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Edward W. Lueninghoener University of Nebraska at Omaha

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AN INVESTIGATION OF THE MELANISTIC PHASE OF THE WESTERN FOX SQUIRREL (Sciurus niger rufiventer) IN EASTERN NEBRASKA AND WESTERN IOWA

A Thesis

Presented to the

Department of Biology

and the

Faculty of the Graduate College
University of Nebraska at Gmaha

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

by

Edward W. Lueninghoener

November, 1973

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THESIS ACCEPTANCE

Accepted for the faculty of The Graduate College of the University of Nebraska at Omaha, in partial fulfillment of the requirements for the degree Master of Arts.

Name	Department
Dairl M. Sutherland	Biology
Selton Herdrick	Psychology

Chairman S. Sharps

Dec. 3, 1973

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INTRODUCTION

The largest member of the tree dwelling North American squirrels is the Fox Squirrel (Sciurus niger Linnaeus). This species inhabits the eastern half of the contiguous United States. Its normal habitat is open woodland though the Fox Squirrel along with the Grey Squirrel (Sciurus carolinensis Linnaeus) may be found in some thickly wooded areas. The Fox Squirrel has extended its range farther west in response to the large number of trees that have been planted on the former prairie of the great plains (Yeager, 1959). The range of the Fox Squirrel is plotted in Appendix I, Figure 1 after Hall and Kelson, 1959.

The species S. niger has been divided into ten subspecies as listed by Hall and Kelson, 1959. The subspecies in the Nebraska and Iowa region is Sciurus niger rufiventer (Western Fox Squirrel) as described by E. Geoffroy St. Hilaire in 1803. The largest range for any of the ten subspecies is the one occupied by the Western Fox Squirrel (Fig. 1).

The normal color phase of the Western Fox Squirrel in the Iowa and Nebraska region is rufous. There are a number of variations in the color phase, one of which is melanistic, the focal point of this study.

The Melanistic Phase

Melanism is very common among the member species of the order Rodentia. The species S. niger is no exception. All the subspecies other than S. n. rufiventer have common melanistic phases, but their melanistic phases have areas of white hair, usually on the ears, chin, feet or tail. The above mixture of characteristics is not normally found in S. n. rufiventer. Furthermore of the 112 black individuals that I observed none had white areas visible on any parts of the body. This is not to say that there are not Western Fox Squirrels with white

areas or completely white bodies within the study area. There has been a small population of completely white Fox Squirrels in southwestern Douglas County, Nebraska for at least the last five years (per. com. Richard Wilson, game warden). There is also documentation in southern Missouri of melanistic Western Fox Squirrels with white areas of hair similar to those previously described. The white squirrels in Douglas County are an example of albinism and the ones in Missouri are caused by the mixing of the gene pools of S. n. rufiventer and S. n. ludovivianus, S. n. subauratus or S. n. bachmani (Terrill, 1941).

Audubon in his Missouri River Journals (1843) gave an accurate description of the melanistic phase of the Western Fox Squirrel. He mentions having first seen the black phase close to St. Joseph, Missouri and continued sighting it until his boat had passed Council Bluffs. What he calls Council Bluffs is a bluff on which Lewis and Clark met with a group of chiefs of the Otoe and Missouri tribes. This is believed to be just north of the present town of Missouri Valley, Iowa.

After examining the black squirrel, Bachman, who was with Audubon, gave it species rank (Sciurus audubonii), believing it to be separate from S. n. rufiventer which at that time was known as S. macroura (Say, 1819) or S. magnicaudatas as the squirrel was listed in Harlans's Fauna Americana (1825). This discrepancy was later resolved by recognition of the black squirrel as simply a melanistic phase of S. n. rufiventer.

Baumgartner (1943b) mentions in his pelage study having seen two stuffed black phase Western Fox Squirrels in taxidermist's shops in Ohio. Terrill (1941) mentions that the completely black phase is common in southern Missouri along with the previously mentioned black phase individuals with areas of white hair. Townspeople of Marysville, Kansas call the town the black squirrel community. There is little else of a scientific nature printed concerning the black phase.

Causes for the maintenance of melanism in an animal population and the reasons for its occurrence along with the distribution of phases have been studied by many. There are two main points that have been fairly well established. The first is that melanism is present in the gene pool of almost all animal genera and actually in most animal species. The second is that melanistic populations are greatest in number close to the equator and become fewer further north or south. Hamilton (1973) claims that melanin actually proves to be an advantage to desert species in that most deserts have tremendous temperature fluctuations daily and the black individuals are able to maintain activity later in the evenings and start activity earlier in the mornings than similar individuals with other than black coloration. The reason is that heat absorbtion by the black color is more efficient than any other color. During mid-day when temperatures are extremely warm almost all desert species have retreated to their burrows or shade of some sort. At these times the melanistic individuals do lose some activity time because of the heat buildup and retention in their bodies, but Hamilton believes this to be more than made up for by the activity periods gained in the cold early mornings and late evenings.

Hamilton (1973) also tried to apply his theory to tropical areas and species. If these observations are correct they might explain the high rate of melanism in the southern subspecies of the Fox Squirrel. It is easy to hypothesize that melanism decreases in the higher latitudes because even though its heat absorbtion capability would be an advantage, its obviousness to an enemy during periods of snow cover would be a definite disadvantage.

Life History

The Western Fox Squirrel normally breeds from December 15 to the end of March with a second season possible during May, June and July. The gestation period is 45 days and those squirrels that mate early have their young in early February. The young are hairless, weighing two-thirds of an ounce at birth. The coat is present at

two weeks of age. The young are weaned at five to six weeks of age and leave the nest at six to ten weeks of age. The young are capable of cracking a walnut at 60 days (Svihla, 1931) and leave their parents at 75 to 90 days. Maximum life span is believed to be seven to nine years (Burton, 1962).

Most researchers agree that there is a second breeding season during the late spring and early summer during which two-year-old or older females raise a second litter. First year females usually raise only one litter (Baumgartner, 1940). Since sexual maturity is not reached until at least eight months of age, females must be almost a year old before mating.

Some researchers claim that the Fox Squirrel is monogamous (Allen, 1942 and Burton, 1962), while others believe them to be promiscuous. Most authors do agree that after mating, the male remains solitary and leaves the rearing of the young to the female.

METHODS

This study was originally proposed to have three parts: 1) an attempt to interbreed the two phases to learn something of the genetic control of the melanism; 2) a population study of the Council Bluffs area to estimate the incidence of melanism in the Western Fox Squirrel population; 3) a study of the distribution of the melanistic phase in eastern Nebraska and western Iowa.

The Breeding Experiment

For the breeding attempt, cages were constructed out of two by four's and fine mesh chicken wire. These were made four feet by four feet by eight feet tall. Two story den boxes made twelve inches wide by seven inches deep by eighteen inches high were put in each cage.

Squirrels were then live-trapped in Council Bluffs using four different types of traps. Homemade wooden traps were built resembling those built by Baumgartner (1940) with one exception. He put a pane of double strength glass in the end opposite the door to the trap. I constructed these traps without putting the pane of glass in the blind end of the trap.

Other traps that were used were the Havahart live traps No. 2 and 2A, 3 and 3A and the No. 4 trap. The bait used was ear corn, walnuts, dry dogfood, apples and peanuts. Trapping was carried out in three different locations, all of which were fenced yards in residential districts. After capture the squirrels were transported to the University's Allwine Farm where the cages were located. The diet of the squirrels then consisted of dry dogfood, walnuts, apples and corn.

Estimate of the Population in Council Bluffs

The next portion of the study was to estimate the squirrel population in Council Bluffs. The population study was done using

an inventory method described by Hicks (1942) called the spot count method. To use this method two adjacent areas are chosen, each of the same size and vegetational characteristics. Each must be large enough so that it takes approximately 30 minutes to walk through, covering the entire area.

After walking through the first area and recording the squirrels seen, the observer enters the second area and repeats the process. After walking through the second area the observer returns to the first area and begins again, repeating the process in both areas. Each area has then been visited twice for a total of 60 minutes. The total number of squirrels seen on both tours through each area is totaled. This is done regardless of squirrels that may have been counted twice. It is assumed that those observed repeatedly will make up for those that were not seen on either survey of the areas. The total number observed is then considered the population for these areas.

In Council Bluffs the city blocks are rectangular in shape, narrow enough so that walking along a street the observer could cover a half block area on either side during the winter when trees are leafless. What the observer actually is covering would be a full block from alley to alley if the observer walks along the street. It took between 25 and 35 minutes to walk four linear blocks and then walk over a block and back along the four blocks and across to the starting point. Then, by skipping one block, the observer could sample a new area of the same size (Appendix II, Fig. 2).

The actual size of each one of the sample areas would then be ten square blocks with two of these sample areas, or 20 square blocks, being covered in each spot count area. There were seven of these spot counts made in the city, totaling 140 square blocks of area sampled.

Because there are three different city block sizes in Council Bluffs and because part of the town is built in the bluff area along winding streets with no definite blocks, it was difficult to compare results of the population survey between areas. Therefore an aerial

photograph of the city of Council Bluffs was obtained from the U. S. Soil and Water Conservation Service Office in Pottawattamie County. A grid was made with the squares corresponding to the middle sized city blocks on the floodplain area of the city (Appendix II, Fig. 3). This grid was then applied to the total aerial photograph with the number of habitable blocks being counted. Since the photographs used were taken during the late spring or early summer it was easy to pick out large business areas and other treeless areas that would offer no squirrel habitat. These areas could then be subtracted from the total habitable area of the city.

Later I returned to each of the sample areas and counted all the prominent trees in each of the 140 blocks of sample area. Prominent trees were those that could be considered squirrel habitat. The smallest of those counted were at least 15 feet tall.

It would also appear to be simpler to find the total acreage of the city and use the number of squirrels per acre as a basis for finding the total population. Though it might appear easier it really is not in an urban area. For the spot count method, blocks make excellent units of measure. They are well defined and even though there is some variation in size, by making the grid that was described earlier and applying this to an aerial photo and not counting treeless areas, the habitable block area of the city should be accurate. The biggest problem is selecting blocks of the same size to match those used to make the grid, in order to implement the actual spot count.

From January through April all squirrels seen at any time in Council Bluffs were recorded. This was done to obtain a large sampling on which to base an estimate of the percentage of the total population of Fox Squirrels that is made up by the black phase. Records were kept of location, type of tree if on a tree, time of day and atmospheric conditions. The method used was simply driving through Council Bluffs residential districts at ten miles per hour and recording all squirrels observed. There was always a driver plus a passenger doing the observing for maximum coverage. Areas observed

were selected randomly within all vegetational and geographical areas of the city.

The Distribution of the Melanistic Phase in Eastern Nebraska and Western Iowa

The last part of the study, plotting the distribution of the melanistic phase in eastern Nebraska and western Iowa was accomplished with the aid of the conservation officers of both states. A letter and questionnaire were sent to 18 officers in Iowa and 21 officers in Nebraska (Appendix V, Figs. 17 and 18).

RESULTS OF THE STUDY

Results of the Breeding Experiment

In the trapping for the breeding experiment, the wooden traps lacking the glass pane were unsuccessful. In fact these traps were not visited at all by the squirrels. It became obvious that previous literature was correct in suggesting a squirrel would not enter the trap unless it could see all the way through it.

Havahart rodent traps No. 2 and 2A were tried but they proved unsuccessful. There were two reasons for this: 1) both traps are too short to cover the Fox Squirrel's tail at the time the animal tripped the trap; 2) the mesh along the bait area is large enough so that a squirrel could reach through the side for the bait and trip the trap without ever entering the trap.

The ways to get around these problems are to use either a larger trap such as the 3 or 3A Havahart series or to use the Havahart No. 4 which is made much longer than the No. 2 and 2A. The No. 4 is also made of hardware cloth. The mesh is fine enough to protect the bait from being obtained by reaching through the side of the trap. The Havahart live traps 3, 3A and 4 all worked well with the No. 4 working the best.

After being trapped the squirrels were taken to the cages previously described. Trapping started the second week in September and continued until December 1st. It was originally believed that the squirrels would breed later in December.

The above part of the study proved unsuccessful because of following problems. The area in which the cages were kept proved to be too remote for me to care adequately for the animals during the winter, the effects of the shock factor described by Allen (1942) and Baumgartner (1940) and the wire used in constructing the cages proved inadequate.

Since breeding in captivity was not possible the major emphasis of the study became the investigation of individuals in a wild setting. This was done in Council Bluffs, Iowa. Two different instances of mating or attempted mating between the melanistic and rufous phases were observed. The first instance observed on January 25, 1973 occurred in a cottonwood tree at 23rd and I Street. In this case there were two red males and one black male attempting to mate with a single red female. The action was watched for approximately 45 minutes, during which time the female remained extremely unresponsive. During this time it also became obvious that the dominant male would drive away the other two males to win the favor of the female. One of the red males proved to be dominant over the remaining red male and the black male. The black male, though, proved to be dominant over the remaining red male. The black male stood second in the dominant hierarchy that was established concerning mating attempts with the single red female.

The normal chain of events during this mating chase were that the dominant male would advance toward the female and be refused, he would then turn and attack the black male and drive him a greater distance from the female. The black male would then do the same thing to the other red male. After the attack on the black male the dominant red male would resume attempts to mate with the red female. During the dominant male's courting attempts, the black male would slowly approach the female and behind him the third male would approach until the black male came too close to the dominant red male and was driven off. This process was repeated several times.

The second mating observed occurred in an ash tree along the school yard that is on the northeast corner of 32nd Street and Avenue B. In this case two red males were attempting to mate with a single black female. This time one red male was driven off during actions similar

to those related above and mating was accomplished at least once and possibly twice in the approximately 30 minutes that was spent observing these three squirrels.

The results of this mating were not observable because the tree in which the mating took place had neither den holes or a nest, suggesting that the tree may not have been important in this female's home range. The area in which the mating was observed averaged over 1.1 squirrels per square block of which almost 30% were black (see Appendix III, Fig. 5). Even though each squirrel would have a home range, each one's home range is overlapped by many others. Therefore, any attempt to identify this specific female was impossible since she bore no distinguishing marks.

From the few mating attempts observed it is tentatively concluded that random mating does occur without regard to the color phase of the squirrels involved and with neither phase being dominant in the "peck order" that might be established. Furthermore, whereas many researchers have claimed that Fox Squirrels mate for life (Burton, 1962 and Allen, 1942), it seems that the mating chase as described by Baumgartner (1940) was participated in by more than one male squirrel and a single female. In both instances cited, the dominant male mated with or was obviously in position to mate with the female when she was receptive. The actions of the female in both cases resembled in many ways those of a female domestic cat during mating. Both observations tended to refute the belief that Fox Squirrels mate for life.

During observations of the Western Fox Squirrel population in Council Bluffs, a red and black mixed individual was seen at 2323 South 8th Street. This individual had a distinctly black body including the base of its tail, with the rest of the tail being red. There was only one other individual out of almost 300 squirrels that I observed that might possibly have been bicolored. This one was never observed distinctly enough to determine the color distribution.

Since the breeding experiment had failed, but mating between the phases had been observed in the wild, it seemed logical that a two-colored squirrel could be the result of such a mating, provided the genotype for melanism is not a simple Mendelian trait.

In an attempt to gather additional information on partial melanism, I published a request in a local newspaper requesting information from Umaha and Council Bluffs residents who had observed bicolored squirrels in their neighborhood. The response included five separate locations and descriptions of black squirrels with red tails. There was also one call describing a squirrel that was black dorsally with the ventral side red. Later a letter was received, along with a color slide, from a conservation officer in Fort Dodge, Iowa, who had never observed a completely black squirrel in his area, but had periodically seen those that are black ventrally with the back and tail red.

Baumgartner (1943b) describes two variations from full melanism he found in Ohio. His pelage study revealed morphological types which were completely black, black ventrally with the dorsal side and tail red and black dorsally including the tail with the ventral side red. The slide received from the conservation officer and one response to the published request matched Baumgartner's color variations. Notice that all of Baumgartner's variations have the back and the tail the same color.

My observation of the melanistic phase apparently adds a fourth color combination, that of black with a red tail. This combination, as previously described, has a totally black body and tail base with the rest of the tail red.

Genetic Control

A logical explanation for the above is that the melanin is controlled by at least three different sets of alleles, probably many more (Quevedo, 1971), combined in a supergene complex. The basis for this statement is that since common interbreeding between the phases appears to take place in the wild, and since it cannot be

a single gene that controls at least five different color combinations. and since the majority of the offspring must be either black or red or the mixed individuals would be more common, it logically follows that melanism in the Western Fox Squirrel is controlled by a supergene that has two weak points. The genes would have to be so arranged so that all those responsible for ventral coloration would have to be close together, those responsible for dorsal and tail coloration would have to be close together, with a weak point between those genes controlling dorsal and tail coloration and another weak point between the genes controlling ventral coloration and those governing dorsal coloration. More support for this theory is present in the work by Quevedo (1971) in which Mus musculus, also a member of the order Rodentia, has been shown to have as many as 70 genes at 40 different loci controlling the various aspects of melanism. actual number of genes controlling melanism in the Western Fox Squirrel could only be estimated after extensive interbreeding of the two phases.

Normally it appears that the "supergene" is inherited as a simple dominant, acting as one gene that causes complete melanism. Support for this comes in reports from Omaha and Council Bluffs residents that have observed mixed mating on their property and that the results of these matings were offspring colored either completely black or completely red. It cannot be stated positively, but from the limited reports it appeared that the black offspring may outnumber the red offspring from a mixed mating.

There does seem to be a slight variation in the degree of expression of this supposed "supergene". Many black squirrels have a reddish tinge but some of this was explained by Moore (1956) who stated that he considered reddish-black hair to be old hair which was replaced with dark black hair during the yearly moult in the spring. This yearly moult can make a squirrel appear slightly bicolored since it normally proceeds from the nose to the tip of the tail with a strongly defined line between the new and the old hair (Baumgartner, 1943b).

Results of the Population Study

Beginning in January, 1973 all squirrels seen while I was in Council Bluffs were recorded as to color, location and type of tree or other object that they were seen upon. The information in Appendix III, Figure 4 and Appendix IV, Figure 8 was gathered by the method of driving through residential areas at approximately ten miles per hour. This sampling was done randomly so that residential and business areas were sampled in both the floodplain and bluffs area of the city.

An interesting result of this is shown in Appendix III, Figure 6. Though statistically insignificant, it appears that on cold days (below 44° F.) more black phase than red phase squirrels were seen. There are a number of possible reasons for this. One is that the black phase may be easier to spot than the red phase when snow is present. Since these observations were made in January, February and March during which snow was present most of the time, this could have been a factor.

Another explanation is that the black hair absorbs much more warmth from the sun, making activity possible during colder temperatures than those at which the red phase would be active. Studies of this type involving desert insects were mentioned earlier (Hamilton, 1973). To obtain statistically significant evidence careful studies of the same areas on different days when temperatures were above or below 44° F. would have to be conducted. The reason for selecting 44° F. is that this is the median of the optimum temperature range of 40° to 48° F. suggested by Hicks (1949).

The population estimation method implemented was that used by Hicks (1942) which has previously been described. During the survey 109 squirrels were sighted in 140 blocks of survey area, an average of .78 squirrel per square block. Using the aerial photograph described in the methods section, the city blocks that I considered good squirrel habitat were counted. This totaled 2,162 habitable blocks. Extrapolating, the Western Fox Squirrel population in Council Bluffs approximates 1,685 individuals.

As was mentioned earlier all squirrels observed in Council Bluffs were recorded. This included many more squirrels than those counted in the population study. All the squirrels counted, including those in the population study, totaled 248. Of this, 112 (45.2%) were black and 136 (54.8%) were red. For the total population it would be 762 (45.2% of 1,685) black phase and 923 (54.8% of 1,685) red phase squirrels.

A completely different impression for the squirrel population can be derived if the habitable blocks are divided into floodplain blocks and upland blocks. Of the 2,162 blocks in the city, 1,126 are floodplain blocks and 1,036 are in the bluffs area of the city and would be considered upland blocks. The floodplain blocks surveyed by the spot count method averaged 1.01 squirrels per block. Extrapolating for the 1,126 floodplain blocks, there would be 1,137 squirrels on the floodplain.

The upland area only averaged .20 squirrels per block. The uplands, according to the above method, would then have a population of 207 squirrels. Using this method, Council Bluffs would then have a Western Fox Squirrel population of 1,344 individuals. Applying the phase percentages previously stated it would mean that there are 607 (45.2% of 1,344) black phase and 737 (54.8% of 1,344) red phase squirrels within the city limits of Council Bluffs, Iowa.

The above figures appear very low. One probable cause for this is that the survey was conducted in March, before any newborn squirrels had left the nest. This theory is supported by the fact that no immature squirrels were recorded during the spot count survey. The actual population that was counted, the adult population, was at its yearly low. There could easily be a high during the summer months, counting immature squirrels, that could exceed 2,500 individuals greater than the population estimate. This statement is based on an estimate that approximately half the adult population consists of females capable of bearing at least one and possibly two litters of young that average four young per litter (Baumgartner, 1938 and Jackson, 1961).

While the population study was being conducted, the species of tree that each squirrel occupied at the time of sighting was recorded and later these areas were surveyed to determine the species composition and relative density of the predominate trees in each of the areas. This data is contained in Appendix IV, Figures 7, 8, 14, 15 and 16. A combination of the various data contained in these Figures is presented on the graphs in Appendix IV, Figures 9 through 13. Each of the first seven graphs records the vegetational characteristics for each study site combined with the number of squirrels of each color phase that were observed upon each tree type. The eighth graph combines this data.

The graphs 1 through 4 and 7 represent floodplain areas, while 5 and 6 represent surveys in the bluffs area of the city. In most areas of the city the elm is still the dominant tree despite the effect of dutch elm disease. There were several species of elm but these were not separated. The number of squirrels seen in the elm trees was also the highest number seen in any of the tree types, 21 red and nine black within the survey region.

Maples were the next most common tree. The maples also had the next highest number of squirrels recorded, 13 red phase and 13 black phase. Within the survey area of 140 square blocks the elms and maples outnumbered all other trees tall enough to be considered squirrel habitat. The squirrels seen in the elms and maples also outnumbered all the squirrels in all the other tree types in the survey area, including those not seen upon trees and recorded as seen on "other" (Appendix IV, Figure 7).

Ash trees were third high in numbers but ranked fourth high in squirrel occupants. Cottonwoods, by far the tallest trees in the survey area, ranked fourth in abundance but third in squirrel inhabitants. Some tree species such as sycamores seldom contained squirrels.

Of the seven sample areas, three had obviously fewer trees than the other four areas. These areas are the two areas in the bluffs district of Council Bluffs and an area in south central Council Bluffs. This last area is relatively isolated from the rest of the city having large railroad yards on the north and east side, a newly constructed Interstate highway on the south and open farmland on the west.

In the bluffs area there were very few squirrels observed, .20 per block as compared to 1.01 per block for the floodplain. This may reflect the scarcity of good habitat in the bluffs. Though there were many trees on the sides of the steep bluffs, many of these being non-residential areas, the majority of the trees were young and not yet large enough to be good habitat. Another reason was the reduced numbers of favored trees such as elms and maples. Since squirrels make extensive use of buds as food, Baumgartner (1939) rates elm and maple buds and seeds more important than walnuts and acorns, the lack of these trees could reduce the squirrel population the area can support.

The other area with few trees is between 8th and 11th Streets and 23rd and 27th Avenues. This area contained a mixture of old residential with a few large old trees and new residential with many young trees but few large enough to be considered good squirrel habitat. There was also a school and a park in the sample area, each covering one city block and each block then having very few trees. This area did have a better than average squirrel count however, containing .85 squirrels per block as compared to .78 squirrels per block for the whole survey. Of course this is less than the average for only floodplain blocks (1.01 to .85).

The reason why this area with fewer than average trees was able to support the squirrel population that it did could be explained by the fact that the majority of the trees in the area were old trees providing excellent squirrel habitat. This area was also one of only two areas where maples are more numerous than elms.

Human Effects Upon an Urban Squirrel Activity

There was one other problem in observing these squirrels that has not as yet been mentioned. Human activity had a definite effect on the urban squirrel. Where most researchers studying rural squirrels

claimed that activity was greatest from 7 to 8 A.M. and least from 2 to 5 P.M. (Hicks, 1949), it appeared that rush hour traffic and children going to and from school altered the squirrel activity during these periods, with greatest squirrel activity occurring between 9 A.M. and 3 P.M. There also was observed a period of reduced activity centered about noon, probably caused by increased human activity at lunch time.

Distribution of the Melanistic Phase in Eastern Nebraska and Western Iowa

The last portion of this study was concerned with the distribution of the black phase in eastern Nebraska and western Iowa. One of the original hypothesis concerning the melanistic phase was that it was probably present only in urban areas. This theory was based on a belief that during the winter months the black phase would be much easier for a predator to see and much easier for a hunter to find. The urban squirrel would be protected from both types of predation.

The first hint that this hypothesis was not correct was contained in Audubon's Missouri River Journals (1843). The fact that Audubon saw the black phase here at that time meant that the black phase was able to survive its natural predators without any help from a city's protection.

To plot the black phase distribution and to find out if the black phase could survive the increased pressures in rural areas, questionnaires were sent to 18 conservation officers in Iowa and 21 conservation officers in Nebraska. Baumgartner (1943a) obtained similar help from rural postmen. Examples of the questionnaire and letter sent with it to explain it are shown in Appendix V, Figures 17 and 18.

Of the 18 questionnaires sent to Iowa officers 17 were returned. The results show that the black phase is present in rural areas. The map in Appendix V, Figure 19 has areas shaded in which conservation officers reported seeing the black phase. Where counties were

mentioned as containing black phase squirrels, the entire county was shaded, but where specific areas were stated, only those areas were shaded. As can be seen from the map, not all melanistic individuals are distributed along the Missouri River drainage system. Those in Webster, Worth and Cerro Guardo counties are all along the Mississippi River drainage system. This casts doubt upon any theory that the black phase migrated along the Missouri and spread into Iowa along the Missouri's tributaries. The black phase is also present in Evanston, Indiana and Rock Island, Illinois, proving that the black phase is well established along the Mississippi drainage system.

The Nebraska conservation officers returned 16 of the 21 that were sent. The results are shown in the shaded areas on the map in Appendix V, Figure 20. Nebraska doesn't have as high a population of the black phase nor as dense vegetation as Iowa. There are black squirrels present in small numbers in Omaha, Bellevue and other towns in eastern Douglas, Sarpy, Cass, Otoe, Nemaha and Richardson counties. They are also present in small numbers in the rural areas of these counties. All of the above counties are along the Missouri River.

There is a good chance that imported black phase individuals have altered the population distribution picture in the two states. The conservation officer in Council Bluffs knew of many instances where black squirrels were trapped and relocated. The conservation officer at Onawa, Iowa stated that black squirrels had been imported from Council Bluffs, but so far the stocking had proven unsuccessful.

The above probably explains the populations in three central Nebraska towns, Fremont, Fairbury and Hastings. Though little is known about Fairbury and Hastings, the Fremont population is supposed to have descended from black phase squirrels imported from Council Bluffs.

Whereas most of the populations do occur in urban areas, there are many of the black phase in rural areas, particularly in Iowa and extreme southeastern Nebraska. The environment, including predators and hunters, does not seem to have selected against the black phase strongly enough to confine it just to urban areas.

SUMMARY

The study was proposed to have three parts, a breeding attempt, a population study of Council Bluffs and a study of the distribution of the melanistic phase in eastern Nebraska and western Iowa.

Squirrels were live-trapped in Council Bluffs and then transported to the University's Allwine Farm. The trap that worked best was the Havahart No. 4. Because of difficulties that arose such as the distance to the farm, difficulty in confining the squirrels and the losses to what was probably a drop in blood sugar in the caged animals, the breeding experiment was dropped.

In field observations two specific instances of mixed matings were observed. In addition, one bicolored squirrel was observed. Seeking more information concerning the number of bicolored squirrels in the area, a request for information was published in the Cmaha newspaper. Five of the responses to this were descriptions of squirrels with black bodies and red tails. These matched the color combination of the one I had observed in Council Bluffs. There was also one description from a Council Bluffs resident and a slide from a game official in Fort Dodge, Iowa that matched Baumgartner's pelage study (1943b). The black squirrel with a red tail that I observed does add another variation to the Western Fox Squirrel's coloration as described by Baumgartner (1943b).

It can be hypothesised from the information gathered that the two phases interbreed in the wild and that the genes controlling the color of the individual are at least composed of three different sets of alleles, probably many more, combined in a supergene complex.

The estimate of the population for Council Bluffs was completed using the spot count method described by Hicks (1943). Using this method, 140 blocks, in various areas of the city, were inventoried. A total of 109 squirrels were seen during the inventory, or an average of .78 squirrels per block.

The total number of habitable blocks of the city were counted using an aerial photograph. The total number of blocks within the city that were habitable totaled 2,162. There would then be approximately 1,685 Western Fox Squirrels in Council Bluffs (.78 x 2,162).

During all the observations in Council Bluffs a total of 248 Western Fox Squirrels were observed. Of this total, 45.2% were black phase. There would then be approximately 762 black phase and 923 red phase Western Fox Squirrels in Council Bluffs.

The trees in the survey areas were counted and recorded. There was a relationship between the number of trees in an area and the population of squirrels the area could support. Elms and maples were dominant, these two combined outnumbered all others combined.

Questionnaires were sent to 18 game officials in Iowa and 21 officials in Nebraska in an effort to plot the black phase distribution. It was found that the black phase is present along both sides of the Missouri River from the southern border of either state continuing north until just north of the Omaha-Council Bluffs area. The black phase is present in a number of counties in Iowa east of the Missouri River. Some of these counties actually are on the Mississippi River drainage system. There are also a few isolated cities in both states that contain a small population of black phase squirrels. The accuracy of this information has been affected by the importing of black phase squirrels by residents of these cities. The results of the questionnaires also show that the black phase is more common than previously expected and is present in both urban and rural areas.

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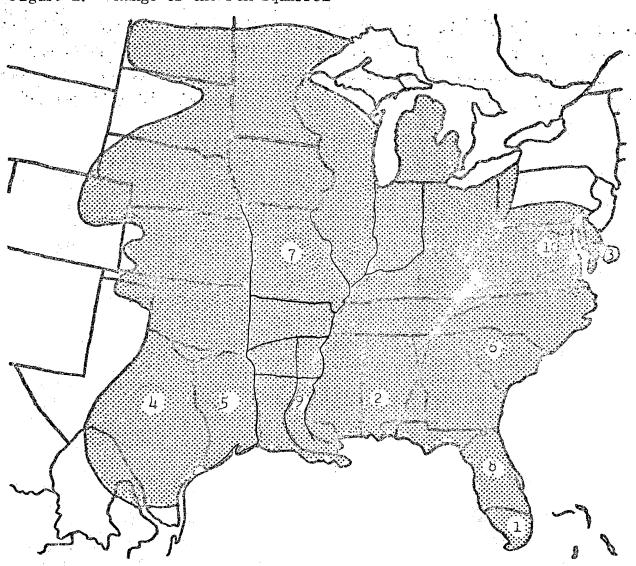
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APPENDIX I

RANGE OF THE WESTERN FOX SQUIRREL

This was taken from Hall and Kelson (1959). The range of the Western Fox Squirrel is area 7 within the shaded portion of the map. Figure 1.— Range of the Fox Squirrel



- 1. S. n. avicennia
- 2. S. n. bachmani
- 3. S. n. cinereus
- 4. S. n. limitis
- 5. S. n. ludovicianus
- 6. S. n. niger
- 7. S. n. rufiventer
- 8. S. n. shermani
- 9. S. n. subauratus
- 10. S. n. vulpinus

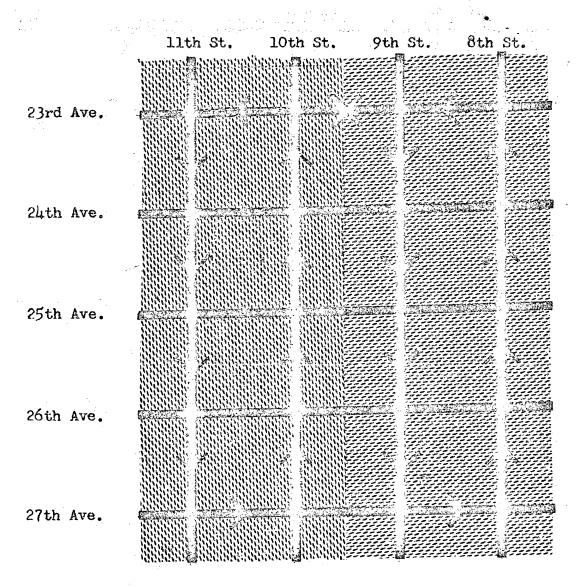
APPENDIX II

METHODS USED DURING THE SPOT COUNT SURVEY

During the actual counting of the squirrels the areas selected were traversed in the method shown by the arrows in figure 2. The actual size of the city blocks as they appeared in the aerial photographs used are represented by the grid in figure 3.

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Figure 2.--Method of Conduction for the Spot Count Population Survey



Represents sample area 1
Represents sample area 2

Arrow represents the direction of movement Each sample area was visited twice

Figure 3.--Example of the Grid Used to Count Habitable Blocks Using an Aerial Photograph of Council Bluffs

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APPENDIX III

RESULTS OF OBSERVATIONS OF THE WESTERN FOX SQUIRREL

Figure 4 represents all the squirrels observed other than those counted on the days when the population study was being conducted. The totals in figure 4 were combined with those in figure 5 (Results of the Population Survey) to obtain a color phase ratio for the entire population. Figure 6 shows what appears to be a relationship between squirrel activity and the temperature.

Figure 4. -- Results of Observations Other Than the Population Survey

Area	Phase	No. Observed	
Lake Manawa	Black Red	l ₁	entroteche entri Principosemi, mento entre consenti esta por
South Central	Black Red	17 14	
Northwest	Black Red	2° 4	
Bluffs North	Black Red	2 1	\$ a d ≥ _{Mare} .
Bluffs North and South	Black Red	8 16	
Northeast	Black Red	6 4	
Southwest	Black Red	15 10	
Northwest	Black Red	7 5	
Total	Black Red	61 54	ngganga mendhing anis maganilanang combernarang mendranca

Figure 5. -- Results of the Population Survey (Spot Count)

Area	Phase	No.	No. of Blocks
Floodplain, southwest (2nd to 5th Ave. and 31st to 35th St.)	Black Red	10 7	20.
Floodplain, northwest (Ave. A to D and 31st to 35th St.)	Black Red	8 20	20
Floodplain, northeast (Ave. D to G and 21st to 25th St.)	Black Red	9 19	20
Floodplain, southeast (3rd Ave. to 6th Ave. and 16th to 20th St.)	Black Red	47	20
Bluffs, south (Franklin, Platner, Bloomer and Carson)	Black Red	0	20
Bluffs, north (Benton, Harrison, Harmony and N. 1st St.)	Black Red	3	20
Floodplain, south (8th to 11th St. and 23rd to 27th Ave.)	Black Red	10 7	20
Total.	Black Red	45 64	140

Figure 6. -- Comparison of Temperature to Squirrel Activity

Date	Temperature	Black	Red	crhess Pibliotic soulists auth
Feb. 15, 1973	17° F.	15	8	
Jan. 28, 1973	22° F.	8	12	
Feb. 17, 1973	29° F.	6	3	
Feb. 8, 1973	22° F.	7	5	
Feb. 18, 1973	37° F.	12	15	
Feb. 25, 1973	33° F.	2	1.	
Total	E CHANGONE PHOTOMOCIONICOS CONTICOS ANGENTOS ESTA CONTICO PRIMES E COMPOSTO POR QUE LA BORRA TRANSPORTAR.	50 .	44	
Date	Temperature	Black	Red	HILLIAN AND THE CONTROL AND
Jan. 25, 1973	46° F.	3	5	
Feb. 22, 1973	48° F.	8	16	
Mar. 30, 1973	49° F.	18	18	
Mar. 26, 1973	58° F.	18	27	
Mar. 6, 1973	56° F.	2	Ls	
Mar. 27, 1973	62° F.	13	19	
Total	Landoninal Cristica Rock in una bissimissione de la AMB Bestinde de Wale Michael Cometic (pepperson	62	89	

APPENDIX IV

COMPARISON OF THE VEGETATIONAL ANALYSIS AND SQUIRREL SIGHTINGS

The figures contained in this Appendix represent the squirrels observed according to the type of tree each was seen upon and the area in which the observation was made. There are also listings of the tree numbers by type per area of observation. The graphs then combine the above so that a comparison of the number of squirrels of each phase and the type of tree they were observed upon can be compared to the number of trees in the area.

Figure 7. -- Squirrels Versus Tree Types in the Study Area

Column Date Area L 23-27 Ave. R 3-30-73 8-11 St. В 3-30-73 Bluffs R Q Q Q O \mathbf{B} O Q Q South 3-6 Ave. R 3-29-73 16-20 St. В 3-29-73 Bluffs R В 3 . North D-G Ave.] 3-27-73 R 21-25 St. В 2-5 Ave. L 3-26-73 R 31-35 St. В Ó 3-26-73 A-D Ave. \mathbf{R} 31-35 St. В Total R

R: Red phase B: Black phase

Ave.: Avenue St.: Street

Bluffs South: Franklin, Platner, Bloomer and Carson Streets.

B

9.

Bluffs North: Harrison, Harmony, Benton and North 1st Streets.

Column	l:	Ash '	6:	Maple		
	2:	Cottonwood	7:	Oak		
	3:	Elm	8:	Sycamor	·e	
	4:	Hackberry	9:	Willow		
	5:	Ironwood	10:	Other:	anything	0

10: Other: anything other than a tree

Figure 8. -- Squirrels Versus Tree Types Outside the Study Area

Date	Area	F-264-9-84	1	2	3	4	5	- 6	7	8	9	10
3-27-73	Lake Manawa	R B	0	0	0	0	0	0 3	0	0	0	0
3-18-73	Far South	R B	0	0 0	0	0	0	5 0	0	0	0	5 0
3-06-73	North West	R B	0	0	0	0	0	3 2	0	0	0	0 0
2-25-73	Bluffs North	R B	0	0 0	0	1	0	0	0	0	0	0
2-22-73	Bluffs No. & So.	R B	0	5	5 1	0 0	l 1	0	3 0	0	0	2 2
2-18-73	Far South	R B	3	1	4	0	0	0	1 3	0	.2	3
2-17-73	North East	R B	2 1	0 0	0	0	0	1 2	0	0	0	1 1
2-15-73	South West	R B	0	4	2 4	0 0	0	2 6	0 2	0	0	2
2-08-73	North West	R B	0	1	2 1	0	0	0 5	0	0	0	2
Total	and the second of the second control of the	R B	5 1	11 5	14,	1 2	1	6 23	4 6	0 1	2	10 12

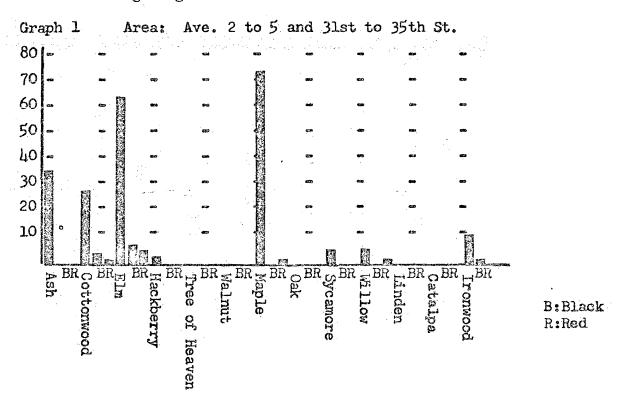
R: Red phase

B: Black phase

Everything not labeled bluffs was on the floodplain area of the city.

Column	1:	Ash	6:	Maple
	2:	Cottonwood	7:	Oak
	3:	Elm	8:	Sycamore
	4:	Hackberry	9:	Willow
	5:	Ironwood	1.0:	Other: anything other than a tree.

Figure 9.—Comparison of the Vegetational Analysis and Squirrel Sightings



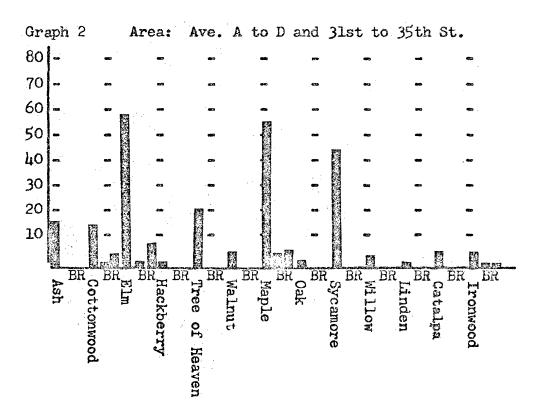
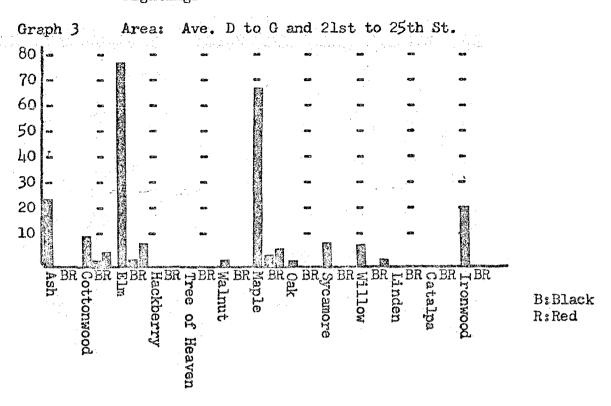


Figure 10. -- Comparison of the Vegetational Analysis and Squirrel Sightings



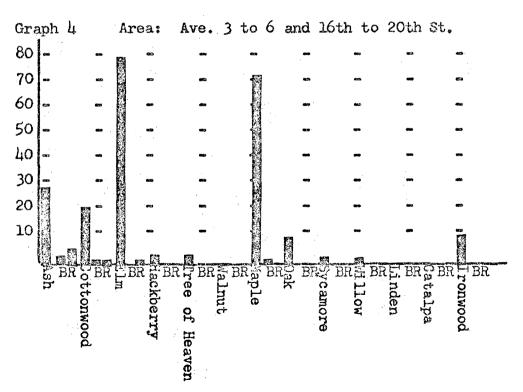
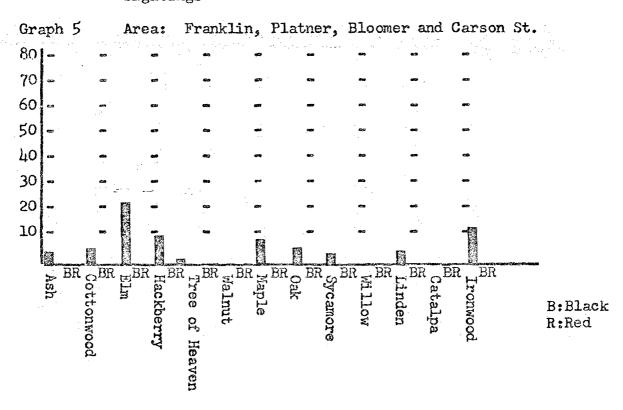


Figure 11.--Comparison of the Vegetational Analysis and Squirrel Sightings



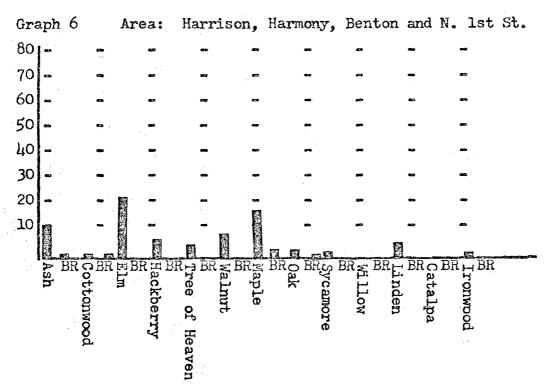


Figure 12.--Comparison of the Vegetational Analysis and Squirrel Sightings

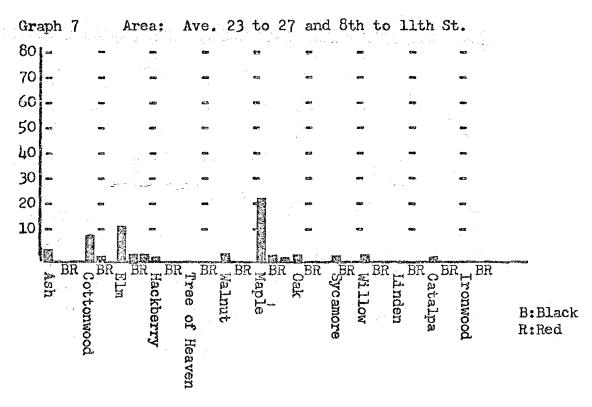


Figure 13

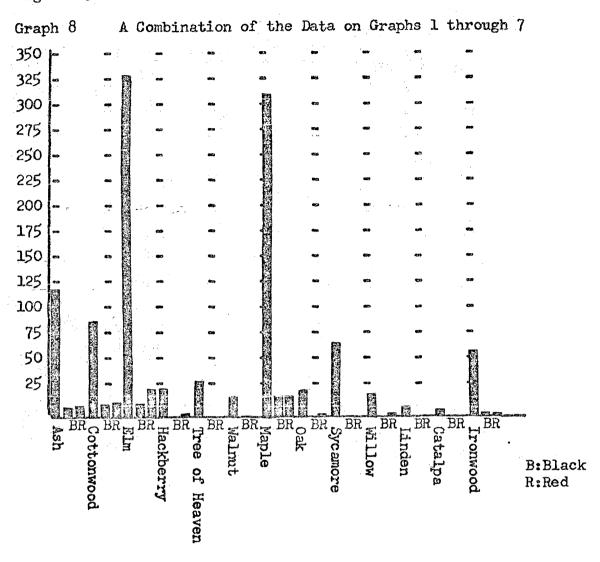


Figure 14. -- Results of the Tree Survey

Table 1	Tree	No.
2nd to 5th Ave.	Ash we have also see see see see see see the see see	34
31st to 35th St.	Cottonwood	
.*	\mathbf{E} \mathbf{I} \mathbf{M} are seen one one one one one one one one one	
	Hackberry	
	Tree of Heaven-	
	Walnut	
	0ak	
	Maple	73
	Sycamore	4
in the second se	Willow	
N.A.	Linden	~~~
	Catalpa	
	Ironwood	
	Total	215
Table 2		·
Ave. A to D	Ashanasaaa	15
31st to 35th St.	Cottonwood][
	Elm == == == == == == == == == == == == ==	_
	Hackberry	
	Tree of Heaven-	
	Walnut	
	Maple	
	0ak	
	Sycamore	
	Willow	
	Linden	
	Catalpa	
	Ironwood	
		228
Table 3	Total	220
Ave. D to G	ASh	23
21st to 25th St.	Cottonwood	
2130 00 27 m 00.	Elmanana	
	Hackberry	•. •
	Tree of Heaven-	
	Walnut-	
	MapleOak	
	Caramana	1
	Sycamore	~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~
	Willow	
	Linden	
	Catalpa	
	Ironwood	-
	Total	211

Figure 15.--Results of the Tree Survey

Table 4	Tree	No.
3rd to 6th Ave. 16th to 20th St.	Ash Cottonwood Elm Hackberry Tree of Heaven Walnut Maple Sycamore Willow	20 79 2 2 71 71
genericus;	Linden	
Table 5		
Franklin, Platner Bloomer, Carson St. Table 6	Ash	
Harrison, Harmony, Benton and No. 1st St.	Ash	21 mm m 21 mm m 21 mm m 2 mm m m m m m m m m m m m m m m m m m m

Figure 16.--Results of the Tree Survey

Table 7	Tree No	٥.
23rd to 27th Ave. 8th to 11th St.	Ashanana and and and and and and and and an	9110222
Table 8	Sycamore 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	
Totals of the seven above areas	Ashananananananananananan 85 Elmananananan 329 Hackberry 21 Tree of Heaven 26 Walnut 312 Oak 3	

APPENDIX V

DISTRIBUTION OF THE MELANISTIC PHASE IN EASTERN NEBRASKA AND WESTERN IOWA

This appendix contains examples of the questionnaires and letter sent to the game wardens in both states. The results of those questionnaires are plotted on figures 19 and 20. The last figure shows the results of the questionnaires as to number returned, number of sightings and the number with no sightings.

Figure 17. -- Sample of Letter Accompanying the Questionnaire

Date

Sir:

I am engaged in graduate work at the University of Nebraska at Omaha. The specific area of interest concerns the black (melanistic) phase of the Western Fox Squirrel. The common red (rufous) phase is present in lightly wooded areas throughout the midwest. The black phase is common in some of the larger metropolitan areas such as the Omaha-Council Bluffs area.

What I am trying to obtain is an accurate distribution of the black phase in western Iowa and eastern Nebraska. It would be of great help if I could get you to fill out the enclosed questionnaire concerning any sightings that you might make during your normal work. There is also a self-addressed stamped envelope enclosed. Filling out the questionnaire would greatly aid the study.

Thank you for your time and assistance.

Sincerely,

Edward Lueninghoener

Figure 18. -- Sample of the Questionnaire Sent to Game Officials

Questionnaire

·	
Number of sightings of the bla Please check one.	ck phase of the Western Fox Squirrel.
None Occasionally (not more than Regularly (more than once a	once a day) day)
Please estimate the amount of and rural% areas during a	
If sighted occasionally or mor are seen.	e please check the area in which most
Rural Name of county If area has the black phase	both in town and in rural areas rural and list the name of the town
If sighted occasionally or mor black phase makes up of the en	e please estimate the percentage the tire Fox Squirrel population.
Rural Sightings	Urban Sightings
0-25% 25-50% 50-75% Over 75%	0-25% 25-50% 50-75% Over 75%

Please feel free to make any additional comments.

Thank you for your time and cooperation.

Figure 19.--Distribution of the Melanistic Phase in Iowa

							Participant of the last of the			SERVICE THE V	
Lyon	Os	sceola	Dicki son	n-	Emm	et	Kos:	suth	Win ba	ne- go	Worth
Sioux) I) EII.	Clay		Pal Al	o to			Han	cock	Cerro Gordo
Plymouth	. 1	rokee	Buena Vist		Poc ta	ahon- s	Huml	ooldt	Wri	ght	Franklin
955655555		The state of the s	Sac		Ca	lhoun		internal prior verse was	Har	nilto	n
Mono	na	Crawf	ord	Car	roll	Gr	eene	Вс	one	St	ory
	arrisor		lby	Aud	*	Guthr	ie	Dalla	ទ	Polk	
Shaded areas indicate the presence of			Control of the second of the s	Cass		Ada	ir	Madi	son	War	ren
melanistic Western Fox					Ada	ms ÷	Umi	Lon	Cla	rke	Lucas
Squirrels.	Fre	rions.	Pace.		Tayl	or	Rimg	gold	Dec	atur	Wayne

Figure 20. -- Distribution of the Melanistic Phase in Nebraska



Shaded areas contain melanistic Western Fox Squirrels.

Figure 21.—Results of the Questionnaire to Game Officials

Iowa

Average time spent in urban areas 24% Rural Areas 76% for all officials surveyed.

	Occasionally	Regularly
Number reporting urban sightings	2	2
Number reporting rural sightings	7	2
Number reporting no sightings 7		
Number of questionnaires not l returned		

Nebraska

Average time spent in urban areas 13.6% Rural Areas 86.4% for all officers surveyed

	Occasionally	Regularly
Number reporting urban sightings	7	0
Number reporting rural sightings	3	0
Number reporting no sightings 8		
Number of questionnaires not 5 returned		