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Author(s): Andrew R. Blaustein

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SEXUAL SELECTION AND MAMMALIAN OLFACTION

Biologists (Darwin 1901, excluded) have generally ignored sexually dimorphic odors among mammals as an important factor in sexual selection. This is interesting because the importance of olfaction in the social lives of mammals is well documented. (See, for examples, reviews by Ralls 1971; Eisenberg and Kleiman 1972; Thiessen and Rice 1976; and in Doty 1976; Seboek 1977.) These reviews suggest that olfaction is important in individual, group, age, and sex recognition and plays an important role in the identification of social status and sexual receptiveness in mammals. Olfaction may play a role in both intersexual (epigamic) and intrasexual selection.

In an excellent review of monogamy in mammals, Kleiman (1977) discussed the relationship of sexual dimorphism and mammalian mating systems. Although she acknowledged the importance of scent marking when considering sexual dimorphism, body size was the main characteristic used in her paper. Recently Ralls (1976, pp. 259–260), discussing mammalian sexual selection, stated that the result of intrasexual selection upon the male sex in mammals has been traditionally viewed as the evolution of larger size and, in some species, such weapons as antlers and large canine teeth. In her stimulating compilation, Ralls (1977) realized that the degree of sexual dimorphism in coloration and in structures used in displays may be more closely related to the intensity of sexual selection than differences in body size, but she did not mention the scent of a mammal in this context. Although Ralls (personal communication) believes that sexual selection may play a role in the evolution of odor dimorphisms, she believes that sexual dimorphism in size is the most common form of dimorphism in mammals (Ralls 1971, 1977). In her discussion of the relationships of mammalian sexual dimorphism, sexual selection, and parental investment (*sensu* Trivers 1972) she states (Ralls 1977) that most mammalian species are small (those in the orders Insectivora, Chiroptera, Rodentia) and are not extremely sexually dimorphic in size. Ralls (1977) believes that models incorporating sexual selection and parental investment apply less well to mammals than to passerine birds upon which many of the models are based.

The many species of small mammals that are regarded as showing little sexual dimorphism in size may in fact be extremely sexually dimorphic through odor. Glandular development is more enhanced in male rodents, and male odor is believed to contain more compounds than female odor (Stoddart 1974, p. 305). The studies of Schultze-Westrum (1965), Goodrich and Mykytowycz (1972), and Stoddart (1974, p. 300) have demonstrated unequivocally that a greater repertoire and intensity of odors are produced in males. Stoddart (1974) stated that there is no species known in which the female produces a greater quantity or a more complex odor than the male. In their review, Thiessen and Rice (1976) showed that marking in 12 species of mammals is sexually dimorphic, with males marking more often than females. Odor is extremely important in communication in these

species (citations above). Certain odors in small mammals are probably functionally equivalent to secondary sexual characteristics such as bird plumage, deer antlers, or the bowers of bower birds. Sexual selection should act upon these odors just as it acts upon visually conspicuous characters.

Darwin (1901, pp. 324–325) recognized the many characters that sexual selection can affect: “. . . weapons of offense and the means of defense of the males for fighting with and driving away their rivals—their courage and pugnacity—their various ornaments—their contrivance for producing vocal or instrumental music—and their *glands for emitting odours* . . .” (italics mine).

Fisher (1930) showed that for sexual selection based on mating preferences in one sex to lead to the evolution of sexually dimorphic characteristics in the other sex, the individual exercising the preference should gain some advantage. The advantage to a male possessing a characteristic preferred by females is obvious. He achieves more matings and produces more offspring. Females mating with such males will, in general, produce male offspring with the desirable trait, if the trait is genetically based. These offspring, in turn, will mate more often and produce more young. Fisher (1930) believed that there was an association (genetically) between high general fitness and certain types of ornamentation. Certain characteristics would be coupled with some other heritable advantage and would persist as markers of increased male fitness, and females would mate with males possessing such characteristics. A familiar example is the ancestral bird with a genetically based long tail. His tail may be slightly longer than other males because long-tailed birds could fly better than shorter-tailed birds and thus avoid predators more easily. Females that preferred characteristics linked with a superior overall genotype would be selected for and their preference would spread in the female population (see Mayr 1972, p. 93).

Intersexual selection could operate upon the scent of a mammal in a similar fashion. For example, hypothetically, certain odors could be associated with efficiency of obtaining food. Mammals may have characteristic odors when they are well fed and other odors when they are less well fed. The scent of a mammal may even give clues as to the quality of food items eaten. There is some evidence that scent-urination in some mammals may give an indication of the mammal's physiological condition and that urine odor changes with diet (see Coblenz 1976; McCullough 1969; but see Stoddart 1977). Additionally, Doane and Porter (1978; Porter and Doane 1977) give evidence that rodent neonatal chemical cues are diet dependent. It is known that small mammals use olfaction in food detection (see for examples Howard et al. 1968; Lockard and Lockard 1971; Maser et al. 1978). Recently, Maser et al. (1978) suggested that there was strong coevolution between the scent of fungi that are dependent upon mammalian seed dispersal and olfactory ability in the mammalian consumer. They suggest that olfaction is more important than sight in many species of small mammals utilizing a fungal food source. In fact, J. M. Trappe (personal communication) states that mammals trapped for his study (Maser et al. 1978) often smell like the fungi they eat. To my knowledge there has been no observed genetic component in these studies. However, genetic aspects should not be ruled out. Some aspect of a mammal's scent could become associated with its ability to acquire food. Females would mate with males displaying this odor. Providing this trait is heritable, the male

offspring would also have this trait, attract more mates, and produce more offspring. It may be less costly for cheater males to evolve mimic chemical cues instead of morphological structures attractive to females. If such males were present, interesting consequences could result. Females mating with such males would be severely penalized and should evolve behaviors to avoid such males. (See discussions by Halliday [1978] and Williams [1978] for differing views.) Males of many rodent species appear to release odorous signals attractive to females (Leshner 1978, pp. 129–130).

The most convincing experimental evidence that olfaction is an important component in sexual selection in mammals comes from studies of rodents. For example, Bowers and Alexander (1967) showed that house mice (*Mus musculus*) can discriminate between closely related species and between sexes on the basis of odor cues alone. Similarly, Huck and Banks (1979) demonstrated that lemmings (*Dicrostonyx groenlandicus*) are capable of discriminating between familiar and unfamiliar conspecifics solely on the basis of odor. Especially interesting is a recent study of Huck et al. (1980). They showed experimentally that estrus female lemmings choose to associate with the odor of dominant male lemmings over the odor of subordinate males.

Odor may also be important in intrasexual selection. Pregnancy blocking (Bruce effect; Bruce 1959, 1960) is a phenomenon in which a pregnant mouse absorbs her litter when she is confronted with the odor of an unfamiliar male after the stud male has been removed. Although certain evolutionary aspects of this phenomenon remain unclear, it may be an effective means of male-male competition among rodents. Also, female rodents may choose to mate with males with the best ability to block pregnancies, since their male offspring presumably will also have this ability if it is genetically based.

It is essential for individuals to mate with members of their own species. In many vertebrate species (including some mammals) elaborate courtship displays and exaggerated secondary sexual characteristics have evolved as premating isolating mechanisms. These are evolutionary checks to avoid mating mistakes. Many species of small mammals lack such obvious behavioral repertoires or conspicuous secondary sexual characteristics. Difference in odor is an important premating isolating mechanism in these species (see for examples Doty 1972; Godfrey 1958; Nevo 1976).

Sexual selection will be most intense in those species displaying polygamous mating systems (see Halliday 1978). Since most species of mammals are polygamous (Orians 1969; Kleiman 1977), it is not unreasonable to assume that extreme sexual dimorphism within the Mammalia exists. It is not easily recognized because its manifestation in many species is probably through scent.

It is not surprising that biologists have keyed upon behavioral displays and conspicuous characteristics such as bright colors, antlers, or body size in discussions of sexual selection in mammals. Biologists use their vision as a major form of perceiving the outside world. So do birds. Many species of mammals probably use olfaction as a major means of perception. This is a difficult sense to comprehend for biologists, because humans have a relatively poor sense of smell. Difficulty in quantifying sexual selection in terms of odor may force us to look at body size in

general when dealing with sexual selection in mammals. However, studies such as those of Bowers and Alexander (1967), Huck and Banks (1979), and Huck et al. (1980) are important steps in quantifying sexual selection through olfaction. (See also Halpin 1974; Dagg and Windsor 1971; and papers reviewed in Stoddart 1980, pp. 124–140.) It may be naive to ignore scent in general models incorporating mammalian sexual dimorphism and sexual selection.

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ANDREW R. BLAUSTEIN

DEPARTMENT OF ZOOLOGY
OREGON STATE UNIVERSITY
CORVALLIS, OREGON 97331

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