

The Evolution of Sexual Dimorphism in Animals: Hypotheses and Tests

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Three major hypotheses, based upon mechanisms of sexual selection, intersexual food competition and reproductive role division, have been advanced to explain the evolution of sexual dimorphism in body size and morphology of animals. Genetic models suggest that all of the hypotheses are plausible, and empirical studies demonstrate that each of the three mechanisms operates in natural populations. However, problems arise in testing hypotheses for the evolution of sexual dimorphism: more than one mechanism may be operating simultaneously, and the demonstrated occurrence of a mechanism does not indicate that it actually results in selection for dimorphism. A recent statistical technique offers a solution to these problems and provides a promising new approach to the study of sexual dimorphism, in which researchers can assess the relative importance of each mechanism in present-day selection for sexual dimorphism within a species.

Sexual differences in size and morphology are widespread in the animal kingdom. Charles Darwin¹ drew attention to these differences, and offered several explanations for their evolution. Darwin's sexual selection hypothesis proposes that sexual dimorphism evolves when characters that confer an advantage in either competition for mates or mate choice are selected for within one sex.

Despite the popularity of this hypothesis, Darwin and others^{2,3} realized that sexual selection could not be the sole explanation for sexual dimorphism and suggested that in some cases, sexual dimorphism might evolve from food competition between the sexes² or intrinsic differences between the reproductive roles of males and females (the 'dimorphic niche' hypothesis³). The three hypotheses are hotly debated today⁴⁻⁸, and some authors even argue that sexual dimorphism can evolve only through sexual selection⁹. How plausible are these hypotheses?

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Genetic models

Several genetic models that specifically address this question have been constructed. Models by Lande¹⁰ and Lande and Arnold¹¹ assume that the genetic basis for sexual dimorphism is polygenic. They demonstrate that sexual dimorphism can evolve from an initial state of monomorphism when selection acts on the two sexes in opposite ways, either through intrasexual selection¹⁰, intersexual selection¹¹ or ecological factors (dimorphic niches, food competition¹⁰). However, the evolution of sexual dimorphism also depends upon the genetic correlation between the sexes in the trait of interest. Such a correlation indicates that male and female traits do not evolve independently; thus, selection on a trait in one sex produces not only a direct evolutionary response in that sex, but also an indirect (i.e. correlated) response in the opposite sex. If the genetic correlation between the sexes is high (close to 1.0) for a particular trait, the rate of evolution of sexual dimorphism in that trait may be very slow. Nonetheless, when the correlation is less than 1.0, a character that is initially found in both sexes can eventually become confined to one sex.

In another series of models, Slatkin¹² examined whether there could be purely ecological causes for the origin of sexual dimorphism. Like Lande and Arnold¹¹, he assumed a polygenic basis for sexual dimorphism and a genetic correlation between the sexes of less than 1.0. He recognized three classes of assumptions about selection for ecological factors: (1) divergent selection pressures on the two sexes, such that each sex has its own optimum value for the trait (i.e. a value that maximizes that sex's total fitness); (2) two or more optimum values for *both* sexes; and (3) competition between males and females for limited resources, e.g. food.

Slatkin's first assumption corresponds to the 'dimorphic niche' hypothesis and was also treated by

Lande¹⁰. When he modelled this case, Slatkin found that each sex would evolve to its own separate optimum unless the genetic correlation between the sexes was 1.0. Thus, the dimorphic niche hypothesis is plausible, and does not require a low genetic correlation between the sexes.

The second assumption proposes that two optima for a species exist, so that each sex has the *same* requirements and the same *two* optima (i.e. either optimum is ideal for either sex). Here, one sex might evolve to one optimum, and the other sex to the other. In this case, Slatkin showed that a genetic correlation between the sexes greatly restricts the possibility that sexual dimorphism can arise. Thus, the presence of two or more optima for each sex probably does not lead to the evolution of sexual dimorphism.

Finally, Slatkin examined the case in which males and females compete for a limiting resource (e.g. food), and asked whether competition alone could lead to the evolution of sexual dimorphism. He demonstrated that as long as the trait in males and females is positively but not perfectly correlated genetically, sexual dimorphism can evolve from food competition alone, even when the genetic correlation is high.

Empirical evidence for the evolution of sexual dimorphism

What empirical evidence do we have for the operation of these mechanisms? Demonstrating that any of the mechanisms could lead to the evolution of sexual dimorphism requires evidence that the mechanism results in differential survival and/or reproduction among the members of one or both sexes, such that the two sexes could experience divergent selection pressures¹³.

Sexual selection

Many empirical studies of sexual selection have documented the occurrence of competition among males for access to mates, and of mate choice by females¹⁴. In some sexually dimorphic species, these processes have been shown to result in differential reproductive success. For example, studies of

several species where males are larger than females (e.g. elephant seals, *Mirounga angustirostris*¹⁵) have demonstrated that males compete for mates, and that males of different sizes have differential reproductive success.

In other species, female mating preferences result in differential reproductive success for males of different body sizes or morphologies. For example, in the neotropical frog *Physalaemus pustulosus*¹⁶, larger males have a mating advantage because females prefer their calls to those of smaller males. Female widowbirds (*Euplectes progne*) prefer males with longer tails to males with short tails¹⁷.

Indirect evidence for differential reproduction among the members of one sex is also provided by comparative studies of sexual dimorphism within groups of related species. Across certain sets of species, the degree of sexual dimorphism is positively correlated with the extent to which some males prevent others from mating¹⁸.

Dimorphic niches

Most studies of the dimorphic niche hypothesis have focused upon selection pressures acting only on females. Myers¹⁹ postulated that larger female size evolved in vespertilionid bats because females (and not males) carry embryos that total 20–30% of their own body weight, and transport young after birth. In support of this hypothesis, he found a greater degree of sexual dimorphism in species in which females carry a greater total weight of young.

Whereas Myers demonstrated a possible advantage to larger female size, he did not investigate differential survival and reproduction of females of different sizes. However, some studies have reported a positive correlation between female size and egg number, supporting the view that being a larger female confers greater fecundity. Wiklund and Karlsson²⁰ found that in satyrid butterflies, larger female size was positively correlated with lifetime fecundity.

Food competition between the sexes

Some authors^{21,22} have suggested that food competition during the nonbreeding season may

maintain sexual dimorphism. Several studies have demonstrated that the sexes compete for food during the nonbreeding season^{21,22}. However, none of these has demonstrated that this competition results in disruptive selection on the sexes (i.e. selection for sexual dimorphism).

Price²³ attempted to measure food competition between the sexes during the breeding season by comparing the reproductive success of highly dimorphic pairs versus less dimorphic pairs of the finch *Geospiza fortis*. If sexual dimorphism lessened food competition between the sexes, he expected to find that the most dimorphic pairs had the highest reproductive success. He found no relationship between degree of dimorphism and reproductive success. However, many factors other than foraging contribute to reproductive success (e.g. territory quality, timing of breeding, predation). Ideally, rates of energy intake²⁴ in addition to reproductive success²³ should be compared among breeding pairs: if food competition is related to the degree of sexual dimorphism, then both rates of energy intake and reproductive success should be greater for more dimorphic pairs than for less dimorphic pairs.

Problems with tests of hypotheses for the evolution of sexual dimorphism

When testing hypotheses for the evolution of sexual dimorphism, most researchers focus on only one of the three mechanisms. However, even if one mechanism is shown to be operating, others also could be important.

Consider a hypothetical species in which males are larger than females, females prefer to mate with larger males, and larger males provide females with more food during courtship. Such observations would lead many researchers to conclude that sexual dimorphism evolved in this species through female mating preferences for larger males (i.e. sexual selection). However, this overlooks the possibility that larger males provide more food to females and their offspring because their larger size reduces food competition between the sexes. Moreover, if males are primarily responsible for defense of offspring, their special role

Box 1. Measuring direct and indirect selection on a sexually dimorphic trait

Net selection occurring within a generation on a trait can be measured by calculating the *selection differential* (s), which is the difference between mean values for the trait before and after selection²⁸. This selection differential may be caused by both selection on that trait (direct selection) and selection on a correlated trait (indirect selection). For example, if bill size and body size are correlated, a change towards smaller bill size might be caused by selection for smaller bill size (direct selection) or by selection for smaller body size (indirect selection).

Lande and Arnold²⁸ have developed a multivariate statistical method for measuring selection on correlated traits, which allows separation of the direct effects of selection from the indirect effects. This method uses the selection differentials and phenotypic intercorrelations for a set of traits to calculate the *selection gradient* (β), which is a measure of the direct force of selection on a trait after the indirect effects from other measured traits are removed. In statistical terms, β equals the partial regression of relative fitness on a trait, holding all other traits constant.

Recently, Arak¹³ used this statistical technique in a simple model to predict the degree of sexual dimorphism in body size for a given species. The model assumes that natural selection (i.e. selection resulting from food competition, predation, etc.) tends to move body size towards an optimum for survival, whereas reproductive selection (i.e. sexual selection plus selection for female fecundity) will tend to drive body size away from the optimum for survival. Total fitness is the product of fitnesses from natural and reproductive selection.

By solving for the body size that represents the optimal trade-off between survival and reproduction (in terms of total fitness), the model shows that the difference in body size between the sexes should be proportional to the difference in their respective *reproductive selection gradients*. However, this result obtains only when a simplifying assumption is made that the optimum and standard deviation of the function relating body size to survival are identical for males and females. Unfortunately, this assumption in effect rules out all explanations for sexual size dimorphism that rely on natural selection acting differently on the two sexes (e.g. the food competition hypothesis). Nonetheless, when the model was tested using data from nine anuran species on the correlation between body size and reproductive success for males and females, its prediction was met. The model could not account, however, for the direction of sexual dimorphism.

The Lande and Arnold²⁸ method for measuring selection on correlated traits is a powerful technique for identifying the targets of present-day selection. To predict the course of evolution, however, knowledge of the heritabilities and genetic correlations of particular traits is required²⁹. Moreover, the method can only pinpoint selection occurring during the observation period; if selection is highly variable in time (or space), inferences to selection in other seasons or populations may be incorrect. Finally, the traits of interest may be responding to selection on traits that are correlated with them, but that were not measured²⁸.

Thus, in studying the evolution of sexual dimorphism, this method's usefulness can be maximized by (1) measuring selection over a number of seasons and populations; (2) measuring as many traits that are potentially correlated with dimorphic traits as possible; and (3) estimating the heritabilities and genetic intercorrelations of these traits.

in parental care also might select for larger size (i.e. males and females have dimorphic niches).

Most empirical studies have focused on species in which dimorphism is already present, and thus are most useful in identifying factors responsible for its maintenance, rather than its origin. However, one factor may have been responsible for the origin of sexual dimorphism, whereas another could be maintaining it¹⁰. Moreover, even where a particular mechanism can be shown to produce differential survival or reproduction, its result may not be net selection for sexual dimorphism if opposing selection pressures are present^{5,7}.

Consider a hypothetical species in which larger males have a higher reproductive success than smaller males because of competition among males for mates. If smaller males tend to live longer than larger ones, there might be no net selection for larger male body size. Similarly, the evolution of sexual dimorphism may sometimes be restricted by the presence of interspecific competition. Some studies have shown that the degree of sexual dimorphism among related species is negatively correlated with their numbers of competing species²⁵.

Finally, selection resulting from a particular mechanism can produce or maintain sexual dimorphism in a trait only if that trait is heritable and its genetic correlation between the sexes is less than 1.0. Few studies of sexual dimorphism in particular populations have presented estimates of heritability for dimorphic traits in these populations, or estimates of the genetic correlation between the sexes when both sexes share a trait²⁶. This problem is especially acute for studies on dimorphic behavioral traits²⁷.

Coping with the problems: a case study

Price's study on *Geospiza fortis*²³ is perhaps the most thorough study of the evolution of sexual dimorphism. First, he examined all three of the suggested mechanisms for the evolution of sexual dimorphism. Second, he used methods outlined by Lande and Arnold²⁸ (Box 1) to demonstrate net selection occurring on a particular trait

(bill size), and to determine how much of this net selection was due to direct selection on the trait, as opposed to indirect selection acting through other correlated traits. Third, he attempted to disentangle the effects of the three mechanisms on net selection by measuring selection during each selection episode within which a particular mechanism was presumed to operate (e.g. mortality during a drought, food competition; male success in obtaining mates, sexual selection). Finally, he measured the heritability of dimorphic traits, as well as the genetic correlations between the sexes for these traits.

Price concluded that sexual dimorphism in *G. fortis* during the period of his study resulted from sexual selection for larger males, and fertility selection for smaller females (because smaller females began breeding at an earlier age). He also noted that selection pressures can act differently on the sexes during different seasons, or in different years.

Future directions for empirical studies

Many questions remain to be answered concerning the evolution of sexual dimorphism. To date, most studies of sexual dimorphism have addressed only one possible mechanism, or have attempted to evaluate the different mechanisms through correlations between the degree of sexual dimorphism in a species and its presumed selection pressures. However, these approaches are limited because competing hypotheses may make similar predictions³⁰.

Moreover, an obvious drawback to these methods, especially the correlational approach, is that they fail to demonstrate whether the mechanism actually results in divergent selection between the sexes. Additional studies like Price's²³ are needed, in which all mechanisms are considered, and the effects of these mechanisms on net selection are measured. Also, because selection pressures may not be constant through time, empirical studies ideally should be carried out over different seasons and years⁷. Finally, even though measures of heritability and genetic correlations are often difficult to obtain, they also may yield some

important information on the potential for the evolution of sexual dimorphism within given populations. Although the precise evolutionary origin of sexual dimorphism in any one species will always remain an enigma, these methods may bring us much closer to understanding the relative importance of different mechanisms for its maintenance.

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