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MATING SYSTEM, MATE PREFERENCE AND RARITY OF BLONDE PRAIRIE VOLES, *MICROTUS OCHROGASTER*

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ABSTRACT

Rarity of the blonde color morph in prairie vole populations is attributed to: a recessive trait requiring breeding between siblings or parents and their offspring for the color morph to be prominent within a population; the mating system of the prairie vole which results in suppression of reproduction between family members, except for young that have dispersed from the natal nest; and a mate preference of blondes for normal-colored individuals and of normal-colored individuals for blondes, which reduces probability of mating between blonde siblings that have dispersed from the natal nest.

INTRODUCTION

Aberrant color morphs are rare in wild populations of the prairie vole, *Microtus ochrogaster*. During the course of a 14-year demographic study of the prairie vole in east-central Illinois more than 12,000 individuals of this species have been handled. Only four distinctly different colored individuals have been observed; all were light cinnamon blonde.

Population genetics models and experimental studies provide explanations for rareness of aberrant color morphs in free-living populations. Brown (1965), Gill (1977) and Slatkin (1985) present models which predict maintenance of rare alleles within a population and phenotypic expression of traits controlled by such alleles. Dice (1947) has shown the importance of predation in eliminating conspicuous color morphs from

a population, thus contributing to rarity of alleles associated with given color morphs. Other factors such as the mating system of the species and preferences for given color morphs in mate choices, also play a role in maintenance of alleles and rarity of expression of unusual color morphs within a population. In this paper we discuss the latter two phenomenons as they apply to maintenance of the blonde allele and to rarity of the blonde color morph within populations of the prairie vole.

A male blonde prairie vole was brought to the laboratory, mated with normal-colored females and inheritance of the coat color determined. The blonde morph proved to be a simple recessive trait (Hofmann and Klatt, unpublished). There is no evidence of reduced reproduction in the blonde morph; the percentage of successful matings of blonde pairs (80%) and the average litter size (3.5) is similar to those for normal-colored individuals in our laboratory colony.

Because blonde is recessive, the trait will be expressed only when heterzygotes and/or recessives mate with each other. Furthermore, since relatives are more likely to share alleles in common, inbreeding would promote the probability of homozygous recessives. However, prairie voles have behavioral mechanisms which reduce or prevent inbreeding (Getz and Carter, 1980; Getz, et al., 1981; McGuire and Getz, 1981; Gruder-Adams and Getz, 1985; Getz and Hofmann, 1986). These studies demonstrate the prairie vole to have a monogamous mating system in which 75% of the young females and 68% of the young males remain at the natal nest. Young females remaining at the natal nest do not become reproductively activated and do not mate with their siblings or father. Siblings may mate only if they disperse from the natal nest and remain apart for at least eight days before meeting again (Gavish, et al., 1984).

If random mate choice is involved, if blondes display a preference for normal-colored mates, or if normal-colored individuals display a preference for blonde mates, it seems unlikely that wandering blonde siblings would remain unpaired sufficiently long to behave as strangers upon meeting again. If, however, blondes display a preference for blonde mates and/or normal-colored animals reject blondes, blondes may delay pairing with normal-colored individuals, thus increasing the probability of encountering a wandering unpaired blonde sibling and forming a breeding pair.

We conducted a behavioral study to determine whether or not the blonde morph is maintained in the population by negative assortative mating. We determined the preference of males and females of each color morph, blonde and normal, to associate with individuals of each color morph of the opposite sex. The experiments simulated the initial mate choices made by unpaired males and females when meeting in a neutral site following dispersal from their natal nests. From these results we can predict the role of mate preference and the mating system in the observed rarity of the blonde color morph in prairie vole populations.

METHODS

Reproductively naive 40-50 day old laboratory-reared voles were used in the trials. All animals were left in sibling litter groups following weaning at 21 days of age until used in the experiments; females remain non-estrous while in sibling groups (McGuire and Getz, 1981). All individuals used in a given trial were from different litters; individuals of each color morph were from breeding pairs of that color morph. The trials were conducted in the animal colony room.

The observation chamber consisted of a 43 x 22 x 30 cm clear plastic breeding cage. The bottom of the cage was covered with a 1 cm layer of hardwood "Beta" wood chip bedding; a clean cage was used for each experiment. To conduct a preference trial one animal of each color morph was tethered at opposite ends of the cage ("choice" animals). A string attached to a plastic cable-tie collar placed around the neck of each choice animal was taped to the end of the cage so as to allow the animal to move around within 1/3 of the chamber. This left a neutral central area equal to 1/3 of the chamber within which neither choice animal could encroach. The end of the cage in which each color morph was tethered was reversed for each trial.

The choice animals were collared and tethered to the ends of the cage for 5 min to become adjusted to the experimental conditions. The animal to be tested for preference of association with a blonde or normal-colored animal ("test" animal) was then introduced into the neutral area. Following a 2 min adjustment period, location of the test animal was recorded for 30 min. The time the test animal spent in the end with the blond or normal-colored animal was recorded on an electronic timer. Subtotals of the time spent with each color morph were recorded at 10 min intervals. There was no consistent difference in the amount of time the test animals associated with each choice animal among the three 10 min periods. Accordingly, total times for the entire 30 min were used in the analysis.

An individual was designated as showing a preference for a given color morph if it spent at least 25% more time in the end of the cage with that animal than with the other color morph. This arbitrary method of designating preference for association with a given color morph was used so as to eliminate errors resulting from inability to determine precisely when the test animal had crossed into the end of the chamber occupied by a given choice animal. The average time spent by all the test animals with each color morph was also used as an indication of the degree of preference of individuals for normal or blonde animals.

RESULTS

Eighteen of 26 (69.2%) blonde test males and females displayed a distinct preference for association with a normal-colored individual of the opposite sex (Table 1). The blonde female not displaying a distinct choice associated with the normal-colored male 0.9 min more than with the blonde male. The average time blonde animals spent with normal and blonde individuals was 19.0 and 8.8 min, respectively (Table 2).

Seventeen of 20 (85%) normal-colored males and females displayed a preference for blonde individuals of the opposite sex; the other three animals exhibited no choice (Table 1). One of the two normal-colored males and the female displaying no choice spent more time with the blonde than with the normal-colored choice animal (1.7 and 2.0 min more, respectively). Normal-colored individuals spent an average of 19.6 and 7.6 min with blonde and normal-colored individuals, respectively (Table 2).

DISCUSSION

The preference of blondes to associate with normal-colored individuals of the opposite sex and of normal-colored individuals to associate with blondes would tend to reduce matings between blonde siblings. Blondes would more readily pair with

normal-colored individuals, reducing the probability of their remaining unpaired sufficiently long to encounter and form a pair with a blonde sibling. Most blondes would be expected to form a pair with a non-sibling normal-colored mate.

Preference for blondes by normal-colored individuals would tend to ensure all blondes would mate and thus increase the frequency of the blonde allele within the population. However, since blonde is a recessive trait, the color preference behavior of blondes (for normal-colored) and normal-colored animals (for blondes) would tend to reduce presence of blonde morphs within the population.

We have few data regarding differential survival of the two color morphs within free-living populations. Two of the three blondes left in the population were first caught as adults and were not present one month later. The third blonde was first caught as a juvenile. It remained on the study area for 128 days. Normal-colored prairie voles first caught as juveniles persist on the study area an average of 52 days (Getz et al., 1979).

Results of this study indicate the following factors contribute to suppression of expression of the blonde allele in prairie vole populations: (1) blonde is a recessive trait requiring breeding between sibling blondes or with their heterozygous parents for the color morph to be prominent within a population; (2) a mating system which prevents young animals from breeding while in the family group and the need for siblings to disperse in order to successfully mate; (3) a low incidence of dispersal of young from the family group; and (4) preference of blondes for normal-colored individuals and vice versa, which greatly reduces the probability of matings between wandering, unpaired blonde siblings.

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Table 1. Preferences of blonde and normal-colored *Microtus ochrogaster* for association with blonde and normal-colored individuals of the opposite sex. Non-estrous females and sexually naive males were used. See text for experimental design.

	Preferred Color Morph		
Test Animal	Blonde	Normal-colored	No Preference
Blonde			
Male	3	10*	0
Female	4	8	1
Total	7	18*	1
Normal-colored			
Male	8	0	2
Female	9*	0	1
Total	17*	0	3

*Preference for this color morph significantly greater (at <.05 level; X^2) than for other color morph and no preference, combined.

Table 2. Amount of time (mean ± 1SE) blonde and normal-colored *Microtus ochrogaster* spent with blonde and normal-colored individuals of the opposite sex during 30-min trials. Non-estrous females and sexually naive males were used. See text for experimental design.

		Amount of time with color morph	
Test animal	N	Blonde	Normal-colored
Blonde			
Male	13	8.1(1.7)	19.9(1.9)**
Female	13	9.7(2.0)	18.0(2.4)**
Total	26	8.8(1.3)	19.0(0.9)**
Normal-colored			
Male	10	19.9(1.5)*	7.3(1.2)
Female	10	19.4(0.6)*	8.0(1.0)
Total	20	19.6(1.0)**	7.6(0.8)

*Difference significant at <0.05 level

**Difference significant at <0.01 level (Wilcoxon matched pairs sign-ranked test).