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Ornamentation

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Definition

A trait used to attract the opposite sex during mate choice.

Introduction

Many animals exhibit conspicuous characteristics such as brightly colored body regions or exaggerated physical structures. When these traits function during mate choice to increase the likelihood of their bearer attracting a mate, they are referred to as ornaments. The quintessential example of an ornament is the peacock's tail: consisting of bright colors and patterns, and enlarged far beyond the relatively small tails of peahens, peacocks' tails are presented to females during mating displays. Peahens then accept or reject a male based in part on his tail characteristics (Petrie et al. 1991). Ornaments are often sexually dimorphic, with one sex ornamented and the other not, but mutual ornamentation is also observed (Andersson 1994).

Ornamentation is linked to reproductive success, with individuals that display more elaborate ornaments enjoying a selective advantage.

Ornamentations are therefore defined not based on appearance but on function, and conspicuous traits are only considered ornaments when they have been shown to influence mate choice. The term ornamentation has generally been used to refer to visual characteristics such as colorful or elaborated body regions, and some authors explicitly define ornamentation as a morphological trait. However, other types of ornaments have also been reported, such as those that involve smell, vocalizations, or electric pulses, and ornaments can also be multimodal (e.g., both visual and acoustic). This entry therefore defines ornaments as any traits that are used to attract the opposite sex during mate choice.

Sexual Selection Dynamics

The extraordinary appearance of conspicuous traits such as the peacock's tail puzzled early biologists because such traits would seemingly make their bearer more vulnerable to predators. To explain the evolution of these ostentatious characteristics, Charles Darwin (1871) developed the theory of sexual selection, which posits that such traits can evolve when they increase individuals' reproductive success. Darwin separated sexually selected traits into two categories based on their function: armaments – such as large antlers or canines – facilitate competition with same-sex individuals for access to mating opportunities (via ▶ Intrasexual Selection, this volume), and

ornaments aid in attracting mates of the opposite sex (via ▶ Intersexual Selection, this volume). Ornamentation therefore results from a competitive regime in which mating decisions are influenced by characteristics of the opposite sex. Individuals with more impressive characteristics will be chosen more often and will therefore enjoy higher reproductive success, leading to an exaggeration of these traits over evolutionary time. Thus, the peacock's tail becomes more elaborate over time because this is linked to higher fitness. While ornaments by definition result from mate choice, it is important to note that intrasexual competition and intersexual mate choice can both support and oppose one another; therefore, a trait can be influenced by both selective processes simultaneously.

Many species are sexually dimorphic, with differential expression of traits like degree of ornamentation between sexes (Andersson 1994). Sexual selection acts on both sexes; however, the strength of selection is dependent upon which sex is the limiting resource in reproduction (see ▶ "Parental Investment", this volume). In many animals, females invest more in offspring and therefore tend to also be choosier in selecting mates. This generates a competitive regime in which males often compete for access to females and are therefore subject to stronger intersexual selection for attractiveness to potential mates. This results in males that are more ornamented relative to females. In ▶ sex role reversed species (this volume) in which females tend to compete for access to males, this trend reverses and females are the more ornamented sex (Andersson 1994). This tendency for differential ornamentation is relative, however, and research is increasingly showing that there is scope for male choosiness and female ornamentation across species (Clutton-Brock 2007).

Selective Advantages and the Evolution of Ornaments

Why are ornaments attractive to members of the opposite sex? The selective advantage and evolution of ornamentation has been a hotly debated and researched topic in evolutionary biology since Darwin's time, and several hypotheses have been presented on the topic (reviewed by Andersson and Simmons 2006).

Some hypotheses are based on nonadaptive mate choice and posit that the expression of ornaments is not linked to any adaptive trait in the individuals expressing them. Rather, they are meaningful only in a mating context. For instance, the sensory bias hypothesis (Ryan 1998) suggests that ornaments evolve because they exploit sensory-response systems in other behavioral domains, such as foraging. A species that forages on red fruit, for example, may have evolved a preference for red, and a red ornament could "piggy back" on this preference. Another commonly cited hypothesis is ▶ runaway selection (this volume), which predicts that ornaments evolve when an originally adaptive trait and a related mating preference are exaggerated via a self-reinforcing positive feedback loop. The mating preference (often considered to arise from a sensory bias) is initially selected for because it leads to offspring that tend to have more adaptive trait values. The runaway process then takes over, with the ornament and the mating preference both increasing proportionally, and often becoming genetically linked such that they are inherited together. Because each yields a mating benefit (i.e., attracting mates via the ornament or producing offspring with ornaments that are attractive to mates), both remain under positive selection. In this way, the ornament becomes far more exaggerated than would be adaptive in a nonmating context. At some point, the costs of the ornament match any mating benefits, and the trait and preference stabilize. Runaway selection models are difficult to test empirically, but remain good candidates for the evolution of particularly elaborate ornaments.

Other hypotheses for the evolution of ornamentation focus on mate choice associated with adaptive traits. Closely tied to research involving signal honesty, these hypotheses focus on ornaments as signals of individual quality, with more elaborate ornaments indicating a higher quality mate. The underlying quality that is signaled can be of varying types. For instance, more elaborate

ornaments may be associated with mates that provide direct benefits to the chooser, such as access to a high quality territory or absence of transmissible disease. Alternatively, the ▶ good genes hypothesis (this volume) suggests that ornaments evolve because they are associated with advantageous characteristics that are heritable (i.e., indirect benefits), such as good foraging skills or a strong immune system. The good genes hypothesis has been of particular interest to biologists because many species lack bi-parental investment, and therefore genetic contributions to offspring are often the only adaptive explanations for ornamentation. However, this hypothesis is theoretically problematic because mate choice based on a heritable trait should reduce associated genetic variability across generations (i.e., because many individuals are choosing the same mates), which would in turn lead to reduced selection on mating preferences. This contradiction is known as the lek paradox (Kirkpatrick and Ryan 1991). Many solutions to the lek paradox have been proposed, which mostly involve identifying mechanisms that can maintain variability in the face of mate choice and positive selection. These include solutions based on environmental change, mutation rates, and parasite co-evolution. A popular model is the genetic capture model (Rowe and Houle 1996), which suggests that ornaments linked to individual condition are influenced by many genetic loci, and this large target for selection helps to maintain variability. Alternatively, trade-offs between selective pressures may maintain trait variability, such as opposing selective pressure from natural and sexual selection, or when a trait is beneficial for one sex but detrimental to the other. New work analyzing the genetic underpinnings of ornaments has helped to further clarify the ways in which trait variability can be maintained in the face of mating preferences (e.g., Johnston et al. 2013).

It is important to note that many proposed hypotheses for the evolution of ornamentation are not mutually exclusive. Different explanations are often supported by different biological systems, and given the diversity of ornaments observed in nature, it seems likely that they have evolved via a variety of mechanisms across the animal kingdom.

Signal Honesty and the Costs of Ornamentation

A major question associated with adaptive explanations for ornament evolution is that of signal honesty (▶ "Honest Signaling", this volume). Many ornaments are condition dependent, with the strength of the ornament associated with individual quality, such that the ornament can be used as a proxy for individual characteristics (Andersson 1994). So what prevents cheaters from engaging in false advertising? In some cases, a signal is directly linked to some physical characteristic that cannot be faked; such signals are referred to as indices. For example, the tones of some acoustic calls are inherently linked to body size. Not all signals follow this pattern, however, so other explanations must be sought. Much of the research in this area has focused on ornaments as "handicaps," which are costly to maintain and therefore more elaborate versions can only be produced by individuals in good condition. Emphasis is often placed on the physiological (e.g., energetic) costs of ornamentation, and from this perspective a particularly elaborate ornament can only be produced by an individual who has characteristics like strong foraging skills or a good immune system (▶ "Handicap Hypothesis", this volume). However, the overall costs associated with producing an ornament are not actually very relevant to the maintenance of signal honesty, and the handicap hypothesis is neither necessary nor sufficient to explain many ornaments (Számadó 2011). Instead of focusing on the costs to each individual of producing their own signal, it is more useful to assess the cost differentials in ornament production. Honest signaling can be maintained when low quality individuals face higher costs to producing high quality ornaments compared to high quality individuals. Punishment of cheaters (e.g., via physical attack) is one such mechanism, although many others have been proposed (Számadó 2011). Ultimately, ornament quality is influenced by a variety of

costs and benefits, not all of which are the same for all individuals within a species; in many cases, this can lead to an honest system where ornaments are generally indicative of some underlying individual quality.

Conclusion

Ornaments are often conspicuous traits that would seemingly be costly in terms of avoiding predators, and as such have been of interest to biologists since the origin of evolutionary thinking. Indeed, such characteristics helped to provide the impetus for Darwin to develop his theory of sexual selection. Much of the research on ornamentation has focused on identifying ornaments across species via mate choice experiments, isolating the mechanisms by which ornaments can evolve, and identifying if and how ornaments can function as honest indicators of individual quality. In studying ornaments, biologists have learned about the nature of evolution and have helped to explain the existence of some of the most impressive phenotypes in the animal kingdom.

Cross-References

▶ Charles Darwin
▶ Female Choice
▶ Good Gene Hypothesis
▶ Handicap Hypothesis
▶ Honest Signaling
▶ Intersexual Selection
▶ Secondary Sex Characteristics
▶ Sexual Attraction
▶ Sexual Selection

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