Does female mortality drive male semelparity in dasyurid marsupials?

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In some members of the marsupial families Didelphidae and Dasyuridae, males are semelparous, that is, they live for only one mating season. Semelparity is proposed to be the result of the high energy demands of competing for matings with many females during a short breeding season. We argue that high adult female mortality rates between mating and weaning of the offspring selects for a 'bet-hedging' mating strategy in males. We tested this hypothesis in a well-studied field population of *Antechinus agilis* by estimating the number of females a male needs to mate with in order to have a high chance of siring at least one offspring that survives to the next breeding season. Our hypothesis predicts that species in which males are semelparous should have higher female mortality rates than species in which males are iteroparous. The limited available data for dasyurid marsupials support this prediction.

Keywords: semelparity; mortality; dasyurid; marsupial; *Antechinus*

1. INTRODUCTION

Semelparity among mammals is restricted to members of the marsupial families Didelphidae and Dasyuridae (Lee & Cockburn 1985; Cockburn 1997). Species in these families share a predisposition for high degrees of post-reproductive senescence (Cockburn 1997), but not all exhibit semelparity. In semelparous species, such as those of the genus *Antechinus*, all males die after a short, highly synchronous mating season. While the physiological features that accompany male die-off are reasonably well understood in a number of species (Bradley 2001; Oakwood *et al.* 2001), the adaptive benefits of a semelparous mating system are largely unknown.

Braithwaite & Lee (1979) demonstrated that the time-interval between conception and weaning in small (less than 1 kg) marsupials is long compared to that of similar-sized eutherian mammals. They also stated that all semelparous mammals live in highly predictable seasonal environments. They argued that these two factors selected for a monoestrous reproductive pattern, synchrony of oestrus and a short mating season. Intense male-male competition during this short mating season, combined

with a low probability of males surviving to the next breeding season, resulted in the highest fitness pay-off to males that invested all reproductive effort in a single breeding event. Recent work has shown that females mate with multiple males and that larger males tend to sire more offspring (Kraaijeveld-Smit *et al.* 2002, 2003), suggesting that male-male competition is indeed intense.

Dickman (1993) suggested that male die-off is a result of selective pressure on males to maximize their success in sperm competition. The costs of producing large amounts of sperm would result in mortality. However, Taggart & Temple-Smith (1994) showed that ejaculates of male *Antechinus* contain rather low numbers of spermatozoa and that the number of ejaculates per male is fixed. The costs of sperm competition are therefore unlikely to explain male semelparity.

We extend the hypothesis of Braithwaite & Lee (1979) to include the effect of female mortality. Female mortality in small marsupials tends to be high, perhaps because the long lactation period makes reproduction relatively stressful. We argue that this selects for a 'bet-hedging' reproductive tactic among males, which in turn leads to selection for male semelparity.

2. DOES HIGH FEMALE MORTALITY SELECT FOR MALE PROMISCUITY?

If many females die between being fertilized and weaning their offspring, and if males are unable to predict which females are likely to survive, the optimal mating strategy for males might be to inseminate as many females as possible. By spreading their sperm among many females, males increase the chance that at least one of these females will survive and successfully wean his offspring. We calculated the likelihood of a male siring at least one offspring that survives to the next breeding season under different female survival rates for a field population of *A. agilis* as

$P\{\text{at least one offspring survives to next season}\} =$
 $P\{\text{at least one offspring survives and at least one mother survives}\} =$
 $\Sigma P\{\text{at least one offspring survives given that } y \text{ mothers survive}\} P\{y \text{ mothers survive}\};$ for all $0 < y \leq \text{number of females fertilized}.$

$P\{\text{at least one offspring survives given that } y \text{ mothers survive}\} = 1 - (k!/x!(k-x)! \times p^x \times q^{(k-x)}),$
 where k is the number of offspring sired per female $\times y$;
 x is the number of surviving offspring surviving between birth and the next breeding season (0); this does not include young that are born, but do not attach to a teat, as these cannot be found in the field and always die immediately after birth;

p^x is the chance that a given offspring survives given that the mother survives;

$q^{(k-x)} = 1 - p$;

$P\{y \text{ mothers survive}\} = n!/y!(n-y)! \times p^y \times q^{(n-y)};$

n is the number of females fertilized;

y is the number of fertilized females surviving between mating and weaning her offspring;

p^y is the female survival rate; and

$q^{(n-y)} = 1 - p.$

The assumption of lack of male selectivity appears to be met in this species because females that weaned offspring

Figure 1. A model for the relation between the number of females fertilized and the chance that a male will sire at least one offspring that survives until the next breeding season for *Antechinus agilis* at three realistic levels of female mortality: 0.7 (continuous line); 0.5 (dashed line); 0.3 (dotted line). See § 2 for the estimates of the model parameters.

were not fertilized by more males, or by bigger males than females that gave birth but did not wean offspring (Kraaijeveld-Smit *et al.* 2003). Estimates for the model parameters were obtained as follows: offspring survival between birth and weaning is approximately 0.5 (Cockburn *et al.* 1985). Offspring survival between weaning and reproductive age could only be estimated for females since males disperse immediately after weaning (Cockburn *et al.* 1985); in the study population, this was 0.42 (Kraaijeveld-Smit 2001). If we assume that this figure is similar for males and females, the overall offspring survival was $0.5 \times 0.42 = 0.21$. Adult female survival in the study population was 0.68 in 1999 and 0.42 in 2000 (Kraaijeveld-Smit *et al.* 2002, 2003). Female survival in other species of dasyurids can be as low as 0.21 (Bradley 1997).

The model shows that mate guarding is unlikely to be a successful strategy. Under the observed level of offspring survival (0.21) and the highest observed level of female survival (0.68), a male that mates with only one female but sires all eight of her offspring has only a 59% chance of having a live offspring during the next breeding season. Field data show that multiple paternity within litters is ubiquitous in this species, and that the median number of young sired per female by a single male was 2 (Kraaijeveld-Smit *et al.* 2002). Figure 1 shows the outcome of the model under these parameter values for three levels of female survival. The results show that when female survival is high (0.7), a male must mate with at least six females to have a greater than 80% chance of gaining an offspring in the next generation. When female survival is low (0.3), this figure rises to at least 14. Field data show that such figures are realistic: single males sired offspring with up to nine of the sampled females (Kraaijeveld-Smit *et al.* 2002). As 0.55% of all females present during the mating season were subsequently caught with offspring, the true number of inseminated females per male may have been as high as 16.

It seems clear that there is intense pressure on males to fertilize as many females as possible. Since the mating

period is restricted to two weeks, and each mating has to last for at least 3 h for sperm to be successfully transported to the storage crypts (Shimmin *et al.* 1999), one can imagine that mating effort will consume large amounts of the males' energy. We propose this as the major cause of death, rather than the production of sperm. Indeed, mating effort might be limiting the resources available for sperm production and therefore account for the low observed sperm counts.

There is a second way in which female mortality could select for male semelparity. When females are philopatric (as in *Antechinus*) and female mortality is high, many of the breeding females in a given area will be replaced by their daughters during the next season. Any male that sired offspring and then survived to the next season would have a relatively high risk of mating with his daughters. Males would either have to disperse or to display kin recognition, both potentially costly. As all males die in *Antechinus*, we have no data to address this question. The prediction in iteroparous species is that second-year males should pair with second-year females.

3. DOES SELECTION FOR MALE PROMISCUITY LEAD TO MALE SEMELPARITY?

Males are likely to face a trade-off between mating effort and post-reproductive survival. If high female mortality rates select for increased male promiscuity, as argued above, there might be a threshold beyond which males must invest all their mating effort in a single season. In other words, a male that invests resources into survival after the first mating season instead of in mating may fertilize insufficient females during his lifetime to ensure his genes are passed on to the next generation. This predicts that species with male semelparity should have higher levels of female mortality. A literature survey yielded data on female mortality for 10 species of dasyurids (table 1). These have similar life histories, except that males of *Dasyurus viverrinus*, *Parantechinus bilarni* and one population of *Parantechinus apicalis* are iteroparous. The female mortality rate of these iteroparous species was significantly lower than that of semelparous species (female mortality arcsine-transformed, Student's $t = -4.88$, d.f. = 9, $p = 0.001$). However, this analysis treats species as independent data points, which may not be justifiable (Harvey & Pagel 1991). Only three independent contrasts could be generated from this dataset, insufficient for analysis. Nevertheless, male semelparity has evolved several times in marsupials (Krajewski *et al.* 2000), so it should be possible to test this hypothesis more rigorously once data on female mortality rates become available for more species in the future.

Perhaps the most interesting species in which to study the evolution of male semelparity are those in which semelparity does not occur in every population. Two such species are known: *P. apicalis* and *Dasyurus hallucatus*. No information on female mortality is available for *D. hallucatus* populations in which males live for more than one season. However, Mills & Bencini (2000) reported trapping data for two populations of *P. apicalis*; one in which males were semelparous, and one in which they were not. In accordance with our prediction, female mortality was much higher in the semelparous population (approximately 0.60) than in the non-semelparous

Table 1. Female mortality rate and ecological variables in dasyurid marsupials.

(All species are monoestrous (although *Dasyurus viverrinus* is facultatively polyoestrous), have seasonal breeding seasons of restricted length and reach sexual maturity at about 11 months of age (Krajewski *et al.* 2000).)

species	breeding seasons per male	female mortality rate	n (female-years)	reference
<i>Dasyurus hallucatus</i>	1	0.68/0.67	22/25	Begg (1981 <i>b</i>), Dickman & Braithwaite (1992)
<i>Dasyurus viverrinus</i>	> 1	0.33	6	Godsell (1982)
<i>Parantechinus apicalis</i> ^a	1	0.44/0.60	70/58	Dickman & Braithwaite (1992), Mills & Bencini (2000)
<i>Parantechinus apicalis</i> ^b	> 1	0.27	55	Mills & Bencini (2000)
<i>Parantechinus bilarni</i>	> 1	0.31	64	Begg (1981 <i>a</i>)
<i>Phascogale tapoatafa</i>	1	0.67/0.67	12/46	Cuttle (1982), Sodderquist (1993)
<i>Phascogale calura</i>	1	0.79	38	Bradley (1997)
<i>Antechinus agilis</i>	1	0.45	94	Kraaijeveld-Smith (2001)
<i>Antechinus bellus</i>	1	0.59	29	Friend (1985)
<i>Antechinus leo</i>	1	0.61	28	Leung (1999)
<i>Antechinus swainsonii</i>	1	0.61	52	Lee & Cockburn (1985)

^a Boullanger Island.

^b Whitlock Island.

population (approximately 0.27; table 1). In *P. apicalis* and *D. hallucatus*, the hypothesis put forward in this paper might be verifiable in field experiments in which females (but not males) are removed from the population after the breeding season.

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