also consistent with predictions concerning the role of meiotic drive in the evolution of polyandry (Haig & Bergstrom 1995; Zeh & Zeh 1996, 1997). The best-known example of meiotic drive in mammals is the *t*-complex in mice (Silver 1985; Ardlie 1998; Fraser & Dudley 1999). Since most of the *t*-haplotypes found in mice, including those found in natural populations, are homozygous lethals (Silver 1985), and driver males are disadvantaged in sperm competition, females that are carriers of *t*-haplotypes can reduce the risk of immediate reproductive failure by mating multiply. Both carrier and wild-type females that mate multiply can also potentially avoid longer-term fitness costs associated with producing offspring that are heterozygous at the *t*-

haplotype (Haig & Bergstrom 1995), although in this case, polyandry does not function to reduce genetic incompatibility *per se*, because all females are expected to prefer non-driving males.

Although females of monandrous species appear to compensate for increased early reproductive failure by producing more ova, the results of the comparative analyses presented indicate that their litter sizes are typically more variable than those of polyandrous females. If this relatively high variation in the litter sizes produced by monandrous females reflects an increased error rate in achieving optimal litter size, it could represent a previously overlooked fitness cost of genetic incompatibility for polytocous female mammals. That is, in addition to producing too few offspring if litter size is reduced owing to high early mortality, monandrous females might also sometimes exceed optimal litter size, as a consequence of adopting a compensation strategy of increased ova production. This could also be costly because exceeding optimal litter size can have long-term fitness consequences both for offspring growth and survival, and/or female survival and future reproductive success (Aparicio 1993; Morris 1996; Sikes & Ylönen 1998; Humphries & Boutin 2000; McAdam *et al.* 2002; Réale *et al.* 2003), although such costs may be avoided in species with paternal or communal care of offspring. Alternatively or additionally, increased variation in litter size associated with monandry might reflect ecological factors that were not considered in the present study (for example, Sikes 1998). Further investigation is thus needed to determine if increased variation in litter size represents a direct fitness cost for monandrous female mammals, and hence if benefits of polyandry are likely to differ for polytocous and monotocous species, with potential consequences for the evolution of parental care strategies.

In conclusion, the findings presented are consistent with predictions of the genetic incompatibility avoidance hypothesis for the evolution of polyandry, although alternative explanations for the results presented cannot be ruled out on the basis of the comparative evidence presented. Further investigation is needed to explore these findings experimentally in a range of mammalian taxa, to determine ecological correlates of multiple-mating behaviour and to identify the causes of reproductive failure in natural populations.

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