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Comparative Methods

THE ORIGINS OF SEXUAL DIMORPHISM IN BODY SIZE IN UNGULATES

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Jarman (1974) proposed a series of relationships between habitat use, food dispersion, and social behavior and hypothesized a series of evolutionary steps leading to sexual dimorphism in body size through sexual selection in African antelope species.
The hypothesis states that sexual size dimorphism evolved in a three-step process. Initially, ancestral monomorphic and monogamous ungulate species occupying closed habitats radiated into open grassland habitats. Polygynous mating systems then rapidly evolved in response to the aggregation of males and females, perhaps in relation to the clumped distribution of food resources in open habitats. Subsequently, size dimorphism evolved in those species occupying open habitats, but not in species that remained in closed habitats or retained monogamy.

In most mammalian groups males are larger than females.

Explanations for the degree of sexual dimorphism in body mass (SD) fall into three main groups:
1. - sexual selection hypotheses suggest that SD is a consequence of either intrasexual competition for mates, mainly males fighting amongst themselves for mating opportunities with females, or epigamic selection in which females choose among males to get mating partners.
2. - large body mass may facilitate the evolution of SD by making polygyny more likely and thus increasing the intensity of sexual selection between the sexes.
3. - SD arises from natural selection by favoring different optimal size for males and females because they occupy different ecological niches.

Food distribution and anti-predator behavior determine the probability of encounters between individuals in space and time, thus influencing their degree of aggregation. Situations in which species feed on low-density food distributed in patches have been linked to strong intraspecific and intersexual competition for food. This may favor increased feeding divergence and thus increased dimorphism in African antelopes and also in primates. But this competition is not only for food. Aggregation of animals around clumps of food may determine the strategies males use in order to maximize their chances of obtaining mates. These strategies lead to sexual selection for or against sexual dimorphism and affect aspects of a species' ecology; for example, adult sex ratio and differential spatial distribution of the sexes.

In this paper they provide a direct test of Jarman's proposed scenario for the evolution of sexual size dimorphism in ungulates, using a phylogenetic approach that can detect the order and direction of evolutionary change in the key traits of habitat use, mating system, and sexual dimorphism in body size. Three variables were analyzed in this study, namely, the main habitat type occupied by the species, the main type of mating system adopted by the species, and sexual dimorphism in body size within a species. Fossil records and paleoecological evidence reveal that ancestral ungulates occupied closed habitats and were monogamous and monomorphic, they took this as the starting point.

Because the comparative method used requires binomial categories for all variables, they coded the three variables into discrete binomial traits:

1. Habitat type: closed-habitat/open-habitat
2. Mating system: monogamous/ polygynous
3. Body size sexual dimorphism: they measured dimorphism as the simple ratio of male to female body mass, and then they classified species as dimorphic or not based on the size of this ratio for that species.

<u>The Comparative Method</u>

They used Pagel's discrete variables method to test all hypotheses concerning correlated evolution in two binary traits. The method compares two models that are fitted by maximum likelihood to the data and the phylogenetic tree. In the model of independent evolution, two binary characters are allowed to evolve on the tree independently. Each character can adopt two states, 0 or 1; calculating ''forward'' and ''backward'' transitions for each requires four parameters.

They compared the rates of evolution from the joint state of closed-habitat/monogamy to open-habitat/monogamy with the transition from the same ancestral state (closed habitat/monogamy) to the derived state of closed-habitat/polygyny. The comparison of these two parameters identifies which evolutionary route away from the ancestral state is more probable.

They found that extant ungulate species that occupy open habitats tend to have a polygynous mating system and are dimorphic in body mass.

<u>Results</u>

The results are consistent with Jarman's hypothesis. Ancestral monogamous and monomorphic ungulate species from closed habitats first radiated into open habitats where polygyny was favored. These were the first two intermediate stages in the development of size dimorphism as the early polygynous species were still monomorphic. Sexual size dimorphism later evolved in the polygynous but not in the monogamous species. This suggests that larger body mass was favored when males fought over mating access to females.

- there is no evidence that polygyny evolved in closed habitats.
- the rate of evolution from open-habitat/monogamy to openhabitat/ polygyny is greater than that from closed-habitat/monogamy to closed-habitat/ polygyny.
- they find evidence in their data that dimorphism does indeed evolve after the occupation of open habitats.
- if, however, they classify as dimorphic species those in which males are approximately 10% or more larger than females they find that dimorphism evolves following the occupation of open habitats.
- polygyny clearly evolves after open habitats and dimorphism evolves in response to polygyny.
- occupation of open habitats preceded the evolution of size dimorphism.
- ungulates were most probably monomorphic when they first occupied open habitats.
- dimorphism was more likely to evolve in open habitats than in closed habitats.
- dimorphism evolved once ungulates occupied open habitats and then dimorphic and monogamous species became polygynous.