



Commentary

Role of fecundity selection on the evolution of sexual size dimorphism in mammals



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Pinnipeds (seals, sea lions and walruses), in particular northern elephant seals, *Mirounga angustirostris*, have been considered among the clearest examples of the role of sexual selection in modulating sexual size dimorphism (SSD) and sexual behaviour (Cassini, 1999; Lindstedt & Boyce, 1985; Staniland, 2005). The largest males defend the largest harems and obtain the largest number of copulations (Le Boeuf, 1974). One photograph of several male and female elephant seals is probably the most widely used example of sexual selection in textbooks.

While writing a 1999 forum piece on the subject (Cassini, 1999), I was surprised by a result described by Cox and Le Boeuf (1977, page 326): 'Females near the end of estrus rarely protest mounts and readily accept copulation with peripheral males. The behaviour of females changed drastically on their last day of estrus..., they were extremely receptive to all males. This was especially noticeable in their response to peripheral males as they moved out beyond the periphery of the harem on their way to the water. We

interpret this change in behaviour as a female's means of insuring fertilization'. This female behaviour contradicts the expectations of sexual selection theory: the largest males were able to monopolize the largest harems, but they should have also been able to monopolize paternity, and this female behaviour appears to reduce male variance in reproductive success.

In the same year my forum paper was published, Le Boeuf and co-workers published an article that confirmed my doubts: DNA fingerprinting and microsatellite DNA analysis indicated significantly lower reproductive success of alpha males (i.e. the largest males) than that predicted by behaviour (Hoelzel, Le Boeuf, Reiter, & Campagna, 1999). In other words, behaviour and body size were poor predictors of paternity, and therefore the role of sexual selection should be reassessed.

A more recent paper on pinnipeds also provided unexpected results: Krüger, Wolf, Jonker, Hoffman, and Trillmich (2014) investigated the co-evolutionary dynamics of 11 life-history traits in pinnipeds. In contrast to expectation, they found support for SSD having evolved prior to changes in the mating system, probably due to niche partitioning during aquatic foraging. Based on these antecedents, we decided to conduct a direct test of sexual theory in pinnipeds (González-Suárez & Cassini, 2014). Using genetic estimates, we did not find support for a positive relationship between

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variance in reproductive success and SSD. In conclusion, the evidence does not clearly support the hypothesis that sexual selection is the main reason for the evolution of SSD in pinnipeds.

PARSIMONIOUS RULE IN THE STUDY OF SEXUAL SIZE DIMORPHISM

Although pinnipeds are just one example of SSD attributed to sexual selection, they are significant because they are the taxon with the greatest size dimorphism among mammals (González-Suárez & Cassini, 2014). Thus, the question regarding the main forces that have modulated the evolution of SSD in mammals should be resolved. At least four selective forces have been suggested: fecundity selection, sexual selection, viability selection and natural selection (Fairbairn, 1997; Slatkin, 1984). Besides these, some general constraints, as well as genetic correlations between the sexes, have been mentioned, which potentially limit the evolution of SSD (Fairbairn, Blackenhorn, & Székely, 2007). Sexual size dimorphism should depend on the strength of these selective forces operating differentially on males and females. Shine (1989) noted that the problem that the interplay between potential evolutionary determinants of SSD may be very complex, and proposed (1) to examine some of the basic tenets of the hypotheses and (2) to focus on the idea with the greatest parsimony, that is, the one that is simplest and, thus, most likely to generate falsifiable predictions, which will, thereby, be more amenable to testing. In the present paper, I evaluate the potential evolutionary mechanisms of SSD in mammals, following the rules proposed by Shine.

The most common explanation for female-biased SSD is Darwin's (1874) fecundity advantage hypothesis (Leather, 1988; Shine, 1989; Wicklund & Karlsson, 1984). In contrast, male-biased SSD is primarily explained through sexual selection theory (Darwin, 1874; Leutenegger, 1978; Price, 1984). This latter theory easily predicts body size in males, but it is more difficult to apply to the evolution of female body size. It must explain not only why males are larger than females, but also (1) why females in more dimorphic species are larger than females in less dimorphic sister taxa, and (2) why females in more dimorphic species are relatively smaller than males, in comparison to females in less dimorphic taxa (Fairbairn, 1997; Fairbairn et al., 2007). These patterns are described by Rensch's rule, which is based on the widespread observation that male body size varies more than female body size, such that male-biased SSD increases with body size (Fairbairn, 1997; Rensch, 1950).

Fairbairn (1997) and Lindenfors, Gittleman, and Jones (2007) formalized a model of the evolution of sexual size dimorphism (SSD) in mammals that included the effect of sexual selection on both sexes (Fig. 1). Under sexual selection on males, females are also selected for larger size in order to produce larger male offspring (Fairbairn, 1997; Lindenfors, Tullberg, & Biuw, 2002). Fecundity selection prevents females from reaching the same size as males (Fig. 1). This sexual model of the evolution of SSD may explain the most important characteristics of SSD in mammals. However, the model is complex, with three explicit mechanisms operating differently: sexual selection on males, sexual selection on females and fecundity selection on females. Moreover, the model lacks an explanation of the role of natural selection in the evolutionary process, which would have complicated it even further.

As stated by Shine (1989), the most parsimonious model is one that requires the fewest mechanisms to explain the phenomenon of SSD. I propose that SSD in mammals can be explained in terms of only one evolutionary mechanism, fecundity selection in females, which is the same mechanism that is largely accepted as an explanation of the evolution of SSD in most animals with sexual

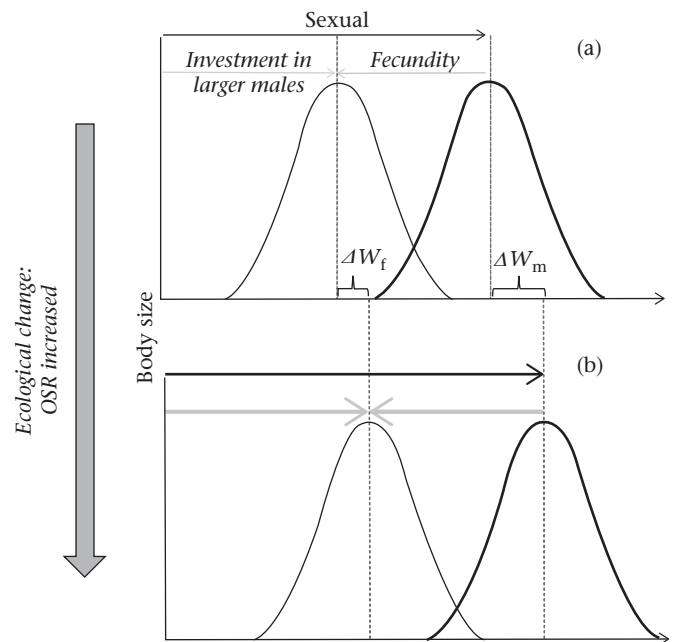


Figure 1. Sexual selection model of sexual size dimorphism. Gaussian distribution of body sizes for females (fine line) and males (gross back line) with (a) low and (b) high operational sex ratios (OSR). The thickness of arrows represent the strength of sexual, fecundity and correlational selections. Fecundity selection prevents females from reaching the same size as males. When an ecological change increases the operational sex ratio (OSR), the intensity of sexual selection increases.

reproduction in which females are larger than males (Darwin, 1874; Fairbairn et al., 2007; Head, 1995).

A SIMPLE EXPLANATION OF THE EVOLUTION OF SSD IN MAMMALS

The role of natural selection in the evolution of animal body size has been investigated since Bergmann's rule was first proposed in 1847. Bergmann (1847) showed that body size increases with latitude and decreasing temperature, and proposed that natural selection favours large size in cold climates to improve thermoregulation. Several studies have shown that species, families and orders of mammals tend to follow this rule (e.g. Clauss, Dittmann, Müller, Meloro, & Codron, 2013; Meiri & Dayan, 2003). Since Bergmann's rule was proposed, geographical patterns in animal size have been extensively investigated, and numerous correlates of body size variation have been proposed, including latitude, latitudinal range, geographical range size, temperature, temperature range, annual precipitation, precipitation range, net primary production, food supply and species richness, yet there is still no consensus on which environmental factors are primarily responsible for these geographical patterns (Huston & Wolvertson, 2011). No matter which ecological mechanism is proposed, there is agreement that natural selection for larger or smaller body size should be involved in the evolution of body size. For example, Huston and Wolvertson (2011) proposed that food availability is the main selective pressure, so, in environments where food availability is chronically low, small individuals will have an advantage over larger individuals because they require less food and, thus, are more likely to avoid starvation and survive. Therefore, over time, natural selection may create genetic constraints on body size.

Assuming that natural selection is a main determinant of body size in mammals, a question remains as to why males and females are of different sizes in many species. In the following paragraphs I

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