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## Secondary Sexual Characteristics

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### Synonyms

[Epigamic traits](#); [Secondary sex characteristics](#); [Secondary sex traits](#); [Secondary sexual characters](#)

### Definition

A secondary sexual characteristic is defined as a sex-specific trait that appears at the onset of sexual maturity and plays a role in sexual selection but is not directly involved in, or essential for, the act of reproduction (Darwin 1871).

### Introduction

In the animal kingdom, an extraordinary diversity of structures exists that cannot be explained by natural selection (Darwin 1871). Consider, for instance, the elaborate antlers in a male deer (Fig. 1a; family Cervidae; Emlen 2008) or the

wonderfully extravagant feathers of the peacock (Fig. 1b; *Pavo cristatus*; Petrie et al., 1991). These remarkable structures, referred to as secondary sexual characteristics, are most commonly observed in males and are thought to have evolved by means of sexual selection (Andersson 1994). These sexual characteristics may be energetically costly to produce and maintain and may be conspicuous, potentially subjecting the bearer to an increased risk of predation (Andersson 1994). Moreover, the use of such structures as advanced “weaponry” during combat with rival males while striving for the attention of females can lead to injury or, in extreme cases, even death (Miller 2013). This raises the question: if these characteristics are so costly, why have they evolved in the first place? In *The Descent of Man, and Selection in Relation to Sex* (1871), Charles Darwin laid the foundation for the two main theories on sexual selection that still persist to this day:

*There are many other structures and instincts which must have been developed through sexual selection - such as the weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals - their courage and pugnacity - their ornaments of many kinds - their organs for producing vocal or instrumental music - and their glands for emitting odours; most of these latter structures serving only to allure or excite the female. (1st Edition, volume 1, p.p. 257–258)*

In this seminal book, Darwin posits that secondary sexual characters may evolve either as “weapons” that enhance a male’s competitive ability in male-to-male competition for access to

females or as “ornaments” that enhance a male’s attractiveness to females (Fig. 1a–d).

### The Evolution of Sexual Characters as Weapons by Means of Male-Male Competition

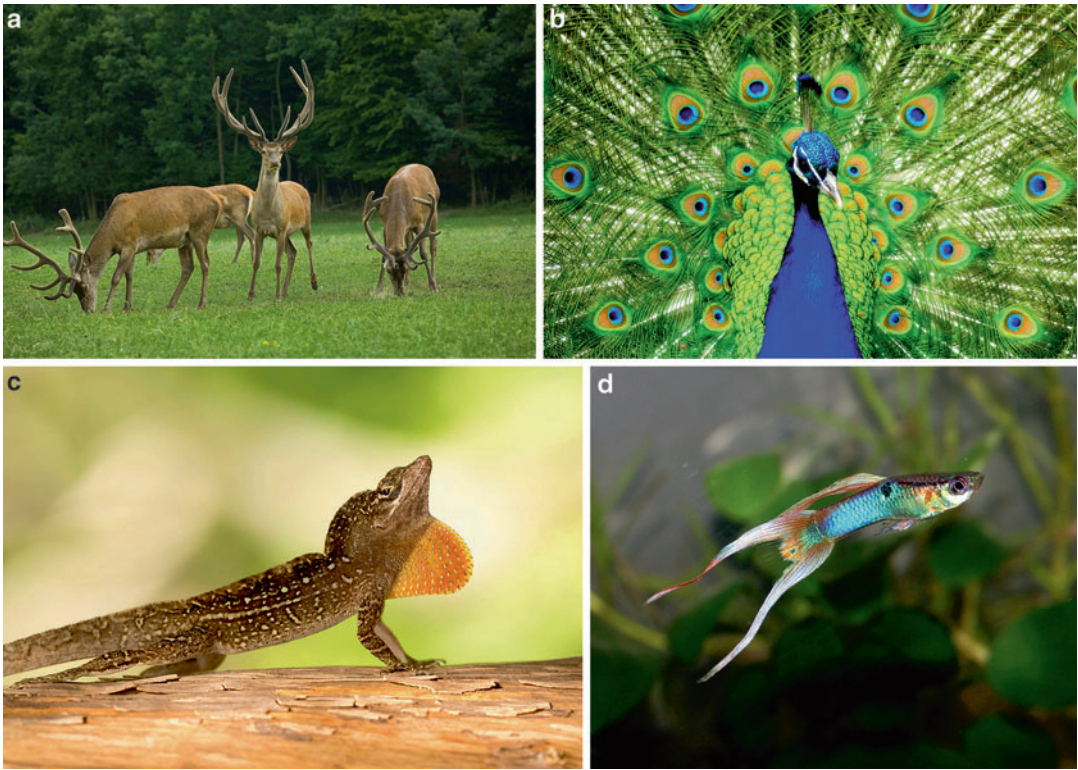
In many species male-male competition is known to play a pivotal role during sexual selection. It is generally accepted that male-male competition can drive the evolution of secondary sexual characteristics by improving a male’s success in competition for mates with rival males (Darwin 1871; Miller 2013). Secondary characters involved in male-male competition can include songs, colors, ornaments, as well as characters involved in direct combat. In systems where males engage in fierce struggles for access to females, traits that enhance a male’s competitive success (either directly by overpowering rivals with weapons during combat or indirectly by deterring rivals with powerful songs or impressive displays) will also directly increase their chance of reproduction. Here, secondary sexual characteristics convey a clear fitness advantage, because the male with the most impressive song or most advanced weapon will chase away its rival and get the chance to mate with the female and produce offspring (Miller 2013). Theory predicts that such sexually selected characters will evolve when the benefits of increased reproductive success outweigh the potential costs of producing and maintaining such structures, and an increasing body of literature on this topic indicates that male-male competition is indeed responsible for the striking diversity of weapons (i.e., antlers, horns, and tusks; Fig. 1a) in the animal kingdom (Emlen 2008; Miller 2013; Panhuis and Wilkinson 1999).

### The Evolution of Secondary Sexual Characteristics as Ornaments by Means of Female Choice

Secondary sexual ornaments can also be selected because they facilitate female mate choice (Andersson 1994). If females show a preference

for a particular male character, then males having that character will have a greater fitness. Male ornaments are thought to have evolved in a variety of animal species, but the most famous examples come from birds, for instance, the extravagant plumage of male birds-of-paradise (family Paradisaeidae), the long tails of long-tailed widowbirds (*Euplectes progne*; Andersson 1982), and, of course, the ornamented tail of peacocks (Petrie et al. 1991). There are two main hypotheses explaining the evolution of male ornaments by female choice:

- (i) Fisher’s (1930) runaway model of sexual selection (also known as Fisher’s “sexy son” hypothesis) proposes a correlation between the expression of a male trait (ornament) and female preference for that ornament. Such genetic correlations between ornament and preference arise when females with a preference for a particular ornament mate with males that have that ornament, leading to the production of offspring that have both the genes for the ornament from the father and genes for the preference of the ornament from the mother (Fisher 1930). Fisher argued that, initially, a “primitive form” of the male trait might have evolved because it was favored by natural selection and that it subsequently evolved into an exaggerated ornament via a self-reinforcing runaway process of trait elaboration (while females simultaneously evolved an enhanced preference for that ornament) that continues until the fitness costs (e.g., reduced survival) of having that ornament outweighs the fitness benefit of increased reproductive success. Houde and Endler (1990) tested this hypothesis in natural populations of the Trinidadian guppy (*Poecilia reticulata*) that varied in the amount of orange coloration on males. They showed that in populations where males had a more pronounced orange coloration, the females also had a stronger preference for this trait, suggesting a genetic correlation between the male trait and female preference consistent with Fisher’s hypothesis (Houde and Endler 1990).



**Secondary Sexual Characteristics, Fig. 1** Photographs showing secondary sexual characters: (a) a male red deer (*Cervus elaphus*) showing off its antlers (Source: Wageningen University), (b) a peacock (*Pavo cristatus*) presenting its extravagant tail (Source: Wageningen

University), (c) a male brown anole lizard (*Anolis sagrei*) displaying its dewlap (Photo: Thijs van den Burg), and (d) a male guppy (*Poecilia reticulata*) with beautiful body coloration and ornamental fins (Photo: Leo van der Meer)

(ii) Zahavi's (1975) "handicap" hypothesis (also referred to as the "good genes" or "condition-dependent indicator" hypothesis) proposes that females choose males with exaggerated ornaments, because these represent a reliable indicator of the male's genetic quality. The presence of a large elaborate ornament is costly and can severely impair a male's chance of survival. The ability to survive despite bearing such a costly feature (or "handicap") provides an honest signal of the condition of the male and, hence, the overall fitness of the male's genotype (Zahavi 1975). Females that mate with males that have exaggerated ornaments will thus produce offspring with a higher fitness, because they pass these "good male genes" on to their offspring. One of the most famous

examples is the extraordinary tail of the male peafowl (*P. cristatus*). A study by Petrie et al. (1991) on a peafowl population from England shows that the number of eyespots of a peacock predicted its mating success, i.e., more eyespots significantly led to more matings. This increased mating success was attributed to female choice (rather than male-male competition), because females always chose from more than one male. Furthermore, offspring sired by males with more eyespots survived better, which supports the "good genes" theory (Petrie et al. 1991). Another classic study was done by Andersson (1982) on long-tailed widowbirds. Male widowbirds can have remarkably long tails: up to half a meter. Andersson experimentally modified the

length of the tail: elongating the tail of some males and shortening it in others. Males with elongated tails attracted significantly more females than males with shortened tails (Andersson 1982). Moreover, males with shortened tails performed better at flying and, hence, presumably were better at escaping from predators, indicating that long tails represent a handicap to males (Andersson 1982). This suggests that female choice can lead to the evolution of costly male traits.

## Conclusion

There are two main hypotheses explaining the evolution of secondary sexual characters by sexual selection. The first states that these characters have evolved as “weapons” to improve a male’s success in combat with rival males. The second hypothesis states that these characters have evolved as attractive “ornaments” by means of female’s choice.

## Cross-References

- ▶ [Cryptic Female Choice](#)
- ▶ [Lekking](#)
- ▶ [Multiple Matings](#)

- ▶ [Sneak Copulation](#)
- ▶ [Sperm Competition](#)
- ▶ [Vocal Competition](#)

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