Ecological dimorphisms: An introduction to the symposium

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Synopsis A growing body of literature is devoted to understanding differences between males and females in numerous behavioral, morphological, and physiological variables that do not appear to play a role in sexual or fecundity selection. Despite the increasing attention paid to such ecological dimorphisms, there has thus far been no attempt to consolidate or review studies in this area. This symposium comprises a series of papers that examine ecological dimorphisms from several diverse perspectives, spanning a range of ecological fields from functional morphology to behavior and evolution of life-history. These studies show that gender exerts considerable effects on individual ecology, even outside of the context of reproduction.

Introduction

The origin and maintenance of intraspecific dimorphisms in animals is a central issue in evolutionary biology. Alternative phenotypes in particular, which encompass irreversible environment-specific (polyphenism) and genotype-specific (polymorphism) phenotypes as well as reversible behavioral polyethisms, are striking examples of the diversifying power of selection, and hence of special interest to students of evolution (West-Eberhard 2003). Variation in behavior and ecology within one sex has therefore been well-studied, particularly over the last 30 years (Brockmann 2001). Intraspecific differences between sexes are also well-known, but by far the majority of research on this topic has been concerned with sexual differences in traits related to reproduction in general, and sexual selection in particular (see Andersson (1994) and Shuster and Wade (2003) for reviews).

The emphasis on sexual differences in reproductive ecology is certainly justified given the striking sexual differences in morphology, behavior, and ecology in breeding animals, but has arguably resulted in the relative neglect of equally striking sexual differences in contexts unrelated to reproduction. Indeed, Darwin himself recognized several cases of ecological differentiation between males and females, although he doubted the efficacy of natural selection alone to drive such changes (particularly compared to the apparent strength of sexual selection; Darwin 1871). Although sexual differences in evolutionary ecology were not entirely ignored (e.g., Clutton-Brock et al. 1982), it was not until a century after Darwin's work that the first quantitative population-genetics models describing the evolution of non-sexually selected dimorphisms were proposed (Slatkin 1984). Specifically, Slatkin's models showed that intersexual resource competition could result in sex-specific adaptations to different ecological niches. In a review of the evidence for ecological causes of sexual size dimorphism to date, Shine (1989) reported evidence supporting the notion of ecologically based dimorphisms in feeding ecology in several taxa, but noted that hypotheses of ecological causation are often difficult to test due to the difficulty of unraveling the effects of natural selection and sexual selection.

In recent years, the literature on ecological dimorphisms has grown to encompass areas of ecology beyond feeding morphology. Sexual differences exist, for example, in locomotion (Snell et al. 1988), use of habitat (Ardia and Bildstein 1997) and escape behavior (Irschick et al. 2005), amongst other variables, and across a broad range of animal taxa. Nevertheless, despite the increasing amount of attention paid to ecological sexual differences, little effort has been devoted toward the synthesis of this recent and exciting work. This symposium draws together a diverse group of studies from a range of ecological and biological disciplines, and presents an overview of the current state of research into this exciting topic. Although ecological dimorphisms are known to occur in both vertebrate and invertebrate animals, this symposium focuses on

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vertebrates primarily because thus far most research into ecological dimorphisms has been conducted on vertebrate groups.

Symposium papers

Vincent and Herrel (2007) discuss the functional and ecological factors driving head shape and feeding dimorphisms in squamate reptiles. In addition to reviewing the literature on this subject, the authors also propose and test two hypotheses regarding the evolution of trophic morphology in snakes and lizards, respectively. Lailvaux (2007) presents an overview of sexual differences in locomotor performance in reptiles, and highlights recent studies showing how sex and temperature interact to affect locomotor ability in lizards. The ecological relevance of locomotor-performance dimorphisms are discussed, as are several potentially important directions for future research. Vanhooydonck and Irschick (2007) continue this examination of ecologically relevant sexual differences by presenting comparative data on sexual dimorphism in habitat use and escape behavior in several species of Caribbean *Anolis* lizards. These data point to important sexual differences in escape behavior that cannot be explained by sexual differences in overall body size or habitat use.

Although the focus of this symposium is on ecological variables that differ between sexes, several contributed papers also offer important insights into the origin of intraspecific phenotypic polymorphisms in vertebrates. In the first of these papers, Huyghe et al. (2007) test a number of functional hypotheses regarding the coexistence of three color morphs in both males and females in the European lizard *Podarcis melliselensis*. Although these data ultimately offer little support for the role of natural selection in driving niche divergence among the three morphs, this study represents a rare attempt at rigorous quantification of functional differences between coexisting morphs within a single population. Badyaev (2007) discusses the evolution of intraspecific polymorphisms from a different perspective, that of environmentally induced plasticity in an introduced bird population, and presents a conceptual framework integrating selection with genetic assimilation of environmental inputs. In a similar vein, Young and Badyaev (2007) highlight the potential importance of bone morphogenic proteins (BMPs) in generating evolutionary novelty via the induction of plastic developmental changes in skeletal morphology, and go on to review recent studies demonstrating the likely role of BMPs in phenotypic evolution.

At the other end of the scale from the origins of sexual differences, existing sexual dimorphisms in body size can also affect other aspects of male and female ecology. The even-toed ungulates are a prime example of this process, and Ruckstuhl (2007) provides a comprehensive overview of the potential proximate and ultimate causes of sexual segregation in this group, and establishes a useful comparative framework for future tests of hypotheses relating to sexual segregation. Sexual size dimorphism is also the subject of the study by John-Alder et al. (2007), who review recent empirical studies addressing the role of testosterone and other factors in directing growth rates and the expression of size differences in several lizard species. Butler (2007) focuses on intraspecific sexual size dimorphisms within adaptive radiations, specifically Caribbean anoles, and uses novel statistical techniques to show that male and female ecomorphs vary in morphology even within the relatively strict confines of ecomorphological niches. Finally, Scales and Butler (2007) return to the topic of sexual differences in locomotion in a detailed study of force and power output during burst acceleration in gravid green iguanas. This study shows that gravid females are able to compensate for the physical or physiological effects of gravidity and maintain performance levels similar to non-gravid females, although the mechanism responsible for this compensation is not apparent.

Conclusions

The variety in subject matter and approach in this collection of papers illustrates how far the understanding of ecological dimorphisms has advanced since Slatkin's (1984) formal elucidation over 20 years ago of the population-genetic processes entailed in intersexual diversification. Indeed, even a casual perusal of the presented papers suggests that ecological dimorphisms are both common and ecologically relevant, and are likely to have important implications for the understanding of sex-specific fitness in nature. Nonetheless, the number of researchers actively working on gender differences exclusive of reproductive contexts is still relatively small. It is hoped that this collection of papers will stimulate further discussion as to the causes and potential consequences of ecological dimorphisms in nature, not only in vertebrates, but in all animal taxa.

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