

Explain how courtship displays evolve and why are they often more exaggerated in males?

Introduction

Courtship displays are behaviours of animals, which in addition often comprise of morphological traits, that evolve under sexual selection in order to attract the opposite sex to mate with them, most commonly in the case of males attracting females. Before analysing in detail how they evolve and why they are often more exaggerated in males, it is important to have a base knowledge of the concepts of sexual selection. This form of selection was first proposed by Charles Darwin in his book *The Descent of Man, and Selection in Relation to Sex* whereby he defined it by stating it is dependent on the “*advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction*” (Darwin, 1871). This has been elaborated on such that it is generally agreed upon that sexual selection can be thought of as arising from differences in reproductive success caused by competition for mate access or fertilisation opportunities (Jones & Ratterman, 2009). The way in which sexual selection acts on organisms can essentially be split into two classes. Firstly, “the law of battle” (Darwin, 1871), whereby males interact with each other competitively to gain access to female mating resulting in the evolution of traits that increase their success in direct combats. Secondly, “female choice”, whereby females show a preference in males with certain traits unrelated to direct combat, and males with such preferred traits will mate with the most females and produce the most offspring thereby deeming them more fit (Davies, Krebs & West, 2012). This essay will assess the evolutionary mechanisms that have led to the development of courtship displays in the animal kingdom, before looking at why they are generally speaking more exaggerated in males.

How do courtship displays evolve?

As briefly discussed previously, courtship displays evolve due to how sexual selection acts on the courtship trait at hand, therefore the mechanisms of this form of selection must be appreciated. Trivers first touched upon the theory of sexual selection with regard to anisogamy and how the distinct sex roles evolve. This is when two gametes from a male and female fuse, each one of different size. Because of their vast difference in size, males produce many more sex gametes. This is thought to have evolved from unicellular isogamous reproduction where the two gametes that fuse are of the same size. As the size of the gametes increase, their survival rates also do. However, this exists in a trade-off because as the size increases they require more energy to produce therefore meaning that a fewer number can be made by the parent cell. The lower abundance means that fusion events would be more rare than otherwise and thus leads to the evolution of cheaters. In this case, these are organisms that produce a large number of much smaller gametes. Even though the survival rate of the individual gametes is lower than larger gametes, the much higher chance of fertilisation outweighs the cost (Scharer, Rowe & Arnqvist, 2012). This process is the main hypothesis as to why directional selection has led to the development of dimorphic gametes in most eukaryotes.

Perhaps the most relevant area of research concerning the action of sexual selection and how it acts to produce courtship displays is with regard to female

choice, given that this is the underlying process that triggers the selective pressure. Female preference arises when the male traits have evolved to either provide direct or indirect benefits. Direct benefits include attributes such as increased ability of territory defence, nuptial gifts or extra parental care (*Jones & Ratterman, 2009*). It is relatively simple to understand why a female might prefer these traits in males seeing as they provide direct fitness benefits. This will lead to assortative mating whereby the males that provide the most benefits will mate the most. Although this provides an obvious suggestion for why female choice has evolved with regard to direct benefits, it does not touch upon indirect benefits provided by males, which might take the form of courtship displays. This is of interest seeing as female choice has evolved in species where it appears that the males that are chosen preferentially provide no obvious direct benefits (*Andersson & Simmons, 2006*).

In order to describe how these indirect benefits might work, models have been created to bring light to how they might prevail and lead to the evolution of courtship displays. Fisher provided the first model whereby he stated that a preferred trait by a female is weakly correlated with fitness and thus the preference and the trait coevolves resulting in an extreme version of both. Theory then predicts that a runaway process then occurs, as the male trait cannot reach an equilibrium as sexual selection driven by the female preference will accelerate more rapidly than the trait can evolve (*Kirkpatrick & Ryan, 1991*). A second model includes, for example, the 'indicator' or 'good genes' model. This suggests that the magnitude of the trait observed in the male is an honest indicator of the male's overall fitness (*Jones & Ratterman, 2009*).

As well as these direct and indirect benefits, it is also possible that certain courtship displays evolve in males without having direct benefits or indicating indirect benefits. For example, it has been suggested that some male morphologies or behaviours have evolved traits by exploiting a female's sensory bias leading to a predisposition of preferential choice without providing any actual benefits. Despite suggestions of such models, it seems that the main support for the evolution of courtship displays with regard to female choice are in the two models described above (*Jones & Ratterman, 2009*). These models will now be assessed in more detail.

The Fisherian model describes how assortative mating takes place due to female preference and male traits that weakly correlate with fitness (*Arnqvist & Rowe, 2005*). In this model, on an evolutionary timescale the female offspring will show a stronger preference for the particular trait and the trait will become exaggerated. In this scenario, at first, the initial offspring will have a slight advantage because of the correlation between the trait and fitness. Due to its slightly higher fitness relative to the population mean, he will be the preferred choice of mating by females. Over time, this will lead to an exaggeration of both the trait and the preference. However, the advantage is not actually being provided by the correlation, but instead, by nature, the males that exhibit the trait are more likely to mate because they dominate the population. This means that the significant advantage that is actually being provided is the higher mating success that the males with said traits have, rather than any other mechanism of higher fitness. It is fairly easy to understand, therefore, how this results in a form of self-reinforcing coevolution (*Kirkpatrick & Ryan, 1991*).

This model is somewhat reliant on the fact that in each generation the female preference and the male trait, or courtship display, have covariance such that assortative mating can occur leading to directional selection. The exaggeration of the trait and preference might be 'checked' by natural selection if the trait cost becomes too large. Therefore the magnitude of the trait will depend on the individual species and the trade-off that exists within it between survival and reproductive rates. This Fisherian model provides explanation as to how courtship displays might escalate on an evolutionary timescale.

The second model is different in the way that it suggests how female preference might evolve in the first place and then how the trait develops over time. As mentioned, this 'good genes' model states that the courtship display is an honest indicator of the male's fitness. Therefore, female choice will evolve such that they have a preference for extreme versions of the display at hand. This can be seen in examples of secondary sexual characteristics such as the tail-length in long-tailed widowbirds (*Andersson, 1982*). This model relies on hypotheses that support honest signals such as 'the handicap principle', which suggests that some signals may be too costly for individuals to fake and therefore cannot be dishonest (*Zahavi, 1975*). In the case of courtship displays (whether morphological or behavioural), they will be tightly correlated with cost and thus the ability to express such displays acts as an indicator of high fitness.

These two models seem to provide strong support for why sexual selection, especially through female choice, acts to produce male traits in the form of courtship displays.

Why are courtship displays often more exaggerated in males?

As previously discussed, natural selection has led to dimorphic sex alleles in many eukaryotic species – a trait common across the animal kingdom. This has significant consequences on the limitations and mechanisms of sexual reproduction. Females need access to a relatively large amount of resources to produce few gametes, their upper limit of reproduction is determined by resource availability. Conversely, the upper limit of male reproduction is determined by their access to females. This entire concept was strongly supported by Bateman when he performed experiments with *Drosophila* showing strong male-male competition for access to females (*Bateman, 1942*).

It is these limitations that result in the biological consequences associated with male competition for access to mates. Specifically with regard to courtship displays, the dimorphic gametes play an important role in intersexual selection, leading to courtship ritual evolution in males as they try and increase their preference for females.

Conclusion

Courtship displays ultimately evolve under strong sexual selection, especially with regard mate preferences and how the courtship traits might either produce direct or indirect benefits. Due to the dimorphic nature of the sex gametes in the animal

kingdom, it is the case that courtship displays evolve much more commonly in males and they compete for access to mate with females.

References

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