Temporal Dynamics of Color Phenotypes in an Isolated Population of Feral Swine

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From 1968 to 1984, frequencies of color phenotypes of feral swine (*Sus scrofa* Linnaeus, 1758) were studied at a site in South Carolina, U.S.A. A Chi-square analysis indicated significant changes in these frequencies across time. There was an abrupt decrease in the frequency of solid black animals and a corresponding increase in the frequency of spotted animals between the 1976—1977 and 1982—1984 sampling periods. There were no significant differences between the 1968—1969 and 1976—1977 frequencies, and there was no significant change in the frequency of solid white animals over the entire study period. The biological significance of the observed changes, if any, is uncertain; however, a larger than usual hunter harvest in 1976 could have shifted color morph frequencies in the surviving population. Results failed to support the contention that feral swine populations tend to revert to all black or dark phenotypes over time.

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1. INTRODUCTION

Animal domestication, through intensive artificial selection for desired characteristics and the relaxation of certain components of natural selection, has had many far-reaching effects upon a variety of traits in the target populations (Berry, 1969; Zeuner, 1963). One of the most common effects has been increased frequencies of variant color phenotypes, particularly white, in a variety of domestic forms (Clutton-Brock, 1981; Zeuner, 1963). This presumably has occurred via the relaxation of natural selection for the more uniform and often cryptic wild-type coloration of these species' wild ancestors (Darwin, 1867; Kowalski, 1976). According to these widely-accepted beliefs, white phenotypes are strongly selected against and eventually should decrease and/or disappear from those domestic populations which return to the feral state. In addition, it is commonly accepted that populations of feral swine (*Sus scrofa* Lin-

naeus, 1758) should revert to an all black or dark coat coloration over time as a result of re-exposure to natural selective forces (Maynard, 1872; McKnight, 1976). We are aware of no studies of feral swine populations which have systematically documented such changes of color morph frequencies. The purpose of this study was to evaluate the changes in the frequency of coat color morphs over a 16-year period in a population of feral swine which had remained almost totally isolated from the input of domestic animals for an extended period of time (>30 years).

2. METHODS

Feral swine were collected on the United States Department of Energy's Savannah River Plant (SRP). The SRP occupies portions of Aiken, Allendale and Barnwell counties in westcentral South Carolina along the Savannah River approximately 25 miles southwest of Augusta, Georgia. Large numbers of free-ranging domestic swine were left behind when the resident farmers were moved from the area in the early 1950s. Since that time, these animals have thrived and multiplied in the riverswamp and adjacent pine plantation habitats on the site (Jenkins & Provost, 1964; Mayer, 1983; Sweeney, 1970). Since 1952, government safety and security considerations have restricted public access to this 780 km² site. During the ensuing 32 years, few if any additional introductions of domestic swine have been made into this population (Brisbin *et al.*, 1977; Mayer, 1983; Smith *et al.*, 1980).

Data were collected from 410 animals during three sampling periods, 1968——1969, 1976—1977, and 1982—1984. Color morph data used in this study were taken from animals which were livetrapped, caught with trained dogs, or collected and examined during the SRP Public Deer Hunts during autumn. Color morphs determined by field observation at a distance may be unreliable due to the fact that these animals often are coated with dry mud or observed while partly concealed by vegetation. Color phenotypes were grouped into one of the following six color morph categories: (1) solid black — all black with no markings; (2) solid red/brown — all red/brown with no markings; (3) solid white — all white with no markings; (4) spotted — various combinations of black, red/brown and white; (5) belted — black with a white band over the shoulders, and (6) miscellaneous — including rare color morphs such as blue and gray roans and combinations of the above categories. Two age classes were defined: juvenile — no permanent second molar present (less than one year old), and adult — permanent second molar present (one year old or older) (Mayer, 1983). Chi-square analyses were used to determine if differences between samples were significant. Only in the 1982—1984 sampling period were sufficient numbers of animals studied to allow comparisons of the frequencies of color morphs between sex and age categories. These analyses indicated no significant differences between the frequencies of color morphs across either sex ($\chi^2 = 4.06$; $d.f. = 5$; $p = 0 54$) or age ($\chi^2 = 2.44$; $d.f. = 6$; $p = 0.78$) groups during that sampling period. Therefore, data from all three sampling periods were combined across sex and age categories for further analyses.

3. RESULTS AND DISCUSSION

There was a significant change in the frequencies of the major color morphs between sampling periods across time ($\chi^2 = 95.22$; $d.f. = 10$; $p < 0.001$); there was, however, no significant difference in the frequencies of color morphs between the 1968—69 and 1976—77 sampling periods ($\chi^2 = 0.23$; $d.f. = 5$; $p = 0.99$). The most salient features of this difference were an abrupt decrease (50% to 13%) in the frequency of solid black animals and a corresponding increase (25% to 68%) in the frequency of spotted animals between 1977 and 1982 (Fig. 1). Of equal importance, there was no change in the percentage of the total population showing the white phenotype either during the entire 16-year study period or during the final 6 years ($\chi^2 = 1.47$; $d.f. = 2$; $p = 0.48$, and $\chi^2 = 0.73$; $d.f. = 2$; $p = 0.69$, respectively).

The reasons for the observed changes in color morph frequencies between 1976—77 and 1982—84, after a period of 8 years of stable color morph distribution, are not clear. The SRP Public Deer Hunts harvested larger numbers of feral swine ($n = 177$) in the fall of 1976
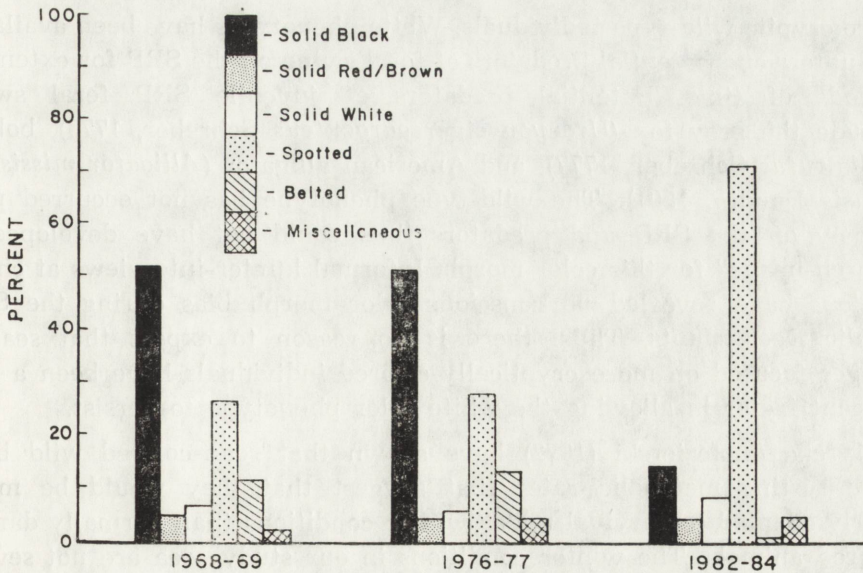

Fig. 1. Changes in the frequencies of the major color morphs occurring in a population of feral swine resident on the U.S. Department of Energy's Savannah River Plant over a 16-year period. Frequencies were calculated on the basis of totals of 57, 61 and 292 animals for the 1968—69, 1976—77 and 1982—84 sampling periods, respectively.

than in any year prior to that time (previous maximum <45). This may have disrupted coat color morph frequencies in the surviving population and caused the shift in frequencies between the 1976—77 and the 1982—84 sampling periods. However, the changes were in the opposite direction that would have been expected if dark phenotypes rendered the animals less vulnerable to hunting pressure. In addition, the changes observed were not in the directions that would be expected if the solid black phenotype tends to predominate in populations of feral swine over extended periods of time.

Reasons for the persistence of the solid white phenotype are equally unclear at this time. Because the solid white color is known to be genetically dominant in swine (Ensminger, 1970; Hetzer, 1945), this phenotype should be easily removable from the population if it confers a selective disadvantage due to increased vulnerability to predation and/or hunting pressure. Other studies (Kaufman, 1973; Kaufman, 1974) have shown that white mice (*Mus musculus* Linnaeus, 1766) are more vulnerable to predation than mice showing agouti (wild-type) coloration. However, it may be that under some conditions, search images of predators which are accustomed to the wild phenotype may result in decreased selection against white-colored individuals as compared to the more cryptic wild-type individuals. White phenotypes have been available to hunters and potential predators of feral swine on the SRP for extended periods of time. Potential predators of juvenile SRP feral swine include the grey fox (*Urocyon cinereoargenteus* Schreber, 1775), bobcat (*Felis rufus* Schreber, 1777), and American alligator (*Alligator mississippiensis* Daudin, 1801). The wild-type phenotype has not occurred previously on the SRP and predators thus could not have developed a "search-image" for this color morph. Informal hunter-interviews at check stations have revealed no conscious color morph bias during the SRP Public Deer Hunts. Thus, there is no reason to expect that search images focused on more cryptically-colored individuals have been a significant factor in allowing the white color phenotype to persist.

Myrcha & Jezierski (1972) have shown that roan-colored wild boar have resting metabolic rates that suggest that they would be more poorly adapted to survival under winter conditions than normally darker colored animals. The winter conditions in our study area are not severe however and neither can this phenomenon explain the decrease in black phenotypes during the latter part of our study. Similarly, wild boar showing a black with white-cream spotty color mutation have been shown to have selectively higher mortality rates than normally-colored animals (Andrzejewski, 1974). If operating in our study population, how-

ever, this factor should have resulted in a decrease rather than the observed increase in spotted phenotypes over time.

Our data do not support the widely-held belief that the all white phenotype is selected against once the animals return to a feral state. These results also suggest that the white color phenotype does not confer an increased vulnerability to predation; the almost universal absence of white individuals from free-living populations of the pig's wild ancestor must be attributable largely to other factors. The proposal that populations of free-living feral swine will, over time, tend to revert to either an all black or uniformly dark phenotype similarly was not supported.

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ZMIENNOŚĆ CZASOWA FENOTYPÓW UBARWIENIA
W IZOLOWANEJ POPULACJI ZDZICZAŁYCH ŚWIŃ

Streszczenie

Badano częstość występowania różnego ubarwienia w izolowanej populacji zdziczałych świń w Południowej Karolinie (USA) w latach 1968—84. Stwierdzono znaczący spadek udziału osobników zupełnie czarnych i odpowiadający mu wzrost udziału osobników o ubarwieniu plamistym w latach 1976—77 oraz 1982—84 (Ryc. 1). Częstość występowania osobników czysto białych nie zmieniała się w ciągu całego okresu badań.

Wydaje się, że zmiany ubarwienia były spowodowane dużym odstrzałem w roku 1976, w wyniku którego uległy zmianie częstości fenotypów ubarwienia w populacji, która przeżyła.