

### Sexy Males and Sterile Females

#### The Ant and the Peacock.

By Helena Cronin.

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A central tenet of evolutionary biology is that natural selection promotes traits that enhance an individual's survivorship and reproduction. If so, then why in some animals, such as ants, are most members of the species sterile? And how is it that males of many animals evolve traits, such as the peacock's tail, that promote the male's early demise? (And even more confusingly, why should females actually prefer to mate with these doomed males?) The ant and the peacock symbolize these two major challenges to Darwinian evolution: altruism and sexual selection. Helena Cronin has examined the historical development of these theories, both analyzing disagreements between Darwin and Wallace and addressing the altercations that now characterize these fields. Cronin has done an excellent job, but, because she courageously ventures into current controversies, it is guaranteed that many will disagree with some of her opinions. This reviewer is no exception; however, this does not dampen my enthusiasm for highly recommending this work to anyone interested in these fields specifically, in evolution in general, or in the history of Darwinism.

The book consists of three parts. The first is a defense of natural selection and adaptation. Cronin promotes a gene-centered view of selection, as championed in the influential works of Richard Dawkins. She characterizes Dawkins as an arch-adaptationist, and much of this book can be characterized as advocacy for this view of life. Many of the arguments between this "selfish gene school" and the "constraints school" of which S. J. Gould is a major proponent are thrashed about. Much of the debate is redundant to the initiated and often turns semantic; it seems that if one merely uses the correct terminology constraints turn into adaptations. The second section, which I view as the strongest, concerns sexual selection. There are two main issues here. First, can female choice explain the extravagance and costliness of traits used by males in courtship? And if so, do females accrue any selective advantage by exerting such choice? Darwin answered yes and no; female choice is an important selection force, but, in an uncharacteristically Darwinian manner, he posited that females gain no advantage from being choosy. They merely find some males more attractive than others; this is Darwin's assertion of animal aesthetics. Darwin and Wallace disagree on both issues. First, Wallace suggested that there was no reason to believe that females choose males, especially if that choice implies aesthetics. And second, if they were to choose, Wallace claimed, then females gain an advantage. He suggested that more vigor-

ous males have more elaborate plumage, based on a bizarre notion of males possessing "super-abundant" energy due to sexual excitement that is channelled into their posteriors. This is where Wallace "out-Darwins" Darwin in his devotion to natural selection.

The transition from Wallace's arguments against female choice to his advocacy of adaptive choice is abrupt. Cronin clearly develops Wallace's reasons for doubting the efficacy of female choice, but then we are suddenly introduced to his arguments for why such choice has evolved. This transition could have been dealt with in more detail. Nevertheless, this brings us to today's controversy, which the author presents as a somewhat oversimplified dichotomy. One popular explanation for the evolution of female choice is Fisher's theory of runaway sexual selection. This hypothesis suggests that choice evolves as an incidental consequence of trait evolution. If there is linkage disequilibrium between alleles for traits and those for preferences (which could result from deterministic or stochastic events), the preferences promote trait evolution, and preferences then evolve as a correlated response to evolution of the trait due to the genetic correlation between the two—what Maynard Smith calls self-reinforcing choice. This is often referred to as a nonadaptive model, since females derive no immediate, direct natural selection advantage from exerting such choice; instead, they produce sons that will be perceived as more and more attractive as the allele for that preference increases in the population. (In her relentless promotion of selfish genes, Cronin argues that if we view this process correctly it is adaptive.)

The alternative hypothesis that Cronin presents is of a class known as "Good Genes"—utilitarian models in which females use traits to evaluate a male's physical vigor, and to the extent that variation in vigor among males is heritable, females increase the genetic quality of their offspring. Cronin leaves us with the impression that there is now overwhelming evidence that female preferences evolved because of such genetic advantages. Some of us have recently taken a more skeptical view of the evidence (e.g., Kirkpatrick and Ryan, *Nature* 350, 33–38, 1991). There is little argument that males with more attractive displays might be more vigorous; it takes time and energy to make a good display—dead males don't grow long tails. This, however, should not be considered strong evidence that female preferences have evolved in order to mate with such males. As an analogy, healthier plants can produce more flowers, and pollinators will be preferentially attracted to plants with more flowers, but no one would argue that the pollinator's behavior has evolved because it results in them pollinating healthier plants. Mere correlation does not argue for cause and effect, and the author does little to suggest how this dilemma can be resolved.

Cronin also points out that there might be preexisting biases in the female's sensory system that could result in them favoring some traits over others. This argument differs critically from the Fisherian and Good Genes hypotheses, and recent data using phylogenetic recon-

structions indicate that in some cases female preferences existed prior to the male trait now favored. For example, platy fish and swordtails are closely related, and only swordtails have caudal fins that are elaborated into sword-like appendages. Female swordtails prefer males with longer swords. Intriguingly, platys prefer their own males to which swords have been artificially attached over their own unadorned males (Basolo, *Science* 250, 808–810, 1990). This is only one example, but there are others involving displays of frogs, birds, crabs, and mites. This is strong evidence that the preference and the trait can be uncoupled. Coupling is required for both Fisherian and Good Genes hypotheses, and thus, in some cases, these hypotheses can be rejected. Unfortunately, Cronin overemphasizes the dichotomy between these two hypotheses at the expense of other alternatives.

The third section of this book deals with altruism and the question of why animals should behave in a manner that benefits others to their own detriment. Here Cronin dispels at least one popular myth about Darwin. In *The Origin of Species*, Darwin stated that sterile castes posed a challenge to his theory of natural selection. Cronin argues convincingly that Darwin was not troubled by sterility per se but instead by caste differentiation. How were workers in ant colonies able to inherit their characteristically distinctive morphology when they didn't reproduce? This is not an issue with knowledge of post-Mendelian genetics. But the question of altruism still persists. The author gives a very readable account of kin selection and reciprocal altruism in the general context of "selfish genes." She does not address the debate about the relative efficacy of kin selection versus reciprocal altruism in the evolution of cooperative behavior. For example, if a queen of a eusocial species such as an ant is multiply inseminated does the geometry of relatedness change to such a degree that altruism can still evolve? Today the theoretical validity of several hypotheses that explain altruism is accepted; the controversial issue is which mechanism or which interaction of mechanisms operates in nature.

Cronin ends this section with a fascinating chapter trying to relate the role of hybrid sterility in speciation to altruism. Although the relationship sometimes seems tenuous, in developing her argument she addresses some other controversies in evolutionary biology, such as whether differences among species in their mate recognition systems are incidental or an adaptive response. Most biologists have suggested that only predated isolating mechanisms can evolve under selection (and many question if the data support this assertion). Cronin makes the radical suggestion that in some cases postmating isolating mechanisms, such as aborting fertilized eggs, can also result from natural selection. If a female "knows" her egg has been fertilized by a heterospecific, she should abort and cut her losses as soon as possible. This appears to be a topic quite worthy of empirical investigation.

I have only touched on some of the topics in this work. Cronin also discusses utilitarian creationism, Wallace's spiritualism, Huxley's politics, conventional signaling, and sympatric speciation. Although I have discussed some aspects of this work with which I disagree, I reiterate that

these controversial topics can not be covered without engendering disagreement. This book is witty and well-informed; it will certainly raise some hackles, but it will not bore. I think this book is an important achievement in evolution biology.

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