Live fast, die young, and win the sperm competition

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Consider the two mammalian species shown in Fig. 1. The brown antechinus (*Antechinus stuartii*) has a fast life cycle and “big bang” reproduction, with males that mate for only a single breeding season in 1 y and then die a programmed death associated with lethal immune system collapse (1). The other mammalian species (*Homo sapiens*) has a long life during which males can mate during up to or beyond 60 y of continuous breeding. This latter species has a slow life cycle, in which reproductive events are spread over an extended period. These contrasting characteristic life cycles of mammalian species remain evident even when the obvious differences in body size are taken into account (2). In short, mammals span the gamut between slow and fast life cycles.

However, it isn't supposed to be this way. Because of lactation (i.e., the extended period of maternal care when young are raised on milk) and generally long developmental periods, mammals should be predisposed to repeated reproduction over the lifetime (3, 4). This type of life cycle is called iteroparous (5). Nonetheless, a few mammals like males of the brown antechinus are semelparous, breeding for only one season: they live fast and die young. Furthermore, male semelparity likely evolved independently in marsupials about six times (6). Such males occur in species in which females may live for additional breeding seasons. So what's so special about these males?

Fisher and colleagues (7) answer this question with a remarkable perspective that draws

from phylogenetic constraint, biogeography, reproductive physiology, and the theory of sexual selection. They take the pattern of historical relationships into account with a rigorous phylogenetic comparative method that applies Bayesian analyses and also accounts statistically for differences in the species' body sizes. They begin with the insight that evolutionary interests in breeding of males and females may be decoupled, an idea anticipated by Darwin (8). Female reproduction is limited, but male reproduction is less so if they can mate with several females. Thus, males may exhibit exceptionally strong competition for matings. This competition will be acute if females are synchronized in their matings.

The phylogenetic groups of marsupials that exhibit semelparous males (dasyurids of Australia and didelphids of Central and South America) are primarily insectivorous. As species in these marsupial groups have diversified and moved into higher latitude regions, the season of peak insect prey abundance is more concentrated by increasingly seasonal climate (7). This produces female breeding and thus female reproductive receptivity to a narrower annual period in more temperate habitats. Due to the long reproductive development period of marsupials, a phylogenetic constraint, only a single breeding season occurs each year. As latitude increases, breeding seasons become shorter and the frequency of marsupial species with male die-off increases.

Synchronized breeding should increase male competition for female mates and make these mates less defensible, important factors for intensifying sexual selection. However, more factors amplify mate competition among semelparous male marsupials. These species may commonly be polygynandrous; that is, they exhibit multiple matings by both males and females (9). For example, the relatively large litters (up to eight offspring) of the brown antechinus can be multiply inseminated by up to four fathers (10). Thus, sperm competition produces strong skew in the reproductive success of males

Fig. 1. The brown antechinus (*Antechinus stuartii*) held by a human (*Homo sapiens*). Only the hand of the latter species is shown. Photograph by Andras Keszey, School of Biological Sciences, The University of Queensland, St Lucia, Queensland 4072, Australia.

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(11), and sexual selection on males is reflected by their larger body size compared with females (12). Sperm competition also reflects the intensity of sexual selection, as marsupial species that have extreme die-offs among males also show long copulation periods and males with significantly larger testes for their body size (7). There is a cost to such extreme reproductive competition, however, as such males exhibit a variety of syndromes that lead to die-off, including weight loss, immune suppression, and disease (6).

Whether extreme die-offs of males in some species of marsupials is adaptive, that is, has been favored by natural selection, has been an ongoing quandary for the last 35 y (3, 4, 6, 12, 13). It is remarkable that two groups of marsupials on different continents exhibit ex-

treme die-offs of reproductive males, but is it a simply a nonadaptive historical anomaly of marsupials? Or worse, is it maladaptive?

Fisher et al. (7) have supplied a robust adaptive scenario by taking a multifaceted ecological and evolutionary approach.

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