# Why Is the World Full of Large Females?

*In most groups of animals, apart from mammals and birds, the female is larger than the male; the ability to produce many offspring may be only part of the reason for this pattern*

ANIMALS come in a vast range of sizes, from the tiniest zooplankton to the largest whale. Absolute body size has a crucial influence on a species' life history, affecting such factors as metabolic rate, longevity, and territorial range. And, within a species, relative body size—females compared with males—is important in behavioral ecology terms too. In most species in the world, females are larger than males, although this rule applies more to groups such as insects, fishes, amphibians, and reptiles than it does to mammals and birds. Nevertheless, the largest animal that has ever lived is a female: the female blue whale.

Why females should attain a larger body size than males has long fascinated biologists. Darwin had an explanation for it, namely: "Increased size must be in some manner of more importance to the females . . . and this perhaps is to allow the production of a vast number of ova." This so-called fecundity-advantage model "has achieved the status of conventional wisdom," says Richard Shine of the University of Sydney, Australia. The model appeals through its simplicity and its consistency with many empirical observations. However, it has not been formally tested, says Shine, a deficiency he has recently repaired. He finds that even though the model may apply in some species it is by no means universal.

It is no easy task, of course, to solve the question of why one sex may be bigger than the other in a particular species, not least because there are two partners in the game. Specifically, the female might be the bigger of the sexes because of the kind of selective advantage that Darwin proposed; but it is equally true that if males evolve small body size for some different adaptive reason, then the same pattern of body size dimorphism would apply. Several biological factors are likely to be operating in any particular case, and this should always be born in mind when looking for "the" factor.

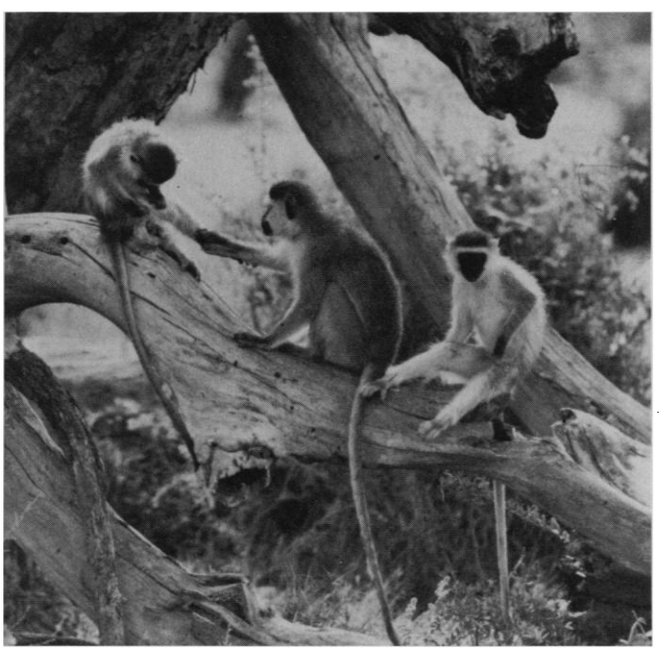
The fecundity-advantage model says simply that the larger a female is, the more eggs it will be able to produce at any one time. Stated boldly like this, however, the model has a "serious flaw," notes Shine: "Life history theory predicts that traits should evolve so as to maximize *lifetime* reproductive success, not *instantaneous* reproductive success at any single breeding season."

In other words, there is little point in growing a big body that will be able to produce large clutches, if attaining that body size has been an expensive process on the way, thus diverting resources from potential reproductive activity earlier in life. The fecundity-advantage model therefore can apply only when energy resources are essentially unlimited, a situation that is likely to be uncommon, although measuring it accurately has proved difficult.

Shine elected to test the model in something of a roundabout fashion, thereby hoping to avoid confounding variables that might affect body size in different directions. He measured male-female body size differences in a series of lizard species, some of which produce variable clutch sizes while in others the clutch size is constant. "If the main selective pressure for large female size is an associated increase in fecundity," says Shine, "the species with invariant clutch sizes would have no such advantage and females should tend to be smaller (relative to males)."

It turns out that in anoline iguanids, which produce a single egg, the proportion of species in which the female is larger than the male is about the same as in other iguanids in which clutch size is variable. "The same tends to be true for other lizards with invariant clutch sizes," says Shine. "These data, involving at least seven separate phylogenetic lineages of lizards, appear to falsify the main prediction of the fecundity-advantage model." This test does not completely invalidate the model, of course, but it does show that if there is a fecundity advantage in females being large, it applies to only a limited set of species.

"Why, then, are females larger than males in most species of animals?" asks Shine. There are several possibilities, some of which may operate singly in some groups, some in concert. "For example, energy limitation may be rare, and the fecundity-advantage model may be valid for many taxa. Alternatively, bigger mothers may produce 'fitter' offspring for many reasons, or other advantages may accrue to large females. There may be circumstances wherein sexual selection favors relatively small size in males, perhaps because of enhanced mobility. Lastly, sexual size dimorphism in some species may simply reflect survival differences if growth continues after maturity; there may be no need to invoke adaptation in such cases." ■ ROGER LEWIN



**Bodies**

*The general rule that females are larger than males applies less to mammals than to other groups. In vervet monkeys, for instance, males are the larger sex.*


ADDITIONAL READING

R. Shine, "The evolution of large body size in females: a critique of Darwin's fecundity advantage model," *Am. Nat.* **131**, 124 (1988).