**Discussion Questions**

to accompany

***Animal Behavior,* Eleventh Edition**

by Dustin Rubenstein and John Alcock

**Chapter 9**

**Reproductive Behavior**

9.1 Darwin defined sexual selection as “the advantage which certain individuals have over others of the same sex and species, in exclusive relation to reproduction” (Darwin 1871). Today most evolutionary biologists consider sexual selection for traits that promote success in acquiring mates to be a form of natural selection. Why? Compare the conditions that cause the process of natural selection to occur with the conditions that must cause sexual selection to occur. Is the factor “differences among individuals in age at death” on your list? Does sexual selection theory have elements in common with game theory?

9.2 Female satin bowerbirds (*Ptilonorhynchus violaceus*) appear to favor males that give very intense, even aggressive, courtship displays. Perhaps that is why females are often “jumpy” when in the presence of a displaying male. Males differ in how they adjust their displays in response to the female’s reaction. Females that often flinch as the male displays tend to leave the site without mating, whereas females that crouch down in the male’s bower are more likely to stay and mate with the displaying male. Why might these observations have led Gerald Borgia and colleagues to hypothesize that the bower enables females to protect themselves against forced copulation attempts by displaying males (Patricelli et al. 2002)? How could males gain by making it harder for themselves to force females to mate? See Patricelli et al.

9.3 Male rats, sheep, cattle, rhesus monkeys, and humans that have copulated to satiation with one female are speedily rejuvenated if they gain access to a new female. This phenomenon is called the Coolidge effect, supposedly because when Mrs. Calvin Coolidge learned on a farm tour that roosters copulate dozens of times each day, she said, “Please tell that to the president.” When the president was told, he asked his guide, “Same hen every time?” Upon learning that roosters select a new hen each time, he said, “Please tell that to Mrs. Coolidge.” Provide a sexual selectionist hypothesis for the evolution of the Coolidge effect. Use your hypothesis to predict what kinds of species should lack the Coolidge effect.

9.4 Gene-centered thinking tells us that sexual reproduction is a Darwinian puzzle in and of itself. Why? Consider the fitness consequences for asexual (i.e., parthenogenetic) females in competition with sexual ones in a given population in which both types produce equal numbers of offspring. When you have dealt with this problem, you should be surprised to learn that in many aphids, females are perfectly capable of cloning themselves, which occurs in one generation after another before one group of females produces a generation of both sons and daughters; these males and females then engage in sexual reproduction before their descendants resume cloning themselves (Moran and Dunbar 2006). What is the Darwinian puzzle here?

9.5 Satellite and attached male horseshoe crabs do not have the same reproductive success. Why hasn’t sexual selection eliminated the low-payoff satellite option if males exercising this option do not leave as many descendants as attached males do?

9.6 Roosters compete with one another for social dominance, and not surprisingly, dominant males have greater copulatory success than subordinate males. Use sexual selection theory to account for these differences among the two categories of males: dominant males release more sperm per ejaculate than subordinates and transfer more and better (faster-moving) sperm to females with large red combs on their heads, whereas subordinates provide all their mates with sperm of the same quality (the same velocity) (Cornwallis and Birkhead 2007). In addition, use conditional strategy theory to predict how males should behave if two dominant males were placed together until one became subordinate.

9.7 Female mimicry by males occurs in many species. For example, in the Broadley’s flat lizard (*Platysaurus broadleyi*), some males have the brown coloration of females while others are far more colorful (Whiting et al. 2009). Female mimics do secure some matings in the territories of their larger, more colorful rivals. Why are the bigger males (and those of the marine isopod *Paracerceis sculpta*) ever fooled into tolerating a female mimic? Why do female mimics occur in any species if the mating success of these individuals is lower than that of the bigger territorial males?

9.8 In the European frog (*Rana temporaria*), some males find and grasp egg-laden females and then release their sperm as the females deposit batches of eggs in a pond. Some other males locate floating egg masses soon after they have been laid. While grasping the egg masses as they would grasp females, these after-the-fact males release their sperm on the eggs, with the result that more than 80 percent of the egg clutches in one pond were found to have multiple paternity (Vieites et al. 2004). Some researchers have argued that the egg-mass-copulating males are ensuring that the maximum amount of genetic diversity is passed on to the next generation, given that the sex ratio is heavily male-biased. Devise another evolutionary explanation, and evaluate the two alternatives.

9.9 The digger bee’s “postcopulatory courtship” consists of elaborate tactile stimulation that the male provides his partner *after* she has accepted his sperm. Why is this behavior a Darwinian puzzle, and what might its adaptive value be?

9.10 Mate guarding should be common in species in which females retain their receptivity after mating and are likely to use the sperm of their last mating partners when fertilizing their eggs. But there are species, including some crab spiders, in which males remain with immature, unreceptive females for long periods and fight with other males that approach these females (Dodson and Beck 1993). How can “guarding” behavior of this sort be adaptive? Produce sexual selectionist hypotheses and some predictions derived from them.

9.11 Although the number of cases of mate choice by females dwarfs the known examples of choosy males, that rarer form of mate choice does occur and may be more widespread than often appreciated. In this light, why might it be adaptive for male jungle fowl to enhance the speed with which their sperm can travel when roosters inseminate attractive versus unattractive females (Cornwallis and O’Connor 2009)? Why might male potbellied seahorses (*Hippocampus* *abdominalis*) strongly prefer to court large females, whereas females show no such preference for large males (Mattle and Wilson 2009)? And why might male black widow spiders bias courtship in favor of well-fed females as opposed to starved ones (Johnson et al. 2011)?

9.12 Indian peacocks (*Pavo cristatus*) have truly extravagant ornaments that could be fairly recently evolved (that is, derived) from an ancestral pattern in which male plumage was not nearly so extreme. In the peacock-pheasants, six species in a genus related to that of the peafowl, there is considerable variation in the degree of male plumage ornamentation. In four species, males have highly elaborate plumage featuring large eyespots, but in two species they do not (Kimball et al. 2001). Draw two phylogenies, one in which elaborate plumage is the derived trait and another in which a reduction in ornamentation is the derived condition.

9.13 Richard Prum argues that researchers need a “null model” of the effects of sexual selection in order to determine whether in fact mate choices lead to adaptive outcomes, with female preferences for certain male attributes providing the choosy females with better genes or superior parents (Prum 2010). For Prum, the Lande–Kirkpatrick models provide the null in which preferences have no utilitarian adaptive effect but instead are the arbitrary products of a nonselectionist process. He argues that we need to test the predictions from the null model first, rather than focusing on predictions from adaptationist hypotheses about such things as signal honesty and fitness benefits of female preferences. Why have so many researchers employed the adaptationist approach? Do we also need a null hypothesis for behavioral traits that adaptationists have assumed (for the purposes of hypothesis development and testing) promote survival by defeating predators?

9.14 When forced copulation results in the death of the female, neither sex benefits. Explain why males may behave in ways that result in the demise of their sexual partners.

9.15 Stuart Wigby and Tracey Chapman formed three populations of fruit flies with different sex ratios: female-biased, having an even sex ratio, and male-biased (Wigby and Chapman 2004). Not surprisingly, the frequency with which females mated increased from the female-biased to the male-biased populations. After 18 and 22 generations of selection, fresh females from the three selected lines were taken from their environments and placed in cages with equal numbers of males. The mortality rate of females from the male-biased line was less than that of females from the even-sex-ratio line and much less than that of females from the female-biased line. What do these results tell us about the evolutionary consequences of sexual conflict between the sexes in this species?

9.16 Males of the parasitic isopod *Ichthyoxenus fushanensis* pair off with females in cavities they construct inside their victims, freshwater fish. At times, sexual cannibalism occurs early in the breeding season, when females eat their partners; males may eat their mates later in the season (Tsai and Dai 2003). Replacement partners of both sexes are readily available. In addition, males can transform themselves into females, a phenomenon that occurs only when males have achieved a fairly large size. The larger the female, the more fecund she is. The smaller the difference in size between male and female, the fewer the number of offspring produced by a pair. Why has conflict between the sexes reached such an extreme state in this species? What kinds of males are females expected to eat? What kinds of males are expected to eat their partners? How can you account for the difference in the timing of cannibalism by males and females?

References

Cornwallis, C. K., and Birkhead, T. R. 2007. Changes in sperm quality and numbers in response to experimental manipulation of male social status and female attractiveness. *American Naturalist* 170: 758–770.

Cornwallis, C. K., and O’Connor, E. A. 2009. Sperm: Seminal fluid interactions and the adjustment of sperm quality in relation to female attractiveness. *Proceedings of the Royal Society B* 276: 3467–3475.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.

Dodson, G. N., and Beck, M. W. 1993. Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes*. *Animal Behaviour* 46: 951–959.

Johnson, J. C., Trubl, P., Blackmore, V., and Miles, L. 2011. Male black widows court well-fed females more than starved females: Silken cues indicate sexual cannibalism risk. *Animal Behaviour* 82: 383–390.

Kimball, R. T., Braun, E. L., Ligon, J. D., Lucchini, V., and Randi, E. 2001. A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. *Biological Journal of the Linnean Society* 73: 187–198.

Mattle, B., and Wilson, A. B. 2009. Body size preferences in the pot-bellied seahorse *Hippocampus abdominalis*: Choosy males and indiscriminate females. *Behavioral Ecology and Sociobiology* 63: 1403–1410.

Moran, N. A., and Dunbar, H. E. 2006. Sexual acquisition of beneficial symbionts in aphids. *Proceedings of the National Academy of Sciences* 103: 12803–12806.

Patricelli, G. L., Uy, J. A. C., Walsh, G., and Borgia, G. 2002. Male displays adjusted to female's response. *Nature* 415: 279–280.

Prum, R. O. 2010. The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty and design in intersexual signals. *Evolution* 64: 3085–3100.

Tsai, M. L., and Dai, C. F. 2003. Cannibalism within mating pairs of the parasitic isopod, *Ichthyoxenus fushanensis*. *Journal of Crustacean Biology* 23: 662–668.

Vieites, D. R., Nieto-Román, S., Barluenga, M., Palanca, A., Vences, M., Meyer, A. 2004. Post-mating clutch piracy in an amphibian. *Nature* 431: 305–308.

Whiting, M. J., Webb, J. K., and Keogh, J. S. 2009. Flat lizard female mimics use sexual deception in visual but not chemical signals. *Proceedings of the Royal Society B* 276: 1585–1591.

Wigby, S., and Chapman, T. 2004. Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution* 58: 1028–1037.