

Exaggerated Traits and Breeding Success in Widowbirds: A Case of Sexual Selection and Evolution

by

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Part I— Introduction

Natural selection is the evolutionary force that shapes the traits of a species in response to the various demands of its environment. Any process or event during the life of an organism that influences the number and/or quality of offspring produced by an organism due to a *heritable* trait(s) of that organism can act as a selective force. Selective forces can be produced by either the biotic or abiotic components of an organism's environment. Hence, natural selection is manifest as not a singular action, but rather as many different events occurring over the life of an organism. In this case study, the different and potentially conflicting manifestations of natural selection will be explored and studied.

The Study Species

Widowbirds are small, finch-like birds in the genus *Euplectes*. They are striking members of the bird community in grasslands and shrubby savannas of southern and eastern Africa. This group is noted for the pronounced *sexual dimorphism* between males and females. During the *non-breeding season*, both male and female widowbirds have a brownish or buff coloration that blends with the grass and other vegetation. During the *breeding season*, however, males molt and produce black feathers on most of their body. Males also produce characteristic bright red and/or yellow epaulets and chevrons on their wings. Additionally, males of several widowbird species grow elaborately long tail feathers that can be up to half a meter in length (see Figures 1 and 2).

During the breeding season, males secure and defend a territory from other males where they then build multiple nest frames. Males then perform a flight display that has a “bouncy rowing” appearance with loops and exaggerated wing beats to attract females to their territory. Females choose a male for breeding, line a nest frame in his territory with fine grass, and then incubate the eggs and feed the nestlings in that frame. After the breeding season, males molt to return to their pre-breeding coloration and appearance. Beyond initially building the nest frame, males do not participate further in raising their offspring.



Figure 1. Long-tailed widowbirds showing breeding and non-breeding plumage. (Long-Tailed Whydah, 1899. Chromolithograph after Frederick William Frohawk, printed by Brumby & Clark Ltd. in Hull and published in Frohawk's *Foreign Finches in Captivity*, 1899. Image courtesy of ancestryimages.com.)

These elaborate behaviors and the striking seasonal sexual dimorphism in male widowbirds have provided researchers with an intriguing system in which to study how natural selection can shape traits of a species.

Sexual Selection

The bright breeding coloration and long tails produced by male widowbirds are thought to be adaptations to attract the attention of female widowbirds. Reproductive systems in which individuals differentiate among potential mates and choose one based upon some characteristic(s) is a form of natural selection called *sexual selection*. The fundamental idea of sexual selection is that choosing the best mate increases the probability of producing high quality offspring who will pass on the parental genes to the next generation. *Intrasexual selection* occurs when members of one sex compete with one another for the opportunity to mate with members of the opposite sex or through actively securing and protecting a territory and its resources. *Intersexual selection*, frequently referred to as *female choice*, occurs when females choose among males based upon some criterion reflecting resources the male can provide or the quality of his genes.



Figure 2. Male long-tailed widowbird during courtship display flight. (Photograph ©Callie de Wet/Wild Images.)

Concept Check

1. Evolution of reproductive characters and behaviors in long-tailed widowbirds has been shaped by natural selection. Develop hypotheses that could be used to test how intrasexual and intersexual selection could be shaping the evolution of traits in male long-tailed widowbirds.
 - a. Hypotheses of intrasexual selection:
 - b. Hypotheses of intersexual selection:
2. Explain the reasoning behind these hypotheses. How would natural selection be acting in them?

Part II—Truth In Advertising

An important part of sexual selection in general and for long-tailed widowbirds in particular is that males need to signal their quality as a potential mate to the females.

Concept Check

3. What are some of the possible signals of male quality in widowbirds and what information might they convey? What are the females choosing and why?
4. Develop an experiment that could be used to test the effectiveness of these signals in regards to the hypotheses of intrasexual and intersexual selection your group described previously.
5. While the signals given by males can indicate their quality, could they also be detrimental to the males? How?

Part III—The Handicap Hypothesis

One idea that has been developed to explain the evolution of elaborate characteristics in males is called the *handicap hypothesis*. The handicap hypothesis proposes that females can assess the quality of a male by his ability to survive despite having a trait that could potentially be detrimental to his health. For example, exaggerated traits such as large horns on rams could be a hindrance to walking through thick brush or inhibit their ability to elude a predator. Similarly, while bright coloration indicates good health, it also increases visibility to predators. Widowbirds, particularly those that produce long tails, present excellent systems for evaluating the handicap hypothesis in sexual selection. As you consider the following studies, think about how they relate to the handicap hypothesis.

Researchers have conducted several studies to investigate the influence of coloration and tail length in widowbird mate choice and reproduction. Results of several experiments are described below.

Epaulet Coloration Study

In a study of the red-collared widowbird (*Euplectes ardens*), researchers compared the brightness of the red epaulet among different males. They found that males with nesting territories tended to have redder epaulets than males without nesting territories. Among males with nesting territories, there was no significant relationship between the number of active nests (nest with a female and eggs) and the redness of the epaulets.

Concept Check

6. How do you interpret the results of the epaulet coloration study in terms of sexual selection?

Tail Length Study

In an initial field study, researchers compared the number of active nests and date of the first egg production in a nest among males with different tail lengths. Results of the study are given in Figures 3 and 4 on the next page.

Concept Check

7. What is the hypothesis being tested in this study?
8. Explain how the results either support or counter this hypothesis.

Figure 3. Number of active nests for males with different tail lengths ($y = 0.038x - 4.84$; $F_{1,40} = 17.3$, $r^2 = 47.4\%$, $p < 0.001$). Data based on Pryke et al. 2001.

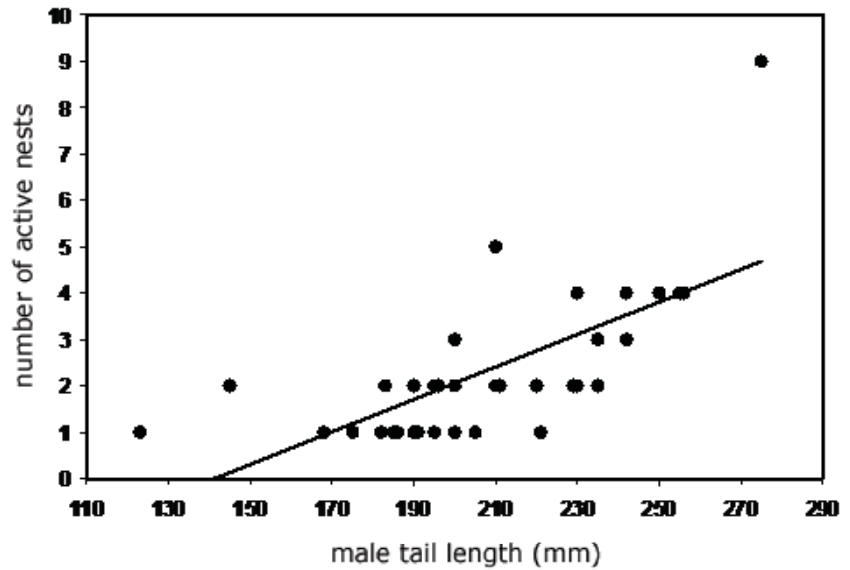
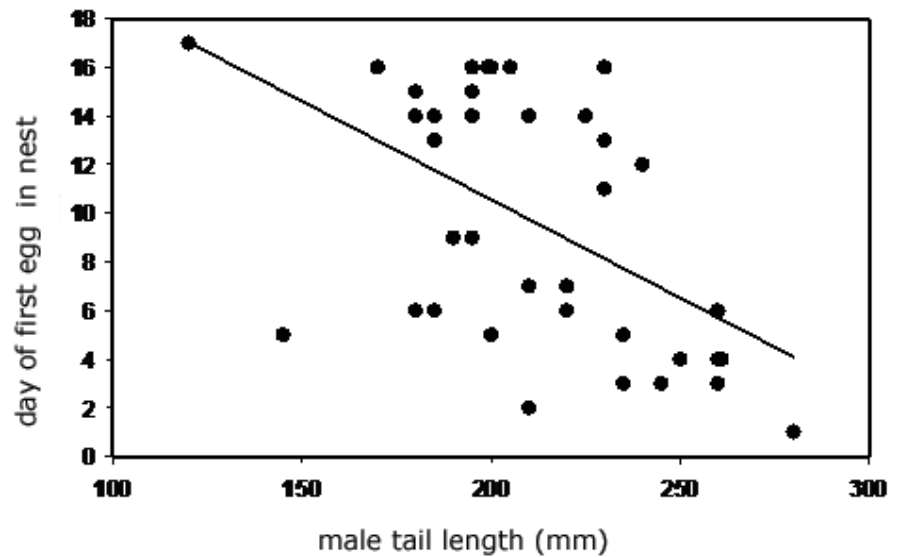


Figure 4. Date of first egg laid in the nest for males with different tail lengths. ($y = -0.085x + 27.32$, $F_{1,40} = 9.3$, $r^2 = 30.0\%$, $p = 0.0003$) Data based on Pryke et al. 2001.



Tail Length Manipulations

In a different study, researchers studied the long-tailed widowbird (*Euplectes progne*). They started by counting the number of active nests among four groups of nine male birds with similar tail lengths (Figure 5). Next, researchers manipulated the four groups of males as follows:

- Group 1—tails shortened
- Group 2—tails uncut
- Group 3—tails cut and re-glued onto the male, length unchanged
- Group 4—tails elongated by gluing on the length cut from Group 1 males

The number of new active nests in the territories of males in the four groups after treatment is given in Figure 6.

Figure 5. Mean number of active nests (\pm standard error) for nine males in four different treatment groups before tail length manipulation. There are no significant differences in mean number of nests among groups. Data based on Andersson 1982.

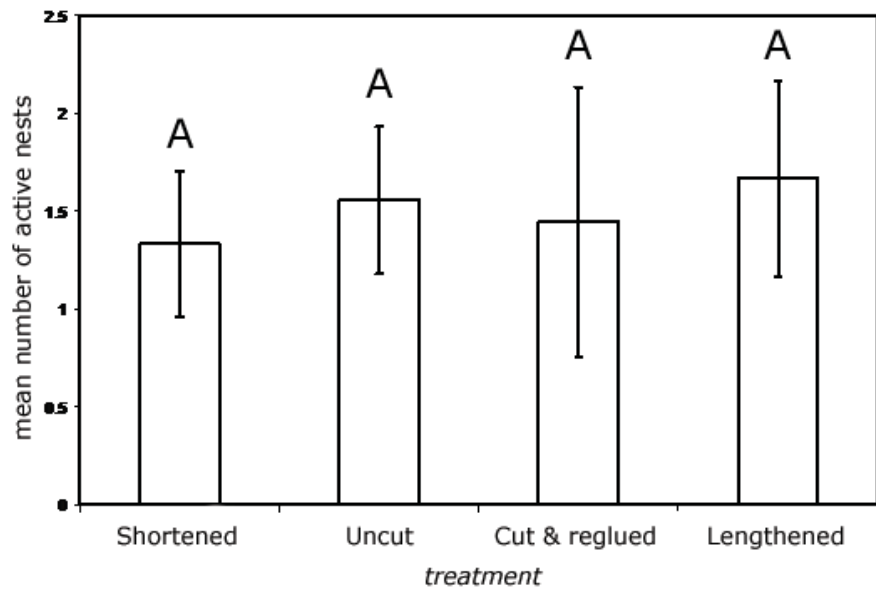
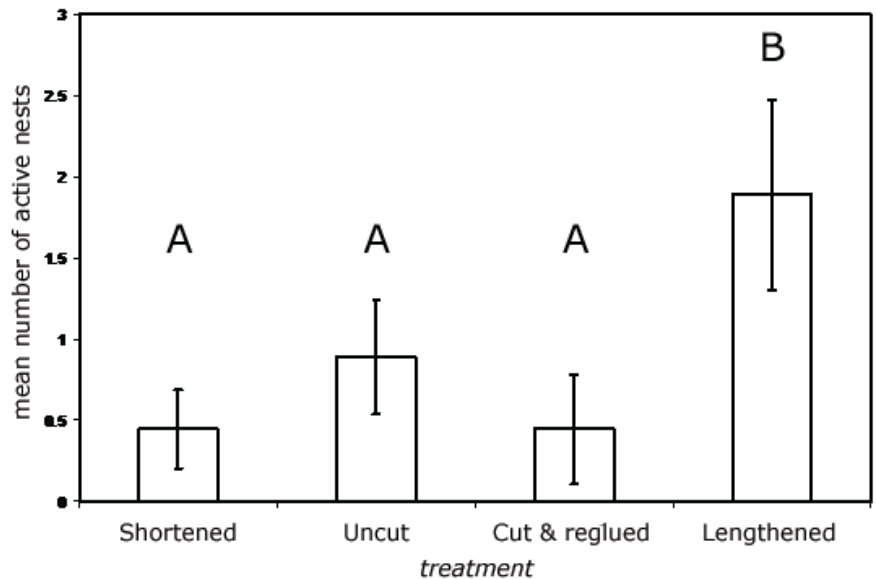


Figure 6. Mean number of new nests (\pm standard error) for nine males in four different treatment groups after tail length manipulation. Groups with different letters above them are significantly different from one another ($p < 0.05$). Data based on Andersson 1982.



Concept Check

9. How do you interpret the results of this experiment in terms of sexual selection?
10. What was the purpose of Groups 2 and 3 in this experiment?
11. Nothing in biology comes without a cost. Describe an experiment you could conduct to follow-up on the results of the tail length manipulation experiment to explore the potential costs of longer tail length in males. Do you think there is any evidence that natural selection has acted on the potential costs of long tails already?

Part IV—Longer Tails in a Short-Tailed Species

Having conducted the studies described above in two long-tailed species, the researchers conducted a similar tail manipulation experiment in a closely related species, the red-shouldered widowbird (*Euplectes axillaris*). Although males in this species have distinctive breeding plumage colors, they do not produce a long tail. Data from this experiment are given in Figures 7 and 8.

Figure 7. Number of males with different tail lengths in a population of red-collared widowbirds. Data based on Pryke and Andersson 2002.

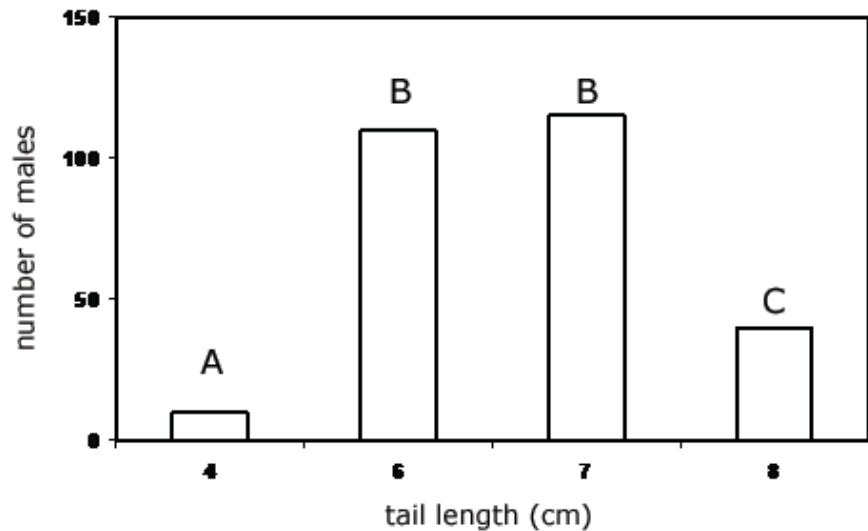
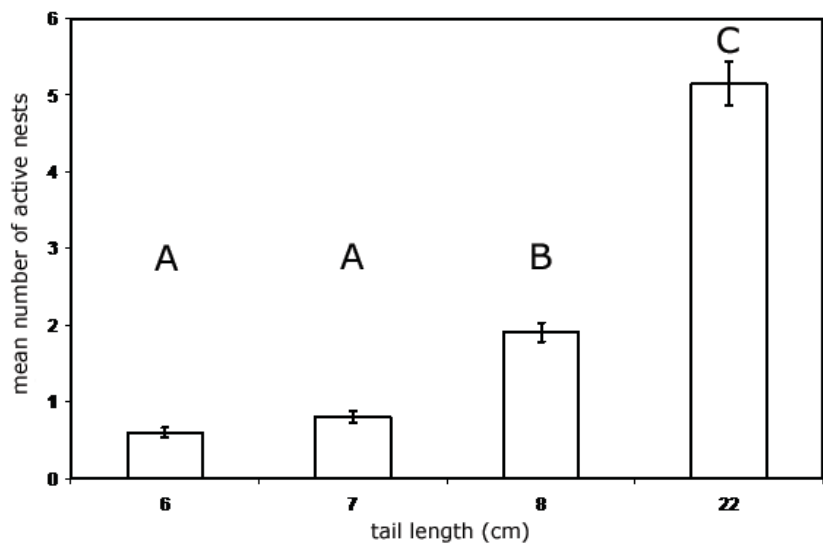


Figure 8. Mean number of active nests (\pm standard error) in a population of red-shouldered widowbirds that had tails shortened (6 cm), elongated (8 cm), or super-elongated (22cm). Groups with different letters above them are significantly different from one another ($p < 0.05$). Data based on Pryke and Andersson 2002.



Concept Check

12. What hypothesis was being tested in this follow-up study? Why was it necessary?
13. What do the data in Figures 7 and 8 show?
14. Do their results support their hypothesis? What do the results mean? Explain.

Question for further thought ...

15. If long tail length is so important to female widowbirds, why don't male tails continue to get longer and longer?

References

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- Pryke, S.R., and S. Andersson. 2002. A generalized female bias for long tails in a short-tailed widowbird. *Proceedings of the Royal Society of London Series B* 269:2141–2146.
- Pryke, S.R., S. Andersson, and M.J. Lawes. 2001. Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463.

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