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Article in *The American Midland Naturalist* · January 1990

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Behavior of Black and Gray Morphs of *Sciurus carolinensis* in an Urban Environment

ERIC J. GUSTAFSON¹ AND LARRY W. VANDRUFF

*College of Environmental Science and Forestry, State University of New York,
Syracuse 13210*

ABSTRACT.—Melanism in the gray squirrel (*Sciurus carolinensis*) is currently found primarily in urban populations and near the northern limit of the species' range. Selected behaviors were examined in Syracuse, New York, to determine if significant differences exist between black and gray morphs which may have survival implications in urban environments and perhaps throughout the range of the gray squirrel. No differences in wariness between the morphs was demonstrated when flight response to approaching humans and dogs was tested. Although males were dominant over females and initiators of encounters usually were victors, neither color morph was more dominant in aggressive encounters at feeding stations. Quantification of sunning behavior during the months of February and March revealed no differences in behavioral thermoregulation between the two morphs. These results suggest that the distribution of color morphs is not due to pleiotropic behavioral trait differences, that neither morph is likely to have a mating advantage, and the variation among demes suggests random factors (drift).

INTRODUCTION

Color polymorphism is a prominent feature of many gray squirrel (*Sciurus carolinensis*) populations, occurring predominantly in the northern half of the species' range (Seton, 1929). Of four distinct and discontinuous color morphs, three involve various degrees of melanism (Kriz, 1959; Robertson, 1973), and the distribution of these color morphs has perplexed biologists for some time (Allen, 1943; Schorger, 1949; Creed and Sharp, 1958; Banfield, 1974). The literature documents three features of the distribution and frequency of the melanistic morphs.

Black color morph frequencies have declined throughout the northern half of the range of the gray squirrel since the late 1700s, especially S of the Great Lakes (Allen, 1943). The black morph was predominant in some areas prior to the advance of civilization (Schorger, 1949). The abundance of the black morph generally increases toward the northern limit of the range. Among exurban populations, the black morph is now abundant only in Canada (Robertson, 1973; Banfield, 1974) and in northern Michigan (Allen, 1943). The frequency of the black morph is higher in some major urban centers than in surrounding areas (Robertson, 1973). We have found demes in Syracuse, New York, in which the frequency of melanism exceeds 60%, whereas in surrounding rural areas the frequency is estimated to be less than 2%.

The selective regime that produces and maintains the color morph cline is not understood. Allen (1943) suggested that heavily forested or wilderness areas result in a predominance of the black morph, but the abundance of this morph in agricultural southern Ontario does not support this hypothesis. Schorger (1949) believed that melanism developed on the borders of the Pleistocene glaciers when the climate was cold and moist, consistent with Gloger's rule. Different rates of mortality among the color morphs may exist. Human alteration of both forest structure and type may have changed vulnerability to natural predators by

¹ Present address: White Pines College, Chester, New Hampshire 03036



creating an environment in which the melanistic morph was more conspicuous. Differential rates of harvest by hunters may continue as an important selective force (Allen, 1943; Creed and Sharp, 1958).

A number of genes are involved in the regulation of coat color in the gray squirrel, and perhaps pleiotropy exists. In the red fox (*Vulpes vulpes*), Keeler *et al.* (1968, 1970) have shown an alteration in adrenal and thyroid gland function and pituitary weight, in the presence of genes regulating melanin production, which led to a decrease in the level of fear exhibited by foxes in startle tests. Thus, coat color may indeed be genetically associated with morphological, physiological and behavioral traits that have survival implications for their bearers.

In general, species with less protection from predation through passive defense go longer distances when they flee (Eibl-Eibesfeldt, 1970). Consequently, the melanistic morph of *Sciurus carolinensis* might be expected to have a longer flight distance. Also, differences in aggressive behavior between the color morphs may affect access to resources, and may determine rates of copulation since the mating system of the gray squirrel involves a dominance hierarchy (Thompson, 1977a). Differences in behavioral thermoregulation may also exist. This study was designed to look for behavioral differences between the black and gray morphs of *Sciurus carolinensis* that may have survival implications in urban environments and perhaps throughout the range of the gray squirrel.

METHODS

Selected behaviors of the black and gray morphs of *Sciurus carolinensis* were quantified between February 1982 and March 1983 in a natural population inhabiting medium-density residential areas and two greenspaces (Thornden Park and Oakwood Cemetery) in Syracuse, New York. Frequencies of the black morph varied widely among demes within the population from less than 5–61%. The exurban frequency is estimated to be less than 2%. Throughout this paper the term melanistic or black squirrel refers to individuals whose pelage was predominantly melanistic.

Wariness.—Wariness was quantified using standardized threat stimuli (man or dog) that approached a squirrel on the ground directly and at constant speed. The distance between the squirrel and the approaching threat stimulus at the instant the squirrel fled to cover was measured as the response variable, STARTLE DISTANCE. Paired tests were employed; after observations were made on a black squirrel, a gray squirrel was tested within 30 min in the same general location. During each wariness test, wire-stake markers were placed at the points where the stimulus and the squirrel were positioned when the squirrel fled. We then measured the distance from the initial point of approach to the squirrel's position before it fled (TOTAL DISTANCE), the distance from the squirrel to the nearest cover when it fled (DISTANCE TO COVER), and the diameter breast height (dbh) of the cover used (DBH OF COVER USED). We also recorded the time, temperature (TEMP), weather conditions and approximate wind speed (WIND). To avoid squirrel habituation to the threat stimulus, tests were not conducted within 200 m of any given trial for at least 5 days. This distance is approximately 30 m greater than the longest reported linear distance of gray squirrel activity ranges (Doebel and McGinnes, 1974; Thompson, 1978).

A squirrel was considered to be unaware of the threat stimulus when the threat stimulus was physically hidden from the squirrel until the test began. Under all other conditions, the squirrel was assumed to be aware of the threat stimulus.

Three different threat stimuli were used to measure squirrel wariness: (1) observer sprinted toward the squirrel without vocalization or other deliberate auditory stimulus; (2)

observer approached the squirrel at a brisk walk while blowing short shrill blasts (approximately one per sec) on a whistle and (3) simulation of a typical urban predator attack. In this third test, a 19.5-kg mongrel dog was allowed to pursue a squirrel, and the markers were placed by the observer. The dog was restrained on a short leash behind a tree or tombstone until it saw the subject squirrel. Upon release, the dog's approach was swift and direct, and the dog never vocalized during an approach.

Aggression between color morphs.—Aggression between the color morphs was observed at feeding stations in the cemetery and at bird feeders in the residential areas. Encounters were recorded only if the sex of the individuals could be determined. Juveniles, recognized by their tail pelage characteristics (Sharp, 1958) or lack of development and turred condition of the scrotum in males, were excluded from the analyses. The activity and color of both the initiator and recipient of aggression were recorded, along with the occurrence of any chase associated with the encounter.

Aggression was defined as an overt agonistic action that elicited an agonistic or submissive response. Dominance was assumed when an individual chased another, was a victor in a "right-to-feed" encounter (Pack *et al.*, 1967), or elicited submissive behaviors, such as avoidance, retreat or rushing past at speed (Taylor, 1966). Repeat encounters between the same two squirrels were excluded as nonindependent observations, unless a role reversal was recorded.

Sunning behavior.—Winter sunning behavior of squirrels was observed during the course of their normal activities, typically foraging and feeding. An activity log (no more than two squirrels at one time) was kept using a stopwatch to determine the time spent in each activity. Eighteen black squirrels ($\bar{x} = 78.2 \pm 45.7$ min) and 23 gray squirrels ($\bar{x} = 67.3 \pm 58.4$ min) were observed for 1408 min and 1584 min, respectively. Activities recorded were foraging, feeding, traveling, alert posture, social interaction, resting, grooming and sunning posture. Duration and location (sun or shade) were recorded for each activity. Our definitions of activities were similar to those of Bakken (1959), Thompson (1977a), and Manski *et al.* (1981).

Data analysis.—The Statistical Analysis System (SAS) computer package at Syracuse University was used for statistical analysis (SAS Institute, Inc., 1982). The wariness tests were analyzed by analysis of covariance, multiple regression, and least squares means linear models. Chi-square analyses were used to test for color-based aggression, and t-tests were used to analyze sunning behavior.

RESULTS

Wariness.—We generated analysis of covariance and multiple regression models, incorporating the uncontrolled variables that may have affected squirrel response. Use of the SAS least squares means procedure, a design based on the analysis of covariance model, estimated the means of STARPLE DISTANCE for both black and gray squirrels when adjusted for the covariates (SAS Institute, Inc., 1982). Results show no differences between the means of STARPLE DISTANCE for black and gray squirrels.

These models explain much of the variation in the dependent variable STARPLE DISTANCE as indicated by the F and R² values (Table 1). The variable TOTAL DISTANCE is consistently the greatest source of variation of STARPLE DISTANCE ($P > 0.01$) in all tests except dog, when squirrel was aware of its presence ($n = 11$, not significant). TEMP was a significant source of variation ($P > 0.05$) in both dog tests and "man with whistle" tests, and WIND was significant ($P > 0.05$) in "man running" tests. The variables COLOR (of squirrel), DISTANCE TO COVER and DBH OF COVER USED were not significant sources of variation in STARPLE DISTANCE. TOTAL DISTANCE is

TABLE 1.—Mean of startle distance for black and gray morphs of *Sciurus carolinensis* adjusted by a least squares means procedure for the covariate total distance, distance to cover, color, wind, temp and DBH of cover used^a for each of the experimental threat stimuli. None of the paired means is significantly different (paired t-test, $P > 0.1$)

Threat stimulus	n (pairs)	F	R ²	Startle distance (m) $\bar{x} \pm SE$	
				Black	Gray
Dog, squirrel unaware	74	10.99**	0.50**	25.70 \pm 1.50	26.27 \pm 1.46
Dog, squirrel aware	11	1.23	0.65	38.24 \pm 7.03	24.68 \pm 4.69
Man running, squirrel aware	49	5.42**	0.44**	14.02 \pm 1.12	14.54 \pm 1.14
Man with whistle, squirrel aware	22	3.36*	0.57	39.07 \pm 2.81	32.32 \pm 3.08
Dog (pooled data)	85	10.90**	0.46**	26.49 \pm 1.45	26.43 \pm 1.37
Man running (pooled data)	57	5.65**	0.40**	13.77 \pm 1.01	13.76 \pm 1.03
Man with whistle (pooled data)	25	3.94*	0.57**	36.52 \pm 2.90	30.52 \pm 3.02
All stimuli, squirrel aware	86	14.72**	0.53**	23.00 \pm 1.44	21.17 \pm 1.44
All stimuli, squirrel unaware	87	17.05**	0.56**	23.34 \pm 1.35	24.10 \pm 1.30
All stimuli (pooled data)	173	27.89**	0.50**	23.37 \pm 1.01	22.46 \pm 0.99

^a See text for variable descriptions

* $P < 0.05$; ** $P < 0.01$

a construct of the test procedure since this initial distance was largely determined by the landscape and the location of cover for the observer, and is thus not a valid measure of squirrel response. The other variables, with the exception of COLOR, were uncontrolled environmental variables that may have biological significance in the response of squirrels to disturbance.

Aggression between color morphs.—Over 200 aggressive encounters were observed; 92 involved both color morphs of adult known-sex individuals. Twenty-one encounters involved two females, 29 involved two males, and 42 involved a male and a female. Males initiated 34 of the 42 (81%) of the male-female encounters ($\chi^2 = 16.09$, $df = 1$, $P < 0.0001$), and males were dominant in 41 encounters (98%) ($\chi^2 = 38.09$, $df = 1$, $P < 0.0001$). Neither color was significantly more dominant; gray individuals were dominant in 24 encounters (57%), and black individuals in 18 (43%) ($\chi^2 = 0.610$, $df = 1$, $P > 0.25$).

Encounters between members of the same sex should be most likely to reveal differences in aggression or dominance between the color morphs. Black and gray individuals were equally likely to initiate interactions among males (45% of 29 by black) and females (48% of 21 by black), and also were equally likely to dominate in same-sex encounters (41% of 29 by black between males; 57% of 21 by black between females). Same-sex encounters were pooled in 2 by 2 contingency tables for chi-square analysis. Comparisons show that initiators of encounters tend to be victors ($\chi^2 = 20.44$, $df = 1$, $P < 0.0001$). They also show that the color of the victor or the initiator was not related to the incidence of chasing by the victor ($\chi^2 = 0.181$, $df = 1$, $P > 0.50$). Again, no difference in aggression ($\chi^2 = 0.32$, $df = 1$, $P > 0.25$) or dominance ($\chi^2 = 0.08$, $df = 1$, $P > 0.75$) was revealed.

Sunning behavior.—No significant difference between the color morphs was found in the average length of sunning bouts, minutes spent in the sun, minutes spent in a sunning posture, or percent of time spent in a sunning posture (Table 2).

DISCUSSION

Wariness.—We found no evidence of color-related differences in wariness between the two morphs in our urban *Sciurus carolinensis* population. This suggests that innate wariness

TABLE 2.—Student's t-tests comparing means of sunning behavior parameters, excluding grooming time, between two color morphs of *Sciurus carolinensis*, n = 18 black, 23 gray. None of the paired means is significantly different ($P > 0.1$)

Variable	$\bar{x} \pm SD$		t
	Black	Gray	
Total time (min) of observation	78.2 \pm 45.7	67.3 \pm 58.4	0.65
Time (min) spent in the sun	51.3 \pm 39.1	35.3 \pm 31.4	1.45
Sunning posture bouts/h	1.9 \pm 1.4	1.8 \pm 1.4	0.29
Time (min) spent in a sunning posture	19.9 \pm 22.7	13.9 \pm 16.0	0.98
Time (%) in sunning posture	25.4 \pm 16.5	20.7 \pm 26.0	-0.52
Mean length (min) of sunning posture bout	8.7 \pm 6.4	10.7 \pm 12.6	-0.63

and conditioned wariness are not factors in the relative fitness of the color morphs. If the black morph is attacked more frequently than the gray morph because it is more conspicuous, then a corresponding increase in wariness or a similar survival strategy would be necessary to maintain a fitness equal to or exceeding that of the gray morph in a stable population (Eibl-Eibesfeldt, 1970). A higher degree of wariness (reflected in STARTLE DISTANCE) was not found. Conversely, if flight response reflects predation pressure on the gray squirrel, the results suggest that differential predation by terrestrial predators on the color morphs is not a significant factor. Dogs, and especially cats, are major predators on urban squirrels (Powell, 1982), and it is probable that neither color morph is particularly cryptic when on the ground in most urban landscapes. Raptors often take squirrels in the treetops (Barkalow and Shorten, 1973) where cryptic coloration would more likely be a factor, but our data are restricted to responses to terrestrial threats.

Some investigators have speculated that the opening up of old-growth forests by settlers made the black morph more conspicuous and vulnerable to hunters (Allen, 1943; Creed and Sharp, 1958). If the absence of behavioral differences between the color morphs exists in rural as in urban populations, then hunting may indeed be a factor in the historical changes in morph frequency. In urban areas, previously hunted populations have been protected from hunting, and the frequency of melanism in various cities may reflect the length and severity of hunting pressure before protection. However, the high incidence of melanism in rural Ontario populations would contradict this hypothesis unless some other attribute of melanism, such as increased absorption of solar radiation, offset the conspicuousness disadvantage. Clearly, further study of this question is needed.

Aggression between color morphs.—Dominance is perhaps the behavioral parameter of most consequence in the reproductive success of gray squirrels, especially among males. Dominance might increase fitness in two ways. Dominant individuals may use available resources at will, although this likely has limited fitness consequences for the gray squirrel (Pack *et al.*, 1967). The mating system of gray squirrels favors dominant males with substantial fitness advantage. When the female comes into estrus, she leads attracted males in a mating chase in which dominance is expressed as the position defended in the queue for copulation (Thompson, 1977b). Pack *et al.* (1967) found that the four dominant males among 18 attracted males were responsible for 65% of sexual contact with females. Since aggression and dominance were not found to differ between the color morphs, it is unlikely that either morph enjoys a reproductive advantage.

Limited dispersal distances of postweaning males and females, and the dominance mating

system, coupled with relatively small breeding ranges (Thompson, 1977b, 1978) result in reduced gene flow and an increase in the average relatedness of mates. This suggests that the effective size of gray squirrel demes may be quite small. This decrease in effective population size serves to promote random drift and to increase the level of inbreeding (Wright, 1938; Shields, 1982). The large variation in the frequency of melanism among adjacent Syracuse neighborhoods suggests restricted gene flow and a large random component to the processes that determine morph frequency.

Sunning behavior.—Dark colors are generally thought to absorb more radiant energy, a concept championed in detail by Hamilton (1973), although Lustick (1969) found that gray, brown and black birds gained about the same advantage from solar radiation, and only white birds absorbed significantly less radiation. Walsberg (1983) concluded that the relation between coat color and solar heating in birds and mammals is not consistent, depending on a combination of environmental and organismal properties.

The lack of differences in sunning behavior between the morphs of the gray squirrel does not provide any conclusive information about the thermal properties of color morph pelages. Should it be shown that the black morph does gain more solar radiation than the gray morph, this lack of behavioral difference will have significance for the distribution of the black morph in the northern limits of the range of the gray squirrel.

In summary, these results show no differences between the color morphs in wariness, aggression and sunning behavior. It is clear that some selective factor is different in some urban areas than in exurban areas. The abundance of melanistic forms in rural Ontario and northern Michigan suggests a somewhat different selection regime there, perhaps related to more rigorous climate. The wide variation in frequency of melanism in Syracuse suggests that drift is a factor in local frequency variations.

Acknowledgments.—We thank Vagn Flyger for encouraging us to do this research and for his critical review of this manuscript. Our appreciation also is extended to Robert L. Burgess, William M. Shields, Richard W. Thorington, Jr., and an anonymous reviewer for their review of earlier drafts of the manuscript.

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SUBMITTED 12 DECEMBER 1988

ACCEPTED 24 APRIL 1989