Population dynamics, predator-prey relationships and management of the red fox in Wisconsin. No. 105 1978

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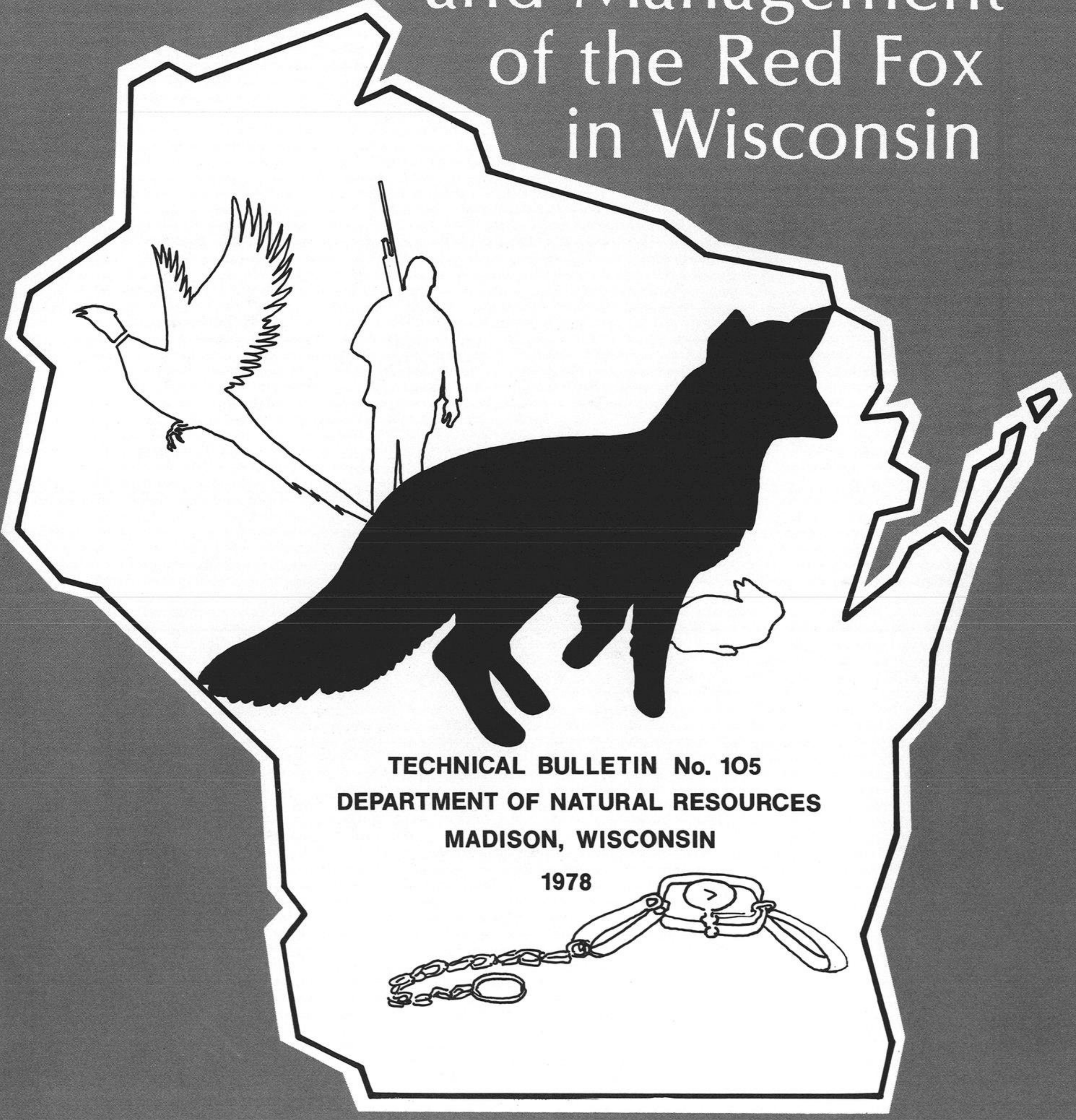

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ABSTRACT

Red fox population dynamics and predator-prey relationships were studied in southern Wisconsin from 1971-75. Spring fox populations and harvest levels were lower than those noted on the Waterloo Study Area (WSA) from 1968-71. The average vixen gave birth to 5.6 pups on 8 March at a den located in strip cover. Three radio-tagged vixens had a mean WSA home range of 598 ha. Return data from 73 tagged foxes indicated that (1) most pups dispersed after 1 October, (2) males dispersed almost twice the mean distance of females, (3) trapping and hunting were the most important causes of mortality, and (4) populations declined as pelt prices increased. Cottontails, small mammals and pheasants were the key foods eaten based on analysis of 1020 scat samples, 132 stomach contents, food items from 58 dens, and foods collected from 182 km of snow tracking. Red fox, other mammalian predators, raptors, winter severity and high spring rainfall appeared to limit pheasant and cottontail abundance at Waterloo. Predator control was deleted from this study because of landowner attitudes, rising pelt prices, establishment of a fox season, mobility of foxes, and interference by non-target species. Management possibilities include shorter trapping and hunting seasons, and mandatory registration of pelts.

POPULATION DYNAMICS, PREDATOR-PREY RELATIONSHIPS AND MANAGEMENT OF THE RED FOX IN WISCONSIN

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INTRODUCTION

The role of the red fox as a predator has been debated for many years. Much of past North American fox research has been directed towards food habits (Scott and Klimstra 1955; Arnold 1956; and Besadny 1966), which documented the number of ring-necked pheasant remains found in red fox stomachs and scats. During the last decade, refinements in aging techniques (Monson et al. 1973) and the use of radio-telemetry (Storm et al. 1976), have given the fox researcher a decided advantage in more thoroughly investigating red fox ecology. Radio-telemetry has especially enhanced analyses of territoriality (Sargeant 1972), dispersal (Phillips et al. 1972) and mortality (Storm et al. 1976).

The studies of Gates (1971) and Dumke and Pils (1973) in Wisconsin singled out predation as the primary limiting factor of ring-necked pheasant populations. Both studies challenged the belief of Errington (1936:252) that good habitat will negate any serious effects of predation on upland game species. These authors implicated the red fox as a formidable pheasant predator, and now, more recently, its value as a game species has also been elevated. The fur value of red foxes has increased 27-fold during the past 15 years, according to the Wisconsin Department of Natural Resources (DNR) Fur Harvest Reports, which has greatly increased the fox's prestige as a furbearer. The first Wisconsin fox season was initiated in October, 1972. Thus, the red fox has been placed between opposing philosophies, one calling for predator control and another for expanded management leading to higher numbers of foxes available for hunting and trapping.

Research on fox ecology in the state therefore, has been of high priority. This report is largely based on field investigations of the red fox on a southern Wisconsin study area during 1971-75. Our objectives were to: (1) determine population trends and compare them with regional and statewide trends, (2) evaluate movements and dispersal of tagged foxes, (3) determine and evaluate their diet, (4) determine age structure and reproductive performance, and (5) evaluate techniques of experimental control. Our investigation was basically divided into two segments; one portion dealt with the population dynamics, movements, dispersal and management of the red fox itself while the remainder analyzed the effects of fox predation on prey species, particularly pheasants, through a detailed analysis of food habits. Originally, research was limited to one geographic location; however, it soon became apparent that data obtained from adjacent areas would greatly strengthen our ultimate conclusions. Consequently, additional information on population trends, age structure, movements and diet was secured elsewhere, essentially creating three geographic areas of comparison: (1) the original study area; (2) other southern Wisconsin locations; and (3) statewide (analyzed through a questionnaire and the preliminary results of a statewide aging study). These data also enabled us to formulate red fox management recommendations compatible with pheasant management procedures.

The current study was established to fill voids in the knowledge of Wisconsin fox-pheasant relationships partially resolved by Gates (1971). Gates (1971:812) felt that the most critical pheasant research need was a detailed predator-prey study to determine the most serious pheasant predator and to evaluate effects of predator control. Dumke and Pils (1973:42) supported the conclusion of Gates that predation, specifically by red foxes and raptors, was the most important direct cause of death; however, they concluded that foxes, red-tailed hawks, and great-horned owls should not be controlled without additional predator ecology research. The Waterloo Study Area (WSA) utilized by Dumke and Pils (1973) was also selected for our red fox investigation because of its past history of habitat manipulation and monitoring of pheasant populations (Frank and Woehler 1969). A raptor ecology study was conducted concurrently with the fox research to fulfill parallel objectives regarding the role of avian predators.

GLOSSARY

Scientific Names: All scientific names are presented in Appendix A.

Fox Family: A distinct aggregate of adults and pups or barren adults occupying separate geographic areas.

Subadult: A fox approaching adult age.

Den: A simple or compounded series of interconnected burrows constructed beneath the ground, connected to the surface by one or more holes or occasionally located above ground. Foxes may live at a series of dens, not connected by burrows, at the same time.

Communal Den: Multiple parents and/or pups living at one or more dens.

Traditional Den: Dens used by any fox family for more than one year.

Survivorship: The probability of survival.

Types of Denning Periods (Sargeant 1972:230): **(1) Pre-emergence:** The first period of the denning season from whelping to emergence of the pups from the underground burrow; **(2) Confined Use:** When all pup activity was confined to the immediate den vicinity; **(3) Dispersed Use:** The third period in which pup activity was more widely dispersed in the den area and several dens were often used simultaneously.

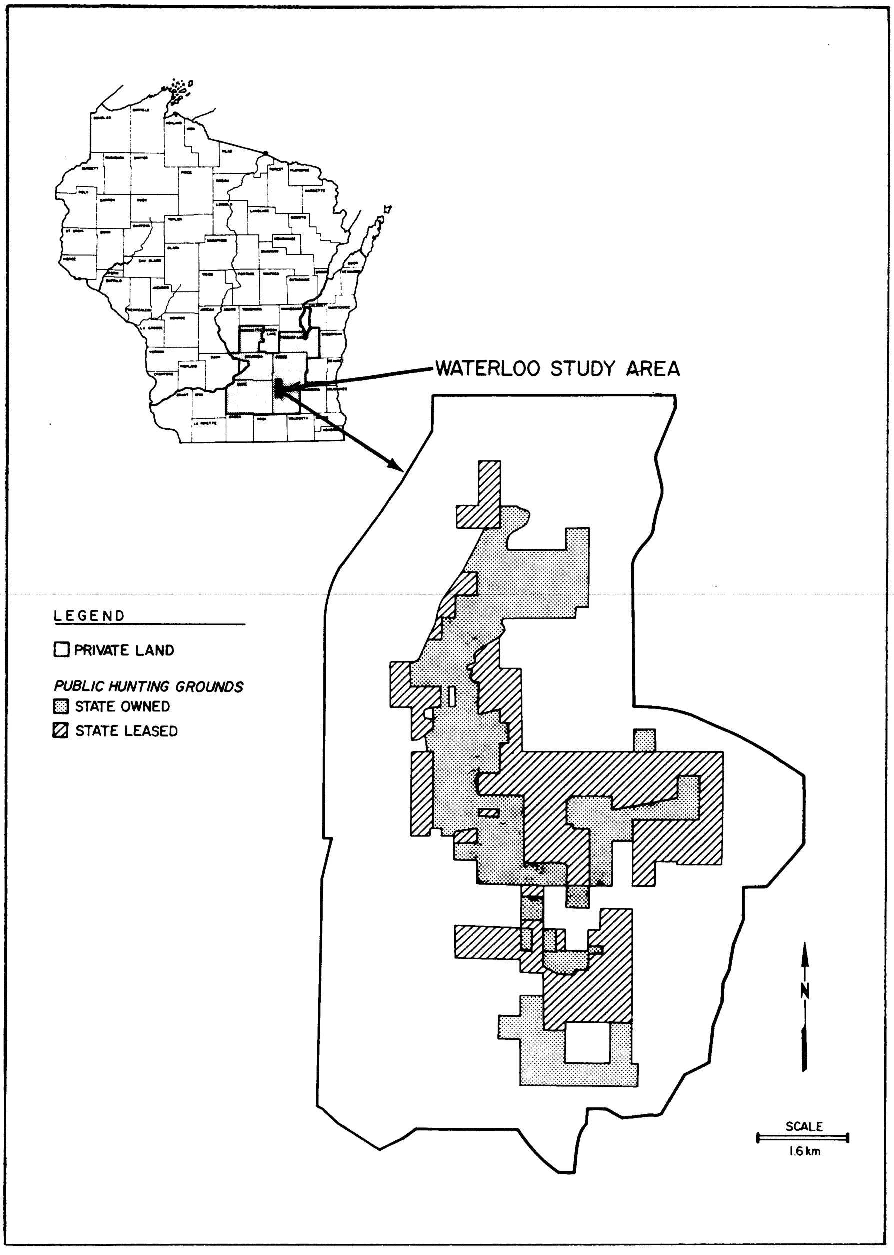


FIGURE 1. *Location and ownership of Waterloo Study Area in relation to the other counties where additional data for the current study were gathered.*

STUDY AREA

Field research was conducted primarily on the WSA, an 8,373 ha complex of state-owned (3,265 ha) and private lands (5,108 ha) located in Dodge and Jefferson counties. A public hunting ground consisting of 3,265 ha of state-owned land and 3,000 ha of leased land was scattered throughout the WSA (Fig. 1). Some additional information was also gathered in nearby portions of Dodge and Jefferson Counties, as well as in Dane, Columbia, Marquette and Fond du Lac counties (Fig. 1).

Geology, land use and climatological characteristics of the WSA are presented in Dumke and Pils (1973:3-4). Table 1 summarizes WSA land use changes from 1969 (Dumke and Pils 1973:4) to 1975 as compiled from aerial photographs and ground checks; 1,764 ha were added to our study in order to obtain more precise information concerning movements of radio-tagged foxes and spring population estimates.

TABLE 1. *Summary of changes in land use on the Waterloo Study Area during 1969-75.*

Land Use	No. Hectares 1969	No. Hectares 1975	Percent of Total Area 1969	Percent of Total Area 1975
Cultivated lands	3,230	4,691	48.8	56.0
Marsh	934	1,069	14.1	12.8
Pasture	1,235	876	18.7	10.5
Upland hardwoods	413*	376	6.3	4.5
Miscellaneous**	296	370	4.5	4.4
Retired cropland	332	346	5.0	4.1
Shrub-carr	--[1]	255		3.0
Tamarack		138		1.6
Lowland hardwood		124		1.5
Strip cover[2]	168	117	2.5	1.4
Conifer plantation		11		0.1
Total	6,608	8,373	99.9	99.9

*Lowland and upland hardwoods, tamarack and conifer plantations.
**Farmsteads, road pavement, gravel pits and open water.
[1]Included with marsh.
[2]Ditchbanks, fencelines, roadsides and R.R. right-of-way.

METHODS

RED FOX CENSUS TECHNIQUES

Questionnaires used to determine the regional and statewide abundance of red foxes were:

1. Summer Wildlife Inquiry: The DNR Technical Services Section has sent rural residents of Jefferson and Dodge counties a questionnaire during the last 12 years, requesting observations of fox numbers and litters (Lemke and Thompson 1960). Results of these inquiries were summarized from 1966-75. They concluded that this questionnaire provided a fox population index that was as good as bounty records, was economical and could provide timely and rapid coverage of the entire state or any part desired.

2. Bounty Records: Money paid for bountied foxes was recorded by Dodge and Jefferson County terminated bounty payments on 31 December 1971 and Dodge County followed suit one year later. Bounty payments from the 2 counties were summarized from 1966-72; Dodge County paid $2.50 for every adult and $1.00 for each pup, while Jefferson County paid $2.50 for each fox.

3. A questionnaire was also sent to all licensed Wisconsin fur buyers incorporating information from the 1974-75 and 1975-76 seasons. Data were gathered concerning the type and month of fox harvest, cases of mange reported, and estimates of red fox populations (Append. B).

Techniques employed to determine the relative abundance of foxes on the WSA were:

1. Annual Mammal Inquiry: Appendix C illustrates the questionnaire used to record numbers of wildlife seen on the WSA by landowners or renters during the year. Information was gathered by a direct interview or telephone conversation, during early January.

2. Survey of Active Dens: The technique of Scott and Selko (1939) was employed during the spring of 1972 in order to thoroughly search for and record all active dens as well as potential denning sites. Observations were made of active dens to obtain a maximum count of litter sizes. Continued surveillance of old dens and potential denning sites was maintained from April through July during 1973-75 by checking dens on foot. April helicopter surveys from 1971-74, Waterloo residents, and our own familiarity with the WSA facilitated the location of traditional denning sites and recently excavated dens.

3. Harvest Summaries: Close contacts were kept with local residents during the fox hunting and trapping season to ascertain locations of harvested foxes on or adjacent to the WSA. Hunters and trappers were given prestamped cardboard tags for recording the location of kill, sex, weight and hunter name. Research personnel filled out most of the cards by periodically checking at residences of the hunters and trappers. Locations of kill were recorded on a map of the WSA. Fur buyers as far as 40 km from the WSA were also frequently contacted for ear-

tagged and marked foxes shot on the WSA which escaped our detection.

PREY CENSUS TECHNIQUES

Ring-necked pheasants. Estimates of pheasant populations on the WSA were made by various DNR personnel (1968-74) as part of a long-term pheasant habitat study. Winter sex ratio and spring crowing counts were used to determine a total (cocks and hens combined) spring population estimate, 1968-74. Intensive hunter interview data were utilized to record a total posthunt population figure during this same period (hunter interviews terminated at the end of the 1974 season).

Small mammals. The relative abundance of small mammals under 400 g was estimated by using lines of 40 snap traps at 12 different stations on a bimonthly basis encompassing six different cover types at Waterloo (Petersen, in press). Results were expressed as captures per 1,000 trap nights.

Cottontail rabbits. Cottontail densities on the WSA were estimated by live-trapped rabbits on 3 areas designated as Faultersack's (3.3) ha), Kerl's (7 ha) and the Quarry (9 ha), during October-November and January-February, 1971-75. Population were calculated by the regression technique of Edwards and Eberhardt (1967) and were expressed as cottontails per ha. Average fall and winter populations were compared from areas with statistically significant population estimates.

CAPTURE AND TAGGING TECHNIQUES

Number 2 Victor and Herter steel traps with off-set jaws were used to capture adult foxes.

During the spring of 1972, pups were captured by inserting a 7.5 m spring steel wire ferret into a den hole and forcing pups out alternate hole(s) where they were netted (Storm and Dauphin 1965).

The majority of pups were captured by excavating dens. This process was simplified by attaching a radio transmitter to the nose of the mechanical ferret. A radio receiver and directional antenna were used to locate the radio-equipped ferret tip and a vertical shaft was dug through to the burrow. This saved considerable time in locating pups in curved burrows. After pups were processed, all burrows except one were filled in and the young foxes were released into the remaining, intact tunnel. Checks were made the following day(s) to determine whether the pups had been moved out of the den.

Although dens were not excavated during the spring of 1972, the direction of slope and number of active openings were recorded and openings measured. Data on direction of slope were used for traditional dens from 1972-75. The general cover type surrounding the den and the distance to the nearest farmstead were also noted during that time period. Additional measurements taken in 1973-75 included total burrow length and maximal burrow depth. Digging operations ceased after all pups were removed and the burrows were completely explored.

Captured foxes were weighed, sexed and ear-tagged. Pup pelage color was noted and measurements were made of the right hind foot length (mm). During the spring of 1972, pups were equipped with expandable metal collars described by Sheldon (1949b); during the remainder of the study ear tags described by Pils and Martin (1974:359) were used to tag all foxes. Pups captured at dens from 1973-75 were also marked with colored streamers described by Knowlton et al. (1964:167).

RADIO TELEMETRY

All adult foxes were equipped with 140 g collars containing radio transmitters similar in design to those reported by Cochran (1967), with the exception of the current drain of the battery which was reduced, resulting in a projected transmitter life of up to 10 months. Old pheasant transmitters used by Dumke and Pils (1973:10) were also modified for short-term use on pups.

Foxes were located by triangulation with portable and vehicle-mounted gear. Locations were taken at intervals varying from 3 to 30 minutes and were plotted on mylar overlays on aerial photos scaled 2.9 cm/km. Calculations of area used by foxes were made with a compensating polar planimeter.

Individual foxes were tracked intermittently from 1 to 78 days over periods ranging from 1 to 171 days in length. The number of foxes per 12-hour period ranged from 1 to 19. All pups were monitored during daylight hours; 40% of the fixes from adult foxes were taken between 6 a.m. and 6 p.m.

Calculations of home range area, previously used by Hayne (1949), Dice and Clark (1953) and Stumpf and Mohr (1962) were not used because of an insufficient number of animals tracked and too few fixes per fox (Storm 1965:5). Therefore, home ranges were constructed by using the minimum area method of Mohr (1947), who calculated the area enclosed by imaginary lines connecting the outermost radio locations.

FOOD HABITS

Food habits data were obtained from the following sources: (1) food items and scats found at dens (items

Most pups were captured by excavating dens.

found outside dens and inside excavated dens), (2) stomach contents taken from shot and trapped foxes, (3) scats found in the field incidentally to other phases of the study, and (4) food items and scats found as a result of tracking foxes in the snow.

Food items found at dens were segregated and identified by portion, such as right leg or left wing to avoid duplication of items. Data concerning food items found above ground level and below ground level were also segregated; ratios could, therefore, be used to calculate estimated numbers of food items present below ground level at those dens not excavated during 1972.

Scats found in the field at one location were counted as a single sample. Large numbers of scats found at denning sites were subjectively divided into samples similar in size to those found in the field; e.g., one sample equaled approximately 3 scats. For analysis, scats were water-soaked in small jars. The softened scat was then broken apart into a water-filled dissecting tray, and food items isolated and identified.

Contents of stomachs taken from harvested and car-killed foxes were analyzed in a manner similar to scats. A reward of $2.00 was paid for untagged foxes shot on the WSA, $3.00 was paid for tagged carcasses and $5.00 was given for fox carcasses bearing radio transmitters.

Foxes were tracked in the snow during portions of three winters from 1972-75 in order to determine cover type used, kill attempts, types of prey and carrion eaten. Distance was computed by counting paces or by using a pedometer. Tracking ceased when suspected resting areas were approached and was not attempted during windy, drifting periods. Carrion was easily distinguished from fresh kills by the condition of the carcass.

Results were expressed in terms of percent frequency of occurrence and biomass. Portions of food items, with the exception of large mammals (pigs, deer and cows) were assumed to represent one animal consumed. For example, if one scat sample (usually 2-3 scats) consisted solely of cottontail hair, one cottontail was assumed to have been eaten. However, if two lower cottontail jaws were found in the scat sample with cottontail hair, two cottontails were considered to have been consumed. Percent frequency of occurrence was found by dividing the total occurrences of a particular food item by the total occurrences of all food items. Percent biomass was calculated by multiplying the mean food item weights (taken from the University of Wisconsin Zoology Museum at Madison) times total occurrences. This product was then divided by the total biomass of all food items. Large mammals were assumed to represent carrion; therefore only a meal-sized portion (454 g) of the carcass was considered as consumed. All food item data were ultimately combined into the 6 seasonal periods used by Dumke and Pils (1973:27) for purposes of comparison. Predation rates were calculated following methods of Rusch et al. (1972) in order to evaluate the impact of predation on the ring-necked pheasant and cottontail rabbit during the spring, the only season when data for the analysis of these rates were available.

REPRODUCTIVE TRACT ANALYSIS

Collection of carcasses. Fox carcasses used for age and reproductive analysis were collected from hunters on and adjacent to the WSA. Through the return of tagged foxes, we were also able to establish contacts with fur buyers, hunters and trappers from the six-county, southern Wisconsin area. Upon request, these individuals periodically furnished carcasses for our use.

Determination of litter size. Number of placental scars and viable embryos were counted in order to determine the reproductive potential of vixens. Mean litter size was determined by observation of pups at den complexes, by averaging numbers of pups taken from excavated dens, by counts of placental scars of the same color (Englund 1970:19) and by counting viable embryos from female foxes killed primarily by hunting and trapping.

AGING TECHNIQUES

Allen's (1974) technique of measuring the enamel line distance of canine teeth facilitated the determination of juveniles and adults and was used during 1974-75. The Monson et al. (1973) technique of counting the annular cementum rings was used to determine yearly age classes. Fox mandibles bearing premolar teeth were sawed off and boiled in water for 30 minutes; premolar teeth were then pulled out and were sent to a commercial histological lab (Matson's, Milltown, Montana 59801) for slide preparation.

All red fox pups captured at dens during 1973-75 were aged (in days) by measuring the right hind foot length (mm) and by fitting the data to a growth curve after the technique of Johnson et al. (1975). Conception dates were determined by backdating 53 days after parturition dates were established (Jackson 1961:303).

RESULTS AND DISCUSSION

REGIONAL RED FOX POPULATIONS

Results of the Summer Wildlife Inquiry suggested a gradual annual decline in the statewide red fox observations on farms during 1967-75. This trend was apparent on the WSA during the years 1971-74 (Fig. 2).

WATERLOO RED FOX POPULATIONS

Spring Fox Family Survey

Annual censuses made of fox families at active dens on the WSA were considered to be the most reliable population indexes obtained during the study. More time was spent locating, observing and tagging foxes at active dens during the spring than was spent for any other census technique. The number, location and family association of dens for each study year is shown in Figure 3. The number of dens used by a WSA fox family ranged from 1 to 6. Fox families ranged from 6-10; densities declined from 1.2 to 0.7 per 10 km^2 throughout the study (Table 2). Three other studies in portions of Michigan, Iowa, and North Dakota found comparable fox family densities (Table 3).

Harvest Summary

Numbers of red foxes harvested during the winter provided a third means for estimating fox abundance at Waterloo. A significant difference was noted in the numbers of foxes harvested at Waterloo (Table 4) between 1968-71 and 1971-75 ($t = 5.91$, 5 d.f., $P < 0.01$). Only 38% of all red foxes harvested from 1968-75 were taken during the current study. We believed that lower harvest levels reflected delining fox densities. This decline in harvest corroborates the diminishing spring populations noted between 1972 and 1974 (Table 2). The amount of snow on the ground during the fox season was possibly reflected in the magnitude of kill, although the degree of influence of snow cover is unknown. Adequate snow cover is essential for effective fox hunting in terms of tracking foxes and for providing a contrasting background for shooting. The severe winters of 1968-71 yielded considerably greater snowfall and longer periods of snow cover than the milder winters of 1971-75.

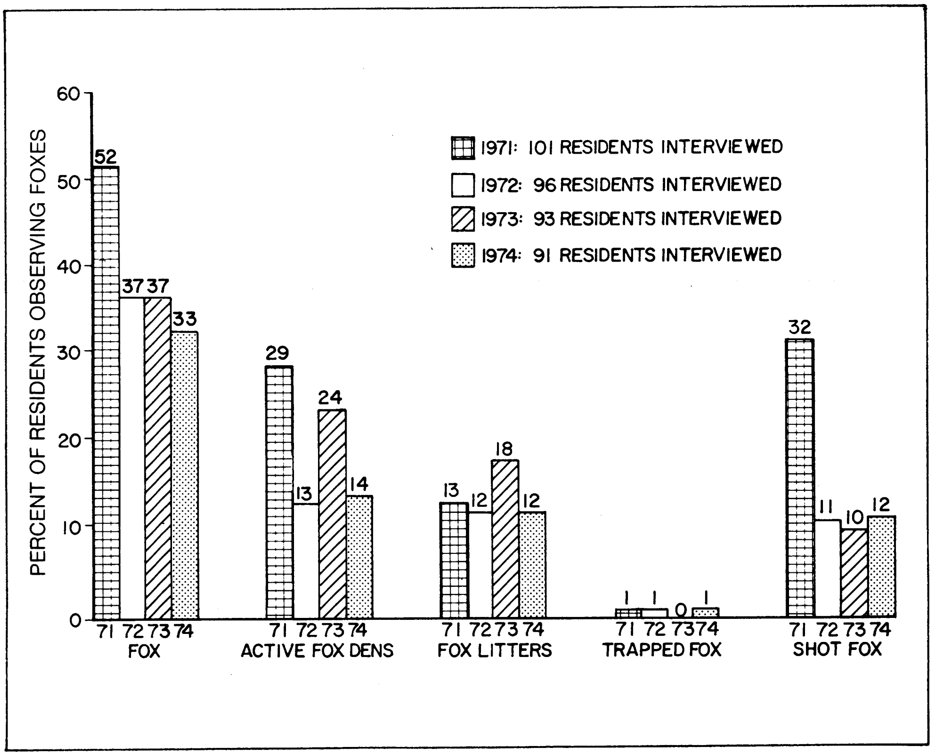


FIGURE 2. *Results of a 1971-74 survey of various fox observations as seen by Waterloo Study Area residents.*

TABLE 2. *Spring populations of red fox on the Waterloo Study Area, 1972-75.*

	1972	1973	1974	1975	1972-75 Mean
Fox families	10	9	6	6	7.8
Number of families per 10 km^2	1.2	1.1	0.7	0.7	0.9
Communal dens	0	1	1	2	1
Mean litter size	4.6*	5.9**	5.9**	5.2**	5.4

*Data calculated from observations of pups at dens.
**Data obtained from counts of pups taken from dens, placental scars and embryos.

DEN ECOLOGY

Red fox dens have been described by Sheldon (1950), Layne and McKeon (1956), Jackson (1961), Stanley (1963) and Storm et al. (1976). Sargeant (1972) discussed the number

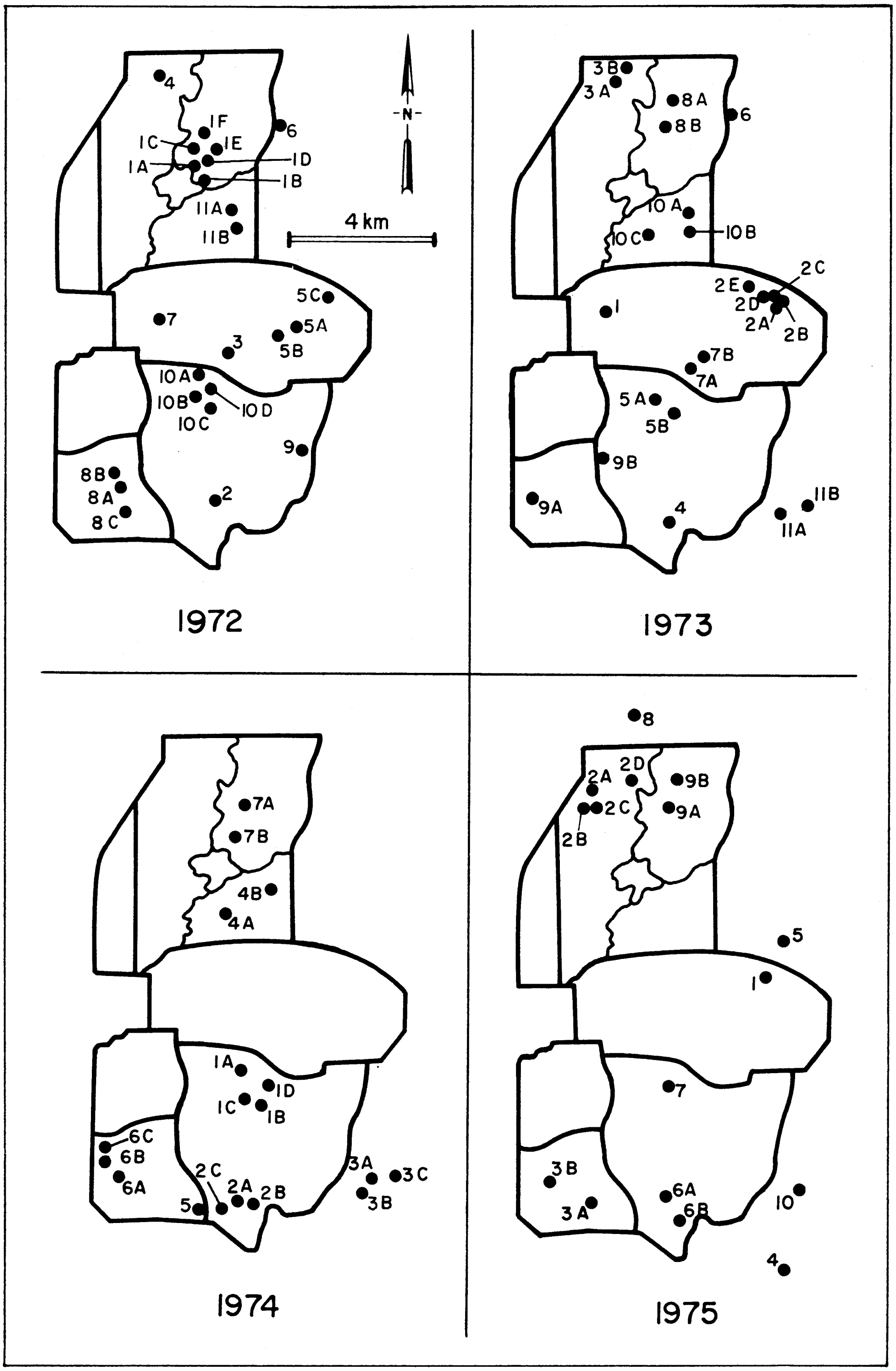


FIGURE 3.
Active dens on the Waterloo Study Area, 1972-75. (Each number represents one den; letters after numbers refer to active dens used by one family.)

TABLE 3. *Comparative population densities of red foxes in spring.*

State	Year(s)	Area (km^2)	Families/km^2	Reference
Eastern Michigan	1942	36	0.1	Shick (1952)
Southeast Iowa	1946-48	10.6	0.1	Scott and Klimstra (1955)
Central North Dakota	1969-73	559.4	0.1	Sargeant et al. (1975)
Southern Wisconsin	1972-75	83.7	0.1	Current Study

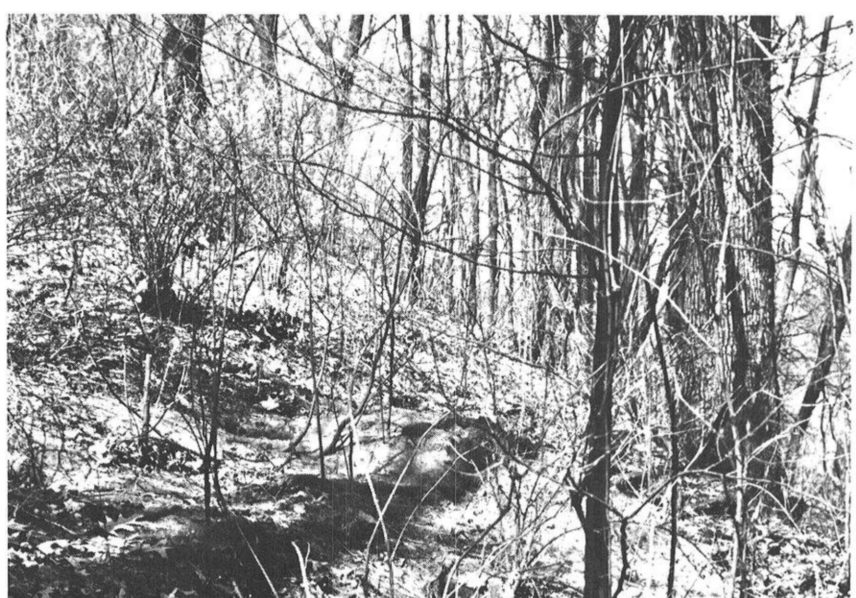
and categorized the types of dens used during the denning season. Layne and McKeon (1956) summarized questionnaires describing physical characteristics of 146 red fox dens. Most recently Storm et al. (1976: 25-28) outlined factors concerning den site selection. In this section we describe possible origins, internal structure, and year-to-year use of southern Wisconsin fox dens, and quantitatively identify major factors influencing den selection.

Den Origins and Structure

Richards and Hine (1953) observed that the majority of dens used by red foxes in southwestern Wisconsin were formerly used by woodchucks and badgers; similar origins were noted in Illinois (Hoffmeister and Mohr 1957) and Michigan (Arnold 1956). Probably the majority of WSA fox dens were dug by badgers and woodchucks. Indirect sign such as the size and shape of den openings (Jackson 1961) and previous observations of badgers and woodchucks in the vicinity of active fox dens supported these beliefs. The only other structures used as spring dwellings by fox families at Waterloo were a brushpile and the crumbled concrete foundation of a razed farm building.

Active fox dens were examined from March through July during 1972; 9 dens contained 5 or more active openings. The mean number of active openings per den (4.0) encountered during 1972 was significantly higher ($t = 3.40$, d.f. = 18, $P < 0.005$) than the 1973-75 mean of 2.1. Dens from 1973-75 averaged 2.1 active openings and varied from 1 to 7 openings per den. Several dens were located near a large number of old openings, but few entrances were used. The maximum distance between active openings at all dens ranged from 0.2 to 91 m, averaging 8.2 m. The mean dimensions of measured den openings (28 × 23 cm) were similar to those found in Illinois by Storm et al. (1976:26).

Dens found on cultivated lands contained the longest burrows (Table 5), possibly due to a high amount of shady loam soil which afforded easier digging. The deepest dens excavated were found in gravel pits in sandy areas. Tree roots and boulders occasionally influenced burrow design and direction, resulting in sharply angled turns and dips. These objects may serve as obstacles to human and animal intrusion. We felt that the most important factor relating to the depth and total distance of the burrow systems was the number of years the den was used. Fox families using traditional dens had the opportunity to lengthen burrows each year, thus making labyrinths out of some older, simpler dens.



Some typical den locations: brush pile (top), hayfield (middle), woods (bottom).

TABLE 4. *Red foxes harvested on the Waterloo Study Area and vicinity, 1968-75.*

Pheasant Mortality Study*		Fox Study	
Year	Foxes Harvested	Year	Foxes Harvested
		1971-72	17
1968-69	88	1972-73	19
1969-70	70	1973-74	34
1970-71	60	1974-75	13
1968-71 Avg.	72	1971-75 Avg.	21

*Dumke and Pils (1973)

TABLE 5. *Mean burrow length and maximum depth of southern Wisconsin fox dens in relation to cover type, 1973-75.*

Cover Type	Number of Active Dens	Mean Maximum Burrow Length Per Den(m)	Mean Maximum Depth(m)
Cultivated lands	10	12.3(2-33.2)*	1.1(.5-1.7)
Strip cover	6	7.7(2.4-17.4)	1.2(.9-1.7)
Retired cropland	8	9.1(3.2-29)	1.2(.9-2.1)
Upland hardwoods	5	7.8(4.6-12.2)	1.3(1.1-1.8)
Miscellaneous (gravel pit)	1	7.6	2.4
Pasture	7	7.5(3.4-12.2)	1.2(.6-2.1)
Total and means	37	9.3(2.4-33.2)	1.2(.5-2.1)

*Range

TABLE 6. *Cover type of 68 red fox dens compared to cover type available on the Waterloo Study Area, 1972-75.*

Cover Type	Number of Dens	Percent of Total Dens	Percent of Total Area
Strip cover	18	26.5	1.4
Cultivated lands	15	22.0	56.0
Upland hardwoods	11	16.2	4.5
Retired cropland	10	14.7	4.1
Miscellaneous	9	13.2	4.5
Pasture	5	7.3	10.5
Marsh	0	--	12.8
Shrub-carr	0	--	3.0
Tamarack	0	--	1.6
Lowland hardwoods	0	--	1.5
Conifer plantation	0	--	.1
Totals	68	99.9	99.9

Factors Influencing Den Selection

Cover Types. The number of dens found in each cover type (Table 6) was compared to the expected number of dens based on percent of area in each type by a single classification Chi-square test. One of the requirements of this test is that not more than 20% of the categories can have an expected number of dens less than 5. Therefore, similar cover-type categories were combined as follows: (1) strip cover, (which incorporated ditchbank spoils, fencelines, roadsides and railroad rights-of-way), and miscellaneous (which included farmsteads, old foundations, road pavement, gravel pits and open water), (2) pasture and retired cropland, (3) marsh, (4) upland and lowland hardwoods, tamarack and shrub-carr (these four were combined because they individually constituted woody cover types representing less than 5% of the total area) and (5) cultivated lands. Results (X^2 = 155.24, d.f. = 4, $P < 0.0001$) indicated that the 5 cover-type categories were not selected by chance, since (1), (2), and (4) were selected with a higher frequency than expected and (3) and (5) with a lower frequency.

Intrinsic factors associated with cover types undoubtedly influenced den selection. For example, woody or herbaceous vegetation growing on spoils may have offered concealment and thus positively influenced den selection. Camouflage may also have been a factor affecting the selection of brushy fenceline and upland hardwoods; these dens were the most difficult to locate because of their association with trees, smaller woody plants and herbaceous vegetation. The woodlots in which dens were found ranged in size from 0.1 ha to 33 ha; understories ranged from heavily pastured to brushy. The selection of den complexes located throughout woodlots did not reflect a relationship with either woodlot size or vegetational density.

Hayfields contained the most dens (14) found in a single cover type. Both hayfield and retired cropland dens were usually located near or on the crests of gently rolling hills. One 1972 red fox family lived for a short period in a brushpile located in a retired cropland field.

Pastures and gravel pits containing active dens were found in well-drained areas that were not associated with any concealing vegetation. Layne and McKeon (1956) found that pasture (34.5%) and woodlots (31.7%) were the two most highly selected cover types in New York. Shrub-carr, tamarack, and lowland hardwoods on the WSA were usually located in poorly drained areas and did not contain any active dens. One active den, located in a roadcut along a heavily travelled state highway, seemed to be situated in a hazardous and conspicuous site without any apparent reason.

Soil. Jackson (1961) suggested that red fox dens in Wisconsin occur more frequently in loose sandy and loamy soils than in heavy clay. Arnold (1956) reported that Michigan fox dens are most commonly found on sandy gravelly soil. Stanley (1963) also found the majority of Kansas fox dens in sandy soils. The most frequent type of soil encountered at Waterloo after breaking through the initial 10 cm of earth was rocky, sandy loam soil, consistent with Sheldon's (1950) observation that preference for this type of soil is almost universal among red foxes. Porous sandy loam soil probably facilitated the drainage of excess water, thus positively influencing the selection of a den. Black peat was the main component of 5 of the 10 dens located in spoils, while pure sand was encountered at gravel pits, especially below a depth of 1.5 m.

Slope. Selection of dens located on certain slopes by foxes was nonrandom in that north-, east- and south-facing slopes were selected more frequently than would be expected from a random sampling of potential slope directions taken off a topographic map. Although dens found on the warmest slope (southeast) in relation to the daily path of the sun were not significantly preferred, individual choices for east and south slopes were significant. Results of a two-sample Chi-square analysis of den preference on slopes indicated no significant preference between use of dens on slopes and level ground. When a comparison was made between dens used on the southeast semicircle of slopes (E, SE, S and SW) versus the northwest semicircle (W, NW, N, and NE), a non-significant ($P<0.20$) a X^2 value of 2.02 (1 d.f.) was obtained. Likewise, comparing the south-facing octants (SE, S, and SW) with their north-facing analogs did not yield a significant value ($X^2 = 0.414$, 1 d.f., $P<0.30$).

Water. Stanley (1963) cited the presence of water as a governing factor in the selection of a den site; only 3 of 34 Kansas dens were farther than 140 m from a permanent source of water. Water was readily accessible near all WSA active dens, and seemed to be an important factor regulating den site selection; Layne and McKeon (1956) came to the opposite conclusion in New York after noting that a third of the dens were more than 152 m from water. Permanent water sources ranged from a distance of 25 to 920 m away from active dens in southern Wisconsin. However, closer temporary sources of water from intermittent creeks, rainwater and flooded marshes undoubtedly were also utilized by foxes.

Long burrow in sandy soil, deep below the surface.

Human Disturbance. The effects of two categories of human disturbance on choice of dens, proximity to farmsteads and human presence at active dens, were examined. The distances from active dens to farmsteads at Waterloo ranged from 0.16 to 1.0 km and averaged 0.5 km. The relative proximity of active dens to farmsteads on the WSA tended to minimize its importance as a factor governing den selection. Storm et al. (1976:25) found that the majority of dens located in Iowa and Illinois were more than 274 m from farmsteads; they concluded that lack of "disturbance by man" is one important factor in the selection of den sites. Although Storm et al. (1976) did not specifically define "disturbance by man", the term implies more than human presence at the den site.

Human presence at or within 25 m of the den caused varied reactions by foxes. Some families living in both traditional and nontraditional dens moved to alternate dens after we walked up to the den for a single visit. Other families remained in spite of repeated visits to the den site. Even though some fox families did move to other denning sites during the spring after they were disturbed, other fox families or possibly the same individuals returned to the original sites during subsequent years. Twenty-three percent of the total dens examined were used for more than one year. The Haberman and Firari dens were used by foxes for 2 years and 1 year, respectively, after being excavated. Layne and McKeon (1956) reported that 3.3% of the New York fox dens were used for 13-15 years. Each year foxes living in traditional dens are able to extend burrows and perhaps add new ones. The Haberman den contained the longest system of burrows and was also used for more years (4) than any den examined at Waterloo. Potentially traditional dens containing shorter and simpler burrow systems were deserted at Waterloo, possibly due to chance alone. Human presence, disturbance from farm machinery (Storm et al. 1976), or digging by dogs may also have forced the foxes to move before the dens could be enlarged.

Den Ecology Conclusions

Our findings on denning by the red fox indicate that the majority of active dens were formerly used by woodchucks and badgers, although other structures such as old foundations and brushpiles were also used. The sequence of den types used on the WSA closely followed the den descriptions associated with the progression of the denning season in North Dakota (Sargeant 1972).

The most important factors influencing den selection were cover type, human disturbance, water and length of use. Although more WSA dens were found in hayfields, dens in strip cover, retired cropland, old foundations, gravel pits and upland hardwood were selected in a significantly higher proportion to their availability as cover types. The longer a fox family was able to stay at a particular site and dig more extensive burrows, the more attractive that den became for future occupancy. Human disturbance encouraged fox families to move before their system of tunnels could be expanded. Soil type and slope were less important; the easy digging and excellent drainage found in sandy loam made this soil the most attractive to red foxes. Although foxes seemingly chose denning sites located on particular directions of slope, it was not statistically possible to define any consistent directional pattern of the choice. Water was readily available near all denning sites and appeared to be an important selective factor.

Denning structure was extremely variable in all excavated burrows and is probably a function of cover types, soil, obstacles within the soil and length of use. Older traditional dens exhibited the longest and most complex system of burrows.

COMMUNAL DENS

Four of five communal dens located during the study were found on the WSA. Communal dens represented 11% of the total dens found in southern Wisconsin during 1972-75. Sheldon (1950:35-38) described some of the possible adult-juvenile combinations at communal dens in New York. Pils and Martin (1974:359-360) saw 3 adults (including 2 females) and 10 pups at a den on the WSA in 1973, during several days of observation. Although factors responsible for communal groupings are little understood, Tullar et al. (1976:92) have suggested that these movements may be stress induced. One example of these movements, a pup which was radio-tagged and released at den 7A (Fig. 3) on 9 May 1973, was later moved to communal den 2 (Fig. 3) 3.2 km to the northeast. The pup was apparently accepted by its new family when trapped 92 m from the communal den on 15 June 1973.

Other Waterloo dens suspected of being communal were never verified. The farmer who owned the land where communal den 2 (Fig. 3) was located during 1973, reported seeing pups of "2 different sizes" on his land during 1972. Den No. 1 found in 1972 (Fig. 3) consisting of 6 different openings provided a maximum count of 10 pups during the confined use period, indicating an unusually large litter or a possible communal concentration.

Pils and Martin (1974) documented the survival of red fox pups associated with a communal den after one of the adults was killed by dogs. They concluded that communal denning may be an adaptation to survival. However, contagious diseases such as sarcoptic mange spread by infected pups adopted by healthy foxes could theoretically cause severe reductions in red fox populations (Tullar et al. 1976:95).

REPRODUCTION

Conception-Birth Dates

Table 7 summarizes range and average conception-birth dates of 35 red fox litters in southern Wisconsin. We used the same aging technique as Johnson et al. (1975) who accurately aged juvenile foxes up to 80 days old. Pups taken from communal dens were segregated into separate litters on the basis of estimated age, from which conception dates were determined. Range of conception dates was 27 December to 3 February (39 days), with a 6-day difference between annual mean conception dates (11-17 January). Birth dates ranged from 16 February to 28 March (40 days), while mean birth dates were 5, 7 and 11 March. Conception dates occur later in the more northerly latitudes of the United States (Layne and McKeon 1956:54). Storm et al. (1976:19-21) discussed the differences in conception dates at varying latitudes.

Influence of Age on Reproduction

Englund (1970) discussed intrauterine losses and litter sizes at birth of vixens of different age classes in Sweden. Fairley (1970), in his extensive discussion of Irish red fox reproduction, was handicapped by the absence of an aged sample for comparing fecundity, placental scar counts, and productivity (mean number of pups born per vixen).

Southern Wisconsin data concerning age-related reproduction from 48 vixens is shown in Table 8. Darkly pigmented scars were used to estimate litter size. Juveniles collected prior to 3 February were not included in the sample because developing embryos cannot be positively detected until at least 10 days after the last day of possible conception (Table 7). Six females aged as juveniles were also eliminated from the sample because they had distinctive placental scars, indicating an error was made in aging. Englund (pers. comm.) has never seen placental scars after examining 1,000 juvenile vixens. However, Allen (pers. comm.) has noted placental scars while examining juvenile uteri. Females aged in a particular year class on the basis of cementum annuli were placed in the previous year class if they exhibited placental scars. The age class was not changed if they were found to be pregnant. The number of females incapable of producing young could then be depicted more accurately. Table 8 compares the productivity of foxes in the various age classes. Adults reproduced at a much higher percent age, possibly due to higher prenatal mortality in pregnant first-year vixens. Allen (1975) has previously indicated that differential embryo mortality occurs. Little differences were noted in ranges of numbers of embryos and placental scars. No significant litter size differences ($P < 0.05$) were found between any of the age classes or between juveniles and all the adult age classes combined.

Litter Size

Mean litter size was calculated by averaging counts of litters captured at dens, placental scars and embryos. No significant difference ($P < 0.05$) was found between mean counts of litters, placental scars and embryos, during 1972-75 (Table 9). From 1 to 13 (communal den) red fox pups were found at excavated dens. The WSA mean litter size varied from 4.6 to 5.7, averaging 5.6 pups overall (Table 9). Any estimate of mean litter size, regardless of the method used, has inherent biases and is subject to criticism. As pointed out by Hoffman and Kirkpatrick (1954), "counts of young foxes seen at or taken from dens permit inaccuracy because of pups overlooked, post-natal mortality or communal denning". Storm et al. (1976:21-23) analyzed different criteria for determining litter size and felt that their estimates of litter size were low because few dens were excavated. During our fox investigation, we were able to dig up 78% of the dens used for calculating litter size (Table 9). Holcomb (1965:530) reported finding 17 pups at a Michigan den and considered it to be a single litter; however, this number far exceeded the mean litter size of 5.5 for southern Michigan (Schofield 1958:313) and probably represented a communal den.

Several authors, including Sheldon (1949a) and Richards and Hine (1953) utilized placental scar counts to obtain estimates of litter size. However, some disagreement persists regarding the interpretation of placental scars as indicators of litter size. Sheldon (1949) used only the more darkly pigmented "fresh scars" for litter size determination. Englund (1970:19) referred to the six distinct placental scar shades in which the darker ones may represent placental remnants of embryos born alive and the other lighter shades may represent the embryos dying in utero or the scars of successful pregnancies of earlier years. However, Englund (1970:23) also stated that *all* scars could possibly fade during the autumn-winter period and thus yield misleading information. Lloyd (1968) and Fairley (1970) stated that previous scars persisted until only mid-February at the latest.

Estimating litter size by embryo counts may also be biased by intrauterine mortality. Allen (1975) reported that prenatal embryo loss is common in juveniles. Englund (1970:15) found that 50% of uterine losses occurred before days 28-29 pregnancy. Therefore, by restricting embryo counts to the second half of gestation when post-implantation losses are reduced, it is possible to achieve a more accurate estimate of viable young born.

SEX RATIOS

An analysis of sex ratios is essential to an understanding of reproduction. The birth rate of monogamous species such as foxes will tend to favor maximum production of young when the sex ration is equal (Dasman 1964:97). Fetus sex ratios were not gathered during our study. Sheldon (1949 a:236), Fairley (1970:124) and Storm et al. (1976:23) however, showed no major departure from an assumed 50:50 ratio.

Our sex ratio information was derived from five sources: (1) pups taken at dens; (2) tagged foxes; (3) untagged foxes killed on the WSA; (4) foxes collected in a 6-county southern Wisconsin area (Table 10); and (5) red foxes collected statewide during the 1975-76 season. Sex ratios of pups from southern Wisconsin dens indicated no significant differences ($P > 0.05$) in the numbers of males and females (Table 10), assuming a 50:50 sex ratio at birth. Fifty-four percent of the 2,063 fox pups examined at dens in Illinois and Iowa were males (Storm et al. 1976:24), which was significantly different ($P < 0.01$, 1 d.f.) from an assumed equal sex ratio at birth. Apparently, more females died during gestation, parturition or their first few days of life.

Sex ratios of categories (2) through (5), with two exceptions, were compared with the den juvenile sex ratio, assuming that the den sample reflected the annual statewide sex ratio. We felt that our den sex ratio was a more realistic point of reference than an assumed 50:50 ratio, especially in light of the disproportionate den sex ratios encountered by Storm et al. (1976:24).

TABLE 7. *Mean conception and birth dates for 35 southern Wisconsin red fox litters, 1973-75.*

Year	Number of Litters	Conception Date Range	Mean Conception Date*	Birth Date Range	Mean Birth Date*
1973	9	27 Dec-2 Feb	11 Jan	16 Feb-27 Mar	5 Mar
1974	13	5 Jan-29 Jan	13 Jan	27 Feb-23 Mar	7 Mar
1975	13	6 Jan-3 Feb	17 Jan	28 Feb-28 Mar	11 Mar
1973-75	35	27 Dec-3 Feb	14 Jan	16 Feb-28 Mar	8 Mar

*S.D. = 9.7 days

TABLE 8. *Reproductive performance of 48 red foxes in southern Wisconsin, 1973-75.*

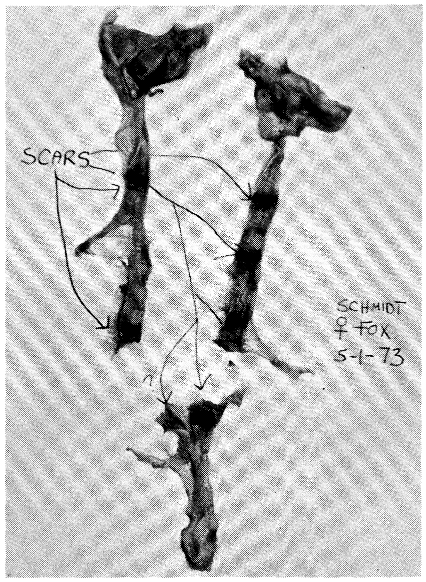
Vixen Year Class	Number	Number Reproducing	Percent Reproducing	Embryo-Placental Scar Range	Mean Litter Size
0-1	22	13	59	2-8	5.9
1-2	10	9	90	3-8	5.4
2-3	9	8	89	4-10	6.8
3-4	4	3	75	5-6	5.3
4(5-7)	3	3	100	4-10	8.0
Total	48	36	75	2-10	6.0
Juveniles	22	13	59	2-8	5.9
Adults	26	23	89	3-10	6.0

TABLE 9. *Mean red fox litter sizes, Waterloo Study Area, 1972-75.*

Year	Criteria	Number Litters Examined	Range	Mean Litter Size
1972	Litter sizes*	6	2-10	4.6
1973	Litter sizes**	8	3-10	4.8
	Placental scars	2	6-10	8.0
	Embryos	1	10	10.0
1974	Litter sizes**	6	4-7	5.7
	Placental scars	17	2-7	5.8
	Embryos	9	4-8	6.3
1975	Litter sizes**	7	2-8	5.6
	Placental scars	7	1-6	4.1
	Embryos	7	2-8	6.0
1972-75	Litter sizes	27	2-10	5.2
	Placental scars	26	1-10	5.5
	Embryos	17	2-10	6.4
1972-75	Total	70	1-10	5.6

*Data based on observations of pups at dens.
**Data obtained from pups taken from dens.

Four of 13 pups from a communal den.



Placental scars in the uterus of a female killed at a communal den by dogs.

TABLE 10. *A Chi-square comparison of sex ratios from pups at dens with sex ratios of tagged foxes, foxes killed at Waterloo, foxes harvested in southern Wisconsin and foxes killed statewide.*

Sample Type	Number of Foxes	Percent Males	Percent Females	X^2
(1) Den juveniles	154	49	51	
(2) Tagged returns	77	45	55	0.32
Trapped	33	45	55	0.02
Hunted	27	37	63	0.93
Other	17	59	41	0.53
(3) Waterloo Study Area Mortality	35	57	43	0.72
(4) Southern Wisconsin**	208	50	50	
Trapped	124	48	52	0.01
Hunted	84	54	46	0.58
(5) Statewide	350	58	42	
Trapped	208	57	43	5.24*
Hunted	142	58	42	4.4*

*Significantly different from den juvenile sex ratio (49:51) at $P < 0.05$, 1 d.f. Chi-square value is 3.84.
**Dane, Dodge, Jefferson, Columbia, Fond du Lac and Marquette Counties.

Sex ratios from southern Wisconsin and statewide foxes (hunted and trapped samples combined) were not compared with den juvenile sex ratios because of a possible bias in the higher number of trapped foxes collected. The statewide samples of trapped and hunted foxes were the only groups whose sex ratios differed significantly from those of the den juveniles (Table 10). Groups (2), (4) and (5) were divided into trapped and hunted segments in order to analyze possible differences. The tagged fox category, because it represented a distinct cohort, was compared collectively as well as individually by trapped, hunted and other (car kill and mange) components. The Waterloo mortality group consisted predominantly of hunted foxes and was classified only as one collection. We were not able to determine why the sex ratio of the statewide foxes differed significantly from the den juveniles, whereas the sample from only southern Wisconsin did not. The statewide male collection (350 foxes) may have been more prone to hunting and trapping as a reflection of their more extensive travel patterns (Storm et al. 1976:24).

The nonsignificant differences in the sex ratios of the 3 other fox groups simply may reflect the small sample sizes (Table 10). Our tagging results indicated that between October and March, male foxes moved significantly farther ($P < 0.01$, 64 d.f.) than females, which may have resulted in higher male mortality. Although a sex ratio comparison of den juveniles with statewide foxes indicated a significantly lower number of females killed, similar southern Wisconsin comparisons with denning pups were not significant.

HOME RANGE AND HABITAT USE

Radio-Telemetry

Eight pups were radio-tagged during the study to determine location of dens and distances between them. Five vixens were radio-equipped to measure home range. Histories of each fox are shown in Table 11.

Red fox radio-telemetry studies have incorporated several methods for describing home range. Storm (1965:4) used length-width ratios, distances between day and night resting areas and maximum area to evaluate red fox home ranges in northern Illinois. Ables (1969b:109) relied upon geometric centers of activity and activity radii for the analysis of home range; he also used telemetry to determine activity patterns (Ables 1969a) of red foxes in southern Wisconsin.

The term "home range" used here is defined as the area travelled by red foxes during their daily activities within the perimeter of the outermost radio-locations.

Radio transmitter, incorporating speedometer cable antenna is placed on a fox...

...which upon release quickly heads for the open field.

Radio-Tagged Pups

Four pups (F28, M29, M32 and M179) moved an average distance of 1.3 km (range 0.3-2.8 km) after release. All 4 pups were marked during May, when the majority of their time was spent at the immediate den site. Pup M32 was recaptured 0.8 km northwest of its den on 25 September 1973 and was sporadically radio-tracked in a 50 ha area north of the second capture point until the signal was lost. Sargeant et al. (1975:36) documented 24 den moves from tagged pups in North Dakota, which ranged from < 0.1 to 2.6 km.

In contrast, radio-equipped pups F8, F42, M43 and F52 were captured and followed later in the denning season (June-August) when the juveniles spent more time away from their dens. Only an estimate could be made of the home range occupied by pups because of the difficulty in receiving transmitted signals. F52 was radio-equipped for a 97-day period, but signals were received for only 19 days. F8 was trapped on 18 June 1972 and moved 300 m southwest into a 2 ha woodlot, where she spent the bulk of her time during the 5-day tracking period. The pup was shot on 31 January 1973, 61 km northeast of the trap site.

F42, M43 and F52 were associated with a communal den. All 3 juveniles were frequently located in an unpicked 9.4 ha corn field, located only 30 m southwest of the southern natal den. F42 was captured twice; the second capture was made 0.6 km southeast of the initial capture during an extremely warm and humid period (31 August 1973). The pup, when found dead in a corn field 4 days later, contained a large number of maggots in its rectum. Death may have been caused by stress induced by hot weather, maggot infestation, and/or the shock of being trapped. M43 was located in the 9.4 ha corn field on four occasions during June 1973. When the pup was last seen, the whip antenna of its transmitter was broken off, negating any further radio contact. Numerous tracks of both juvenile and adult foxes in the mud of the 9.4 ha corn field, together with the radio locations of the tagged pups and F10, indicated that the field was heavily used by foxes. F52, trapped in the same 9.4 ha corn field, was located 44% of the time in corn fields and occupied an area of approximately 11 ha.

Pup radio-telemetry data indicated that F42, M43 and F52 at ages of 10 to 18 weeks travelled less than 1 km from dens independent of their parents, but still centered their activity around several dens.

Radio-Equipped Adults. The five adult vixens equipped with transmitters were radio-located 685 times from 1972 to 1974 (Table 11). Sixty percent of the fixes were made between 6 p.m. to 6 a.m. when the foxes were more active. The five females were tracked for 163, 24-hour periods during the 313 days of transmission.

F9 and F17. F17 was located 8 times during a 3-day period before contact was lost. F9 was found 25 times during 8 days after being fitted with a transmitter that later gave only intermittent signals. When located, F9 occupied an 88 ha area located adjacent to the home range of F11.

F11. F11 was trapped near the center of its 581 ha home range and was radio located 103 times (62 night fixes or 60% of the time) during 5 days in November, 20 days in December and 6 days in January.

F11's total home range consisted primarily of cultivated lands (50%), marsh (15%) and lowland hardwoods (9%). Although the frozen Crawfish River was occasionally crossed by F11, it seemed to form a partial western and southern home range boundary. This fox was never located beyond two paved county highways located a short distance to the north and east. F11 was able to explore all possible cover types within her home range because of the frozen conditions. Hunting pressure exerted by a group of local hunters upon the radioed vixen and her probable mate (based on observations of tracks in the snow), was not known to have forced F11 out of her home range. She was eventually shot (13 January 1973) by hunters off the northwestern corner of her known range.

F10. This vixen was trapped and radio-tagged on a small drumlin in a retired cropland field on 21 November 1972. However, radio contact was not established until 10 January 1973, when F10 was located in an area of shrub-carr 2.2 km northeast of the capture site.

F10 was radio-located 51% of the time between 6 p.m. and 6 a.m.; eve-

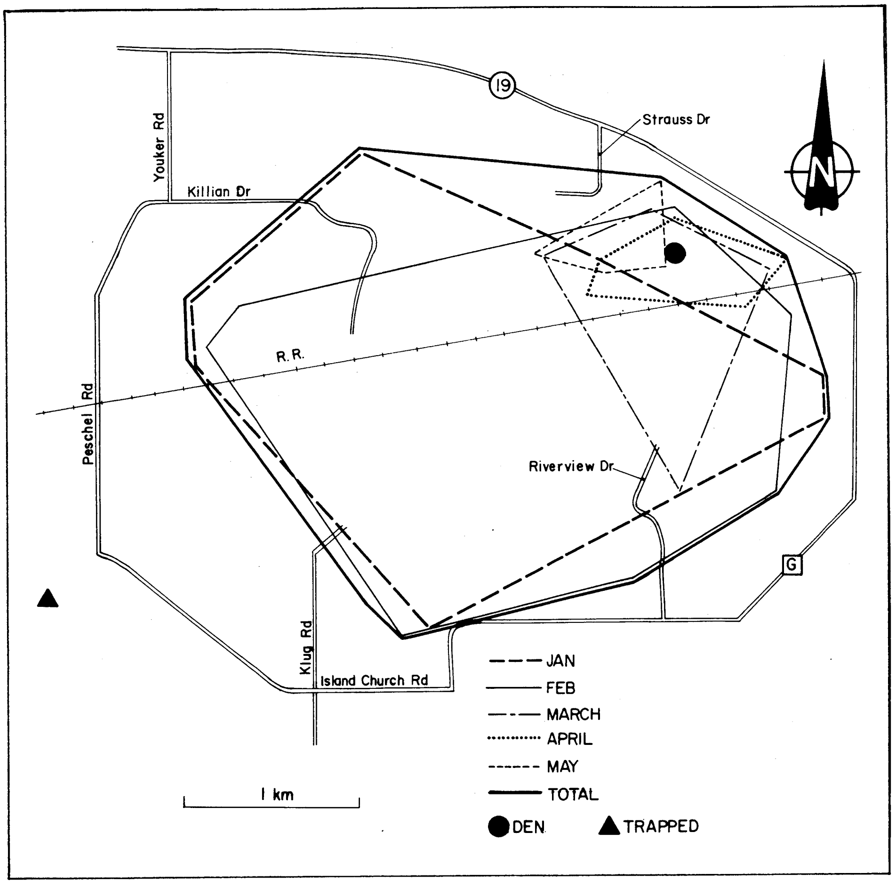


FIGURE 4. *January-May home ranges of F10 on the Waterloo Study Area, 1973.*

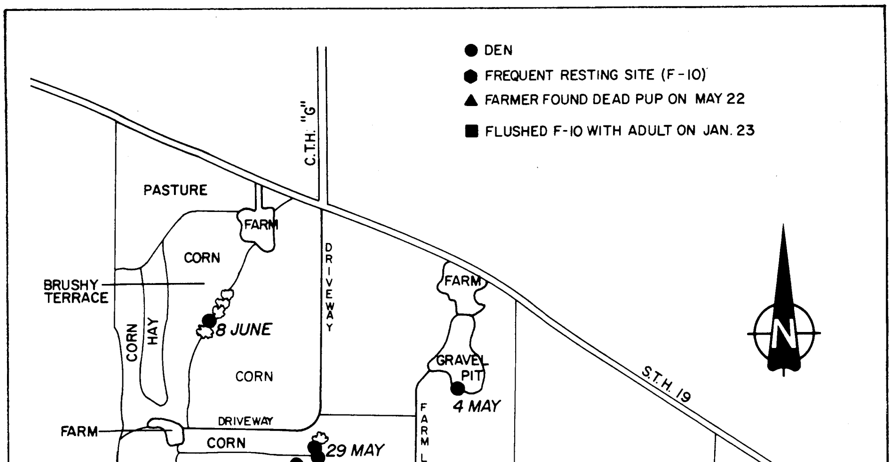


FIGURE 5. *Map of dens associated with F10 on the Waterloo Study Area, 1973.*

ning locations were made as often as manpower was available. The number of days located and day-night fixes per month for the tracking period were: 16 January: 30, 30; 23 February: 41, 61; 21 March: 27, 36; 10 April: 19; 17; and 8 May: 19, 3. The home range of the vixen gradually diminished from 579 ha in January to 18 ha in May (Fig. 4); however, 86% of the May locations were made during the day. Cultivated lands (68%), marsh 9%), retired cropland (5%) and pasture (5%) were the major cover types frequented during each monthly home range.

Two sets of tracks were observed in the snow within F10's January home range and on 23 January 1973, she was flushed from a lowland pasture resting site with another (presumably) male fox. The presence of a mate was further substantiated when she was monitored from 5:30 p.m. on 7 February to 5:40 a.m. on 8 February; two sets of tracks corresponding with radio-locations from the previous night were found within the home range of F10. Radio-telemetry enabled us to make several observations of F10, two other adults and 10 pups near and at subsequent communal denning sites (Pils and Martin 1974). Observations of these pups at dens from 5 April to 11 June together with radio locations made of pups F42, M43 and F52 allowed us to map the location and chronology of dens utilized by F10 and her communal family (Fig. 5). Dates next to the den symbols signify the first observation or radio location of F10 or her family at a den site.

F58. This vixen was trapped on 20 November 1973 on the eastern slope of a heavily grazed hilly pasture located 0.6 km east of The Waterloo city limits. The following day, F58 moved 2.3 km south into the area in which she established her home range.

F58 was located by radio from 6 p.m. to 6 a.m. 68% of the time. The number of days located and day-night fixes per month for the tracking period were: 8 November: 23, 16; 17 December: 36, 145: and 18 January: 25, 21 (Fig. 6). Cultivated lands (57%), pasture (19%), and marsh (10%) were the three principal cover types frequented by F58 during the establishment of her entire November through January home range of 515 ha. Radio-telemetry data were supplemented by tracking F58 during adequate snow cover. The distinctive trail left by the dragging antenna enabled us to distinguish F58 from other foxes in the vicinity. This capability permitted us to compare the radio locations with track locations during the same period, resulting in a high degree of accuracy in estimating our locations of this fox. Radio-tracking data indicated that picked corn fields were a prime area of movement for F58. Persistent snow cover was generally less than 7.6 cm during the winter of 1973-74; fox tracking efforts indicated that extensive small mammal hunting activities took place in these corn fields during a period of small mammal abundance and apparent rodent vulnerability (Petersen unpubl.). The influence of habitat on fox movements and subsequent home ranges was probably affected by climate. Radio locations of F58 made during the freezing conditions of late fall and winter resulted in a meandering pattern of fixes through a variety of cover types, especially wetlands.

F58 and an associated fox were pursued by a group of local fox hunters with dogs during portions of three winter weekends. The hunters claimed that they wounded F58 on 13 January 1974 and found blood on the snow. The vixen, thought to be seriously injured after the shooting, was located in a den on 16 January. However, she was again seen on 23 January in apparently good condition at another den located 1 km east of the 16 January location. Most importantly, F58 did not shift her home range in spite of the severe hunting pressure. Hamilton (1939:304) found that foxes may be chased from their territories, but return when no longer pursued by hounds. Waterloo movement data from F58 and F11 agreed with Storm's (1965:8-9) finding that two adult males stayed well within the limits of their home range in spite of being pursued by dogs.

Radio contact was lost with F58 on 27 January 1974; however, drag marks from her antenna were seen on 15 February, verifying her presence in the area. During May, a farmer reported seeing a den located on the southern edge of F58's home range. This den was subsequently dug up, and 4 pups were tagged. However, F58 was never seen at or near this den. F58 was found dead on 17 November 1974 along Stokes Road (Fig. 6).

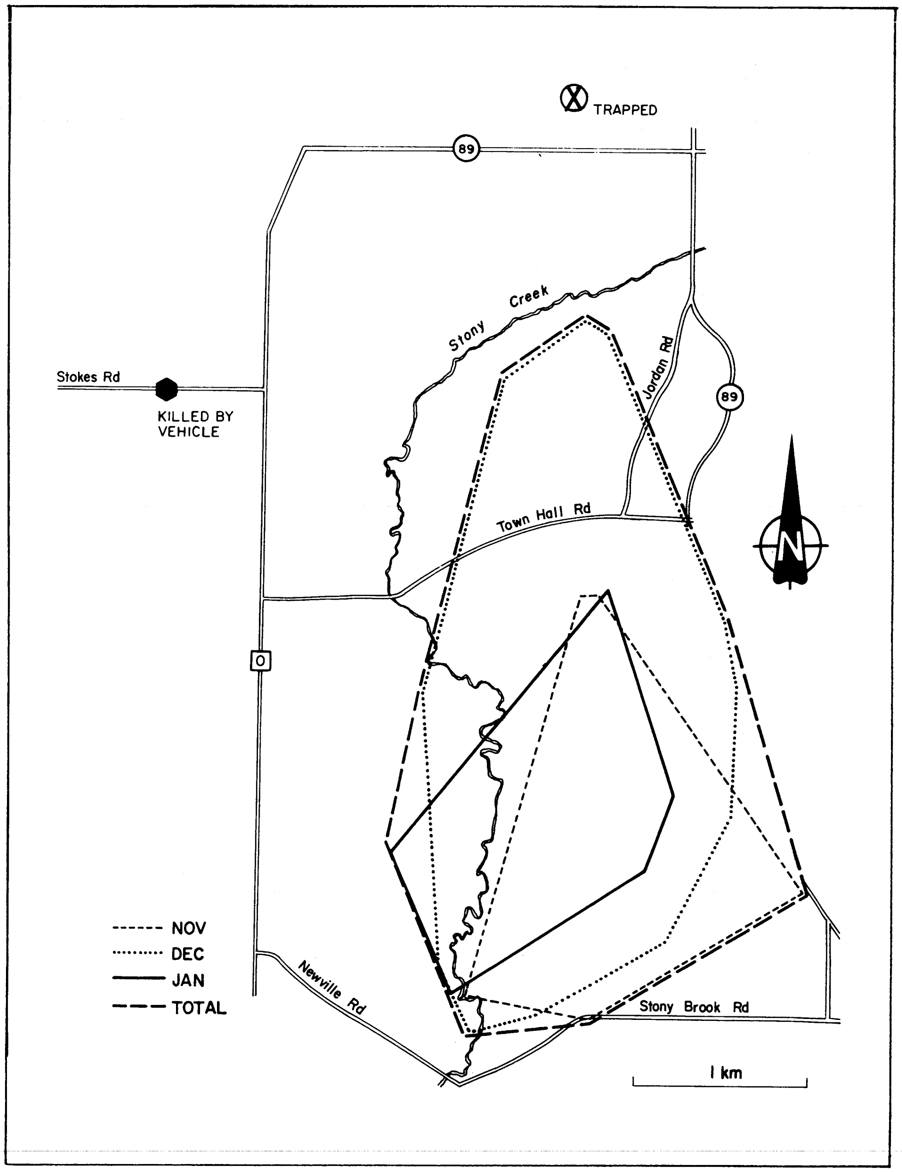


FIGURE 6. *November-January home range of F58 on the Waterloo Study Area, 1973-74.*

Conclusions. Juveniles less than 18 weeks old independently explored most of the habitat within 1 km of their dens. An unpicked corn field was especially preferred by 3 of the 8 radio-tagged pups. Adults frequented a wide variety of cover types within their territories, especially during the night. They were highly territorial during the fall and winter in spite of harassment from hunters and dogs, but were tolerant of other adults and pups during the spring and summer.

Winter Tracking

Red foxes were tracked in the snow at several different locations within the Waterloo Study Area for a total of 182.6 km during December through March of 1972-75. State-owned or leased areas (Fig. 1) were primarily utilized for ease of access. Snow depth varied from 5 to 20 cm during tracking. The three major tracking areas were in cultivated land including plowing, corn (picked and standing), soybeans and food patches. Table 12 lists the percent of fox trails in various cover types compared to the percent of available cover types taken from Table 1. Strip cover, marsh, upland and lowland hardwoods, tamarack, conifer plantations and shrub-carr were used excessively in proportion to the total area that they occupied. Strip cover was highly utilized because it was a continuous travel route also used heavily by rabbits and pheasants. Retired cropland probably contained a high proportion of the small mammal prey source. Frozen conditions probably allowed greater movement in the marsh than would be expected during the warmer months.

We may have inadvertently avoided particular cover types such as shrub-carr, tamaracks and rank vegetation (found in portions of the marsh) because of the difficulty in following trails in these vegetational areas.

Snow tracking efforts were mapped within the home range of F10 on 7-8 February 1973 (Fig. 7) and inside the territory of F58 (which could be identified by its antenna drag marks in the snow) on 15 February 1974 (Fig. 8). Both maps illustrate the meandering pattern (Huff 1964) made in search of food and in the act of patrolling their home range. Foxes regularly used frozen waterways such as drainage ditches (especially those bordering areas of

TABLE 11. *Summary of radio-equipped red foxes on the Waterloo Study Area, 1972-74.*

Sex-Number	Capture Method	Period Tracked	Total Days Tracked	Number of Fixes	Transmitter Fate	Fate of Fox
Pups						
F 8	Steel trap	Jun 72	5	18	*	Shot 31 Jan 73**
F 28	Den	May 73	1	1	Shed	Unknown
	Den	May 73	1		Failed	Moved to alternate den
M 29	Steel trap	Jun-Jul 73	14	22	*	Shot 23 Feb 73[1]
	Den	May 73	4		Shed	Moved to alternate den
M 32	Steel trap	Sep-Oct 73	11	45	*	Trapped 3 Jan 74[2]
	Den	Jun 73	4		Shed	
F 42	Steel trap	Aug-Sep 73	4	2	Still running when fox	found dead 4 Sep 73[3]
F 43	Den	Jun 73	4	3	Broken antenna; weak signal	Unknown
F 52	Steel trap	Jun-Sep 73	19	18	*	Trapped 20 Oct 74[4]
M 179	Den	May 74	2	2	Shed	Unknown
Adults						
F 9	Steel trap	Nov-Dec 72	8	25	Failed	Unknown
F 10	Steel trap	Nov 72-May 73	78	283	Failed	Unknown
F 11	Steel trap	Nov 72-Jan 73	31	103	Still running when fox	shot on 13 Jan 73[3]
F 17	Steel trap	Feb 72	3	8	*	Unknown
F 58	Steel trap	Nov 73-Jan 74	43	266	Failed	Killed by car on 17 Nov 74[5]

*Fox may have moved off Waterloo Study Area or transmitter failed.
**Moved 61 km NE
[1]Moved 42 km NE
[2]Moved 36 km NE
[3]Died on Waterloo Study Area.
[4]Moved 6 km SE
[5]Moved 3 km SW

dense vegetation), rivers and ponds as travel lanes. Foxes often investigated particular landmarks such as muskrat houses and old den openings either for the purpose of scent marking or hunting prey. Fox trails were also followed to dens that evidently were inspected for use as possible future natal dens. However, these dens were not always used later during the spring when pups were born. Bedding sites were found in a variety of cover types including marsh (7), shrub-carr (4), strip cover (4), lowland hardwoods (1) and retired cropland (1).

Storm (1965:9) reported that intraspecific interactions probably are a major influence on the movements of foxes throughout most of the year. Double fox trails were noted on the WSA from December through March, reflecting the close relationship pairs have before the denning season. However, the extent to which pairing influenced movements on the WSA is not clear.

DISPERSAL

Dispersal is here defined as a straight line movement of more than 8 km between first and last captures. Therefore, our results were directly comparable to the findings of Phillips et al. (1972) and Storm et al. (1976), who used the same criterion.

Time of Dispersal

Southern Wisconsin subadult red foxes, tagged as pups, did not start to disperse until October. Between October and March, 81% (59) of the 73 subadult recoveries occurred. Storm et al. (1976:28) found that none of their 57 radio-tagged foxes left natal areas before 1 October. Males in Illinois, Iowa and Minnesota dispersed earlier than females, which may have been related to seasonal changes in reproductive activity (Storm et al. 1976:29).

Proportion Dispersing

Eighty-eight percent (23) of the tagged, subadult males and 58% (19) of the subadult females recovered during October-March of their first year and traveled more than 8 km from their dens, a significantly different proportion ($P < 0.05$, 57 d.f.). Eighty-three percent (5) of the adult males and 56% (5) of the adult females recovered had dispersed. A total of 15 foxes tagged as pups were recovered as adults.

Ten adult-sized foxes were steel-trapped during the late fall; only one male was recovered, 4.5 years after tagging. Storm et al. (1976:31) found that adults also dispersed during fall and winter, but at a lower percentage than juveniles.

Dispersal Distance

Dispersal distances for pups captured at southern Wisconsin dens were a function of sex and age at last capture, as well as the month of recovery. Sixteen males versus 9 females (from all age classes) dispersed over 30 km. The distances subadult males dispersed during the October-March period ranged from 8.8 to 58.8 km, with a mean of 33.6 km. Female dispersals for the same period varied from 8.8 to 85.7 km and averaged 27.6 km, which did not differ significantly from male dispersals. Mean dispersal distances for both juvenile male and female red foxes were progressively greater from October through December for males, but fluctuated thereafter for both sexes (Table 13). Storm et al. (1976:32-33) stated that recovery distances increased significantly for subadult males between October and January, but did not increase significantly for subadult females between October and December. The longest red fox dispersal distance on record is for a male, tagged in southern Wisconsin, that moved 395 km to Indiana one year later (Ables 1965:102). Phillips et al. (1972:240) found that midwestern subadult males traveled almost three times the mean distance of subadult females during the April-March period. In addition, they also discovered that more males left their natal areas than females. No significant differences were found between the mean distances traveled by 23 dispersing juvenile males recovered in their first year ($\bar{x}$ = 33.6 km) and 5 males that were recovered as adults (range 22.4 – 61.2 km; $\bar{x}$ = 37.4 km). Similarly, no significant difference was noted between 18 dispersing females recovered during their first year ($\bar{x}$ = 27.6 km) and 5 vixens recovered as adults (range 11.3 – 62.8 km; $\bar{x}$ = 32.0 km).

Dispersal Direction

Chi-square tests of the directional distribution of dispersing subadult males and females revealed that both sexes did not randomly move into each of the four compass quadrants (Table 14). A significant number of males moved north rather than south, which agreed with the findings of Arnold and Schofield (1956:95) and Storm et al. (1976:34). The northeast quadrant contained at least twice as many recoveries as any of the other Wisconsin quadrants (Fig. 9). Females were recovered east in significantly higher numbers than west. When both sexes were combined, significantly more foxes were recovered in the northeast quadrant.

Storm et al. (1976:34) hypothesized that the foxes taken in the northern quadrants may reflect a greater hunter effort and better snow hunting conditions, rather than more foxes moving north from natal areas. Although it is very difficult to estimate hunter density in southern Wisconsin, we assumed that pressure was similar both in the release and recapture areas. Pelt prices for the 1971-72 to 1975-76 fox seasons averaged $24.42, which resulted in a high hunter density during that period throughout southern Wisconsin. We considered a 10 cm snow cover necessary for marginal fox hunting. Using this criterion, 22 days per year (seasonal mean from the Madison weather station) were available to fox hunters during 1971-75.

Data derived from this study suggested that the interstate highways may alter the direction and rate of dispersal. Storm et al. (1976) cited evidence that large rivers, such as the Mississippi, acted as barriers to dispersing foxes and that features such as lakes, smaller rivers, cities and interstate highways only altered dispersal direction. Fifteen pups (excluding F136 and F137, which moved west and north) tagged in southern Wisconsin (Fig. 10) were recovered during October-February in the southern two compass quadrants (Fig. 9). Six of these subadults were killed south of I-94, which runs east and west between Madison and Milwaukee. The traffic flow on this route is extremely heavy during all hours.

Sixty-five percent of the recoveries illustrated in Figure 10 were foxes killed before they crossed I-94, suggesting that these foxes may have been reluctant to cross the large highway and remained in the area until they were trapped or shot. The presence of a 1.2 m woven wire (15 × 15 cm) fence with a top strand of barbed wire running parallel to both sides of the interstate may have also discouraged these foxes from crossing I-94. A total of 22 possible corridors (culverts, frozen rivers, underpasses, and overpasses) for crossing 27 km of I-94 were available between the locations where F137 and F169 were recovered (Fig. 10). It is possible that trappers, who recovered 65% of the foxes shown in Figure 10, frequented these areas where foxes were concentrated before moving across I-94, over others farther from the interstate. As a result, foxes entering these areas would tend to be more vulnerable to recovery. An example of this type of corridor was the recovery sites of M158, M156, F117 (caught by the same trapper) and F186, all taken within 2 km of each other (Fig. 10). The majority of the tagged pups came from the WSA vicinity, which is relatively close to I-94 (Fig. 10). If the number of foxes killed within 2.1 km of the north side of I-94 is any indication of the superhighway's effectiveness as a partial travel barrier, it is possible that a number of dispersing foxes from the WSA vicinity initially moved south, encountered I-94 and eventually moved into the two northerly quadrants.

Tracks of radio-tagged female in snow, illustrating drag marks from the antenna.

TABLE 12. *Comparison of cover type preferences of red foxes in winter with available cover types.*

Land Use	Fox Trails In Cover Type (Percent)	Area In Cover Type (Percent)
Cultivated lands	21.1	56.0
Marsh	25.7	12.8
Pasture	3.6	10.5
Upland hardwoods	9.6	4.5
Miscellaneous	6.0	4.4
Retired cropland	14.2	4.1
Shrub-carr	8.9	3.0
Tamarack	1.8	1.6
Lowland hardwoods	2.4	1.5
Strip cover	6.0	1.4
Conifer plantation	.8	.1
Total	100	99.9

Dispersal of Littermates

The dispersal pattern of 8 out of 13 pups tagged from a communal litter was extremely widespread (Fig. 11). Dispersal distance of 8 recoveries exceeded 8 km; the 6 males dispersed a

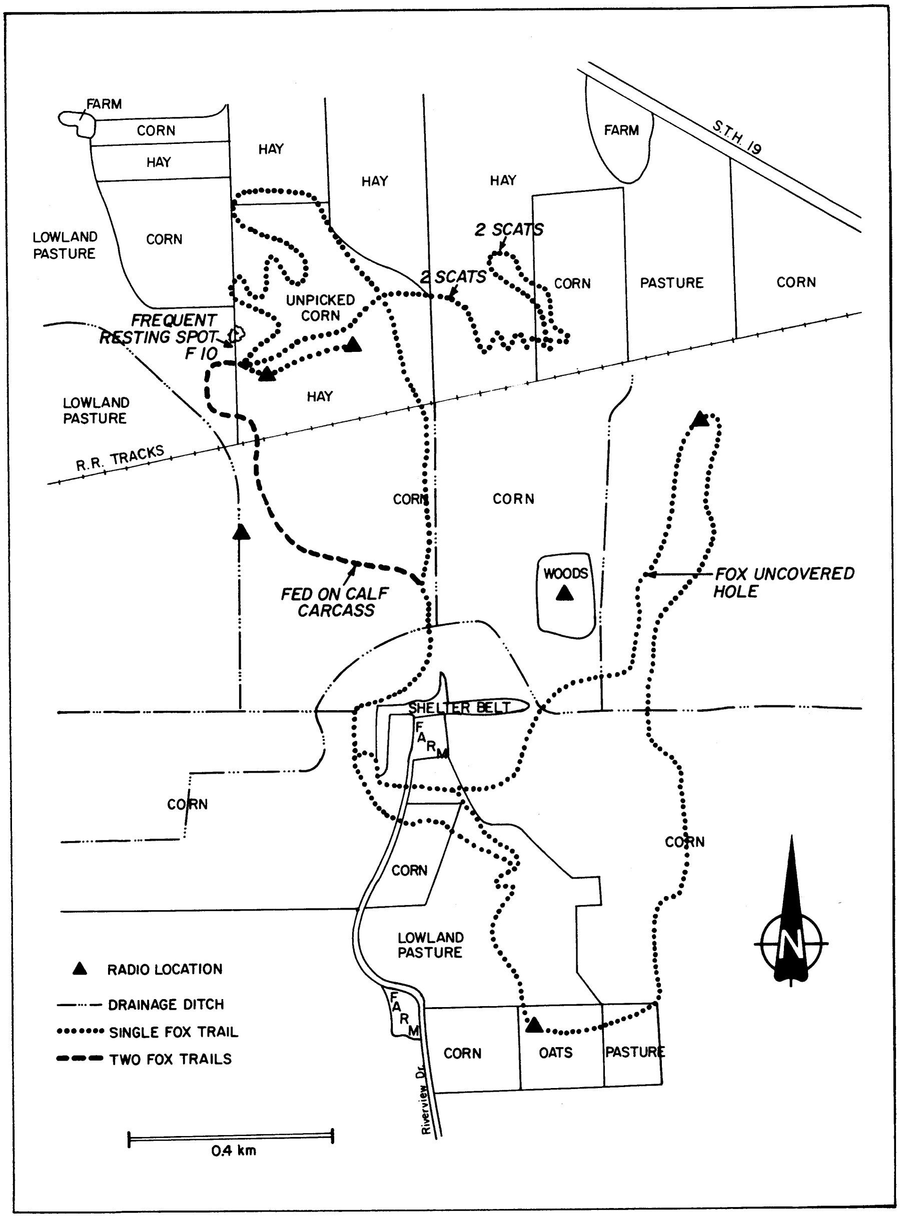


FIGURE 7. *Radio locations of F10 and associated fox trails found in the snow during 7-8 February 1973 on the Waterloo Study Area.*

mean distance of 40 km, while 2 females traveled a mean distance of 14 km. Recoveries from the litter were found in every quadrant except the southwest. Four of the 6 tagged males were recovered from the northeastern quadrant, while the 2 female recoveries were killed in the southeastern quadrant; the reasons for these sex-oriented directional movements remain largely unknown. The main conclusion drawn from analyzing dispersal from large or communal litters is that these pups spread out over an extremely large area (Fig. 11).

Our data suggest that littermates may occasionally disperse together or follow similar routes. A male (M77) and female (M79) juvenile tagged at the same den, were trapped by the same trapper at an identical site on 4 January 1975 and 16 January 1975 respectively. The site was located 11.3 km northeast from the den. It seems unlikely that both pups would independently arrive at the same trap site. Two other tagged littermates (F122 and M125) were killed within 4 km of each other after dispersing north for 55 and 59 km respectively. The male was trapped on 21 October 1975, while the female was shot on 20 January 1976. M125 may have dispersed earlier and reached the trapping vicinity before the female; however, they may have dispersed together, with the female remaining in the vicinity after her littermate was trapped.

MORTALITY

Causes of Mortality

Sources of mortality for 127 foxes examined during the present study (44 foxes recovered on the WSA and 83 foxes from the 6 southern Wisconsin counties outside Waterloo) were summarized into four categories: deaths by fox hunting, trapping, other hunting (deer, pheasant and rabbit) and miscellaneous (car, mange, dog and unknown). Fox hunting and trapping constituted the major source of mortality for both the tagged and untagged samples. We felt that our sample of foxes collected represented the proportion of foxes dying from various causes. Sarcoptic mange was the only disease that we were able to recognize during field work in southern Wisconsin. Such cases were assumed to result in death, based on the findings of Stone et al. (1972). Therefore, if a mangy fox was shot near a farm building after appearing to be listless or unafraid, mange was considered to be the cause of death. Most of the cases diagnosed as mange were in the easily recognized advanced stages. We did not examine all dead foxes for other diseases or parasites.

Figure 12 contrasts the differences in mortality found primarily on private land (southern Wisconsin tagged returns) versus types of deaths occurring principally on public land (WSA tagged and untagged recoveries). Waterloo mortality data included 8 tagged foxes thus some overlap of information occurred between the two areas.

Types of Mortality

Annual mortality was determined from those tagged foxes recovered as subadults and adults (Fig. 13). Seasonal mortality for 69 tagged foxes shown in Figure 13 included one March recovery from a county with an open fox hunting season.

On the Waterloo Study Area. Waterloo losses (both tagged and untagged foxes) included much higher hunting losses than southern Wisconsin samples (tagged and untagged). The trapping harvest was low on the WSA because a public hunting ground was interspersed throughout the study area (Fig. 1). Trappers were reluctant to trap during the first third of the fox season, when trapping conditions were prime, because of the high density of pheasant hunters and dogs. As a result, fox hunting at Waterloo was the leading cause of death. Table 15 categorizes the monthly fox harvest on the WSA according to hunter or trapper intent.

TABLE 13. *Straight-line distances in kilometers between first and last captures of tagged juvenile red foxes during their first year of life in southern Wisconsin, 1973-76.**

	Males			Females		
Month Recaptured	Number of Animals	Mean Distance Traveled	Range	Number of Animals	Mean Distance Traveled	Range
May				1	5.2	5.2-5.2
June	2	1.6	1.6-1.6	2	0.6	0.0-1.2
July	2	2.3	0.8-3.6			
August	1	3.2	3.2-3.2	1	1.3	1.3-1.3
September	4	2.3	0.4-3.2	1	3.2	3.2-3.2
October	5	27.5	2.4-51.1	4	12.7	1.6-29.4
November	7	31.9	2.8-56.7	8	15.4	0.4-46.7
December	6	40.2	3.2-58.8	4	11.4	0.0-31.0
January	5	21.9	11.3-30.0	11	19.5	1.6-55.9
February	2	25.6	16.1-35.0	6	22.2	0.8-85.7
March	1	19.3	19.3-19.3			
May-September	9	2.3	0.4-3.6	5	2.3	0.0-5.2
October-March	26	30.1	2.4-58.8	33	17.5	0.0-85.7
May-March	35	22.8	0.4-58.8	38	17.1	0.0-85.7

*Movements were termed "dispersal" when they exceeded 8 km.

Pup shot by a farmer near its den during 1972.

Rifles or shotguns accounted for 91 percent of the total kill. A miscellaneous category was created for those foxes that were shot after being accidently spotted. These losses were distinct from other types of hunting. Foxes shot by deer and pheasant hunters on the WSA during 1971-75 equaled 22% of all reported mortality (Table 15). These hunting losses probably constitute an important source of fox harvest on public hunting grounds in southern Wisconsin. At Waterloo, such mortality ranked second only to fox hunting losses.

Although rabies is a controlling influence on some red fox populations (Johnston and Beauregard 1969), it has never been a major problem in Wisconsin (Richards and Hine 1953; Trainer 1976). No incidence of rabies were reported on the WSA during this study.

Indiscriminate killing of foxes by man at Waterloo during the spring and summer was minimal during our investigation, probably because of the higher potential fur values in fall (averaging from $10.65 in 1971-72 to $23.61 in 1974-75). We knew of only two instances (both during 1972) where Waterloo pups were deliberately killed at dens by man. After 1972, when fur prices accelerated, landowners assumed a much more protective posture (Pils 1977). Only one WSA juvenile was known to have been injured by farm machinery during our field research. However, Storm et al. (1976:49) speculated that this type of fatality was underestimated.

Dogs were known predators of foxes on the WSA. Although only one tagged pup was reported by a farmer to be

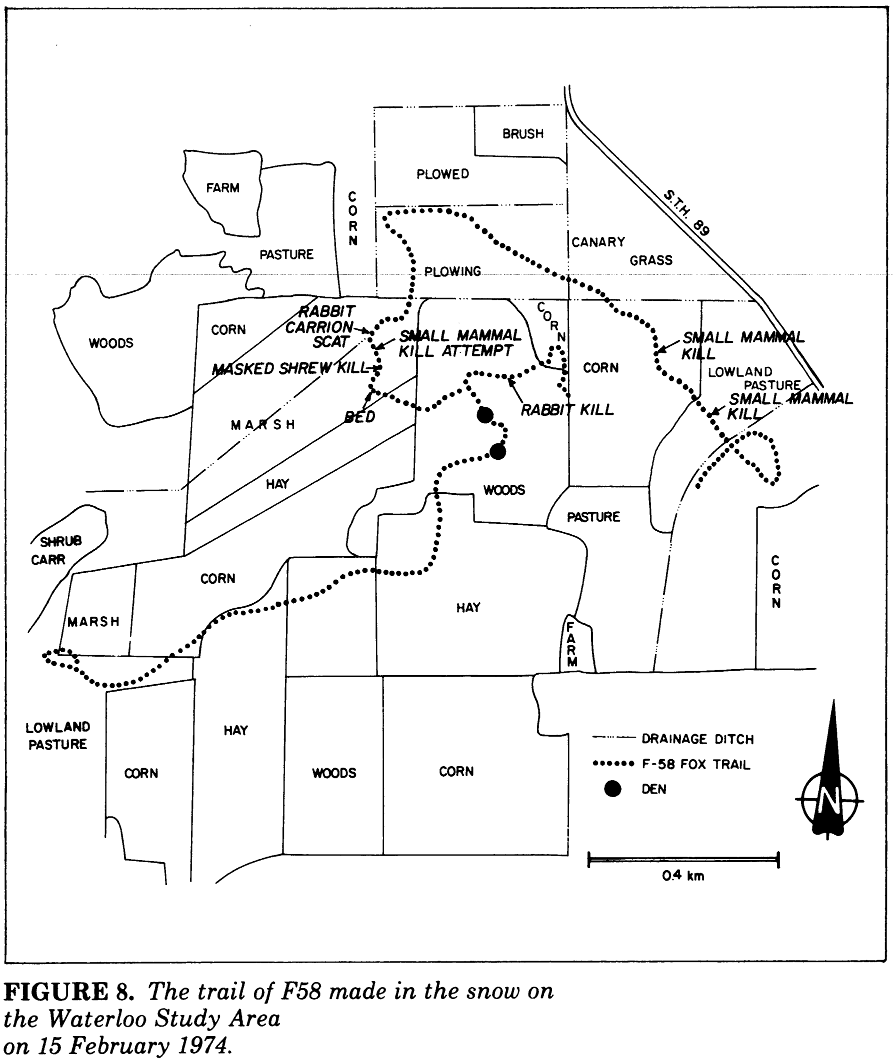


FIGURE 8. *The trail of F58 made in the snow on the Waterloo Study Area on 15 February 1974.*

killed at a Waterloo den, we documented one instance of dog aggression that resulted in the death of an adult female. Dog densities at Waterloo averaged approximately 1.4 dogs per farm. Many of these dogs roamed over wide areas and may have been responsible for additional fox mortalities.

Although miscellaneous causes of death did not constitute large percentages of the reported mortality, these losses may have greater significance when related to unreported, predispersal or pre-October deaths. Pup mortality from unknown causes was observed at Waterloo on three occasions. Collectively, pups killed by dogs, mange, vehicles, unknown disease and possible injuries inflicted by littermates had an extremely low probability of being found and reported during the spring and summer. Therefore, these types of mortality are the major reason that our recovery rates represent minimal values.

In Southern Wisconsin. Tagged foxes from southern Wisconsin were primarily obtained by trapping on private lands, where small game hunting pressure was less intense than on public hunting grounds. The proportion of tagged foxes that were taken by trapping off the WSA was also considerably higher than the proportion of foxes taken by trapping on the WSA (Fig. 12). Although the tagged sample was small, it probably was the best indicator of sources of red fox mortality, since tagged animals recovered also represented miscellaneous causes of death from March to September (months not included in the untagged sample). Results of our Wisconsin fur buyers questionnaire also indicated that trapping was the major source of mortality, accounting for 67% of all furs purchased during 1974-75 and 1975-76 (Table 16). Eighty-six percent of the kill came during the October-January period when furs were of greater value than in February or March.

No significant mortality differences ($P > 0.05$) were noted between males and females in the two categories (Fig. 12); 5 WSA males died from the mange, but the small sample size precluded a meaningful statistical comparison.

The majority of both tagged and unmarked foxes were trapped during October, November and December or were shot by fox hunters during January and February (Fig. 13 and Table 15). Trapping was undoubtedly easier and more efficient during the former three months, while maximum fox hunter efficiency occurred during the latter two months, when snow tracking and spotting conditions were optimal.

TABLE 14. *Directional distribution of recoveries for dispersed foxes, tagged in southern Wisconsin, 1973-75.*

	Semicircle		Semicircle		Quadrant				
	N 270-90	S 90-270	E 0-180	W 180-0	NE 0-90	NW 270-360	SE 90-180	SW 180-270	Value Chi-square
Males	22	6	17	11	13	9	4	2	10.57* (3 d.f.) 9.14**(1 d.f.) 1.28 N.S.(1 d.f.)
Females	14	9	22	1	13	1	9	0	20.65**(3 d.f.) 1.08 N.S.(1 d.f.) 19.18**(1 d.f.)
Males & Females	36	15	39	12	26	10	13	2	23.42**(3 d.f.) 8.64**(1 d.f.) 14.30**(1 d.f.)

*Significant at ($P < 0.05$).
**Significant at ($P < 0.01$).

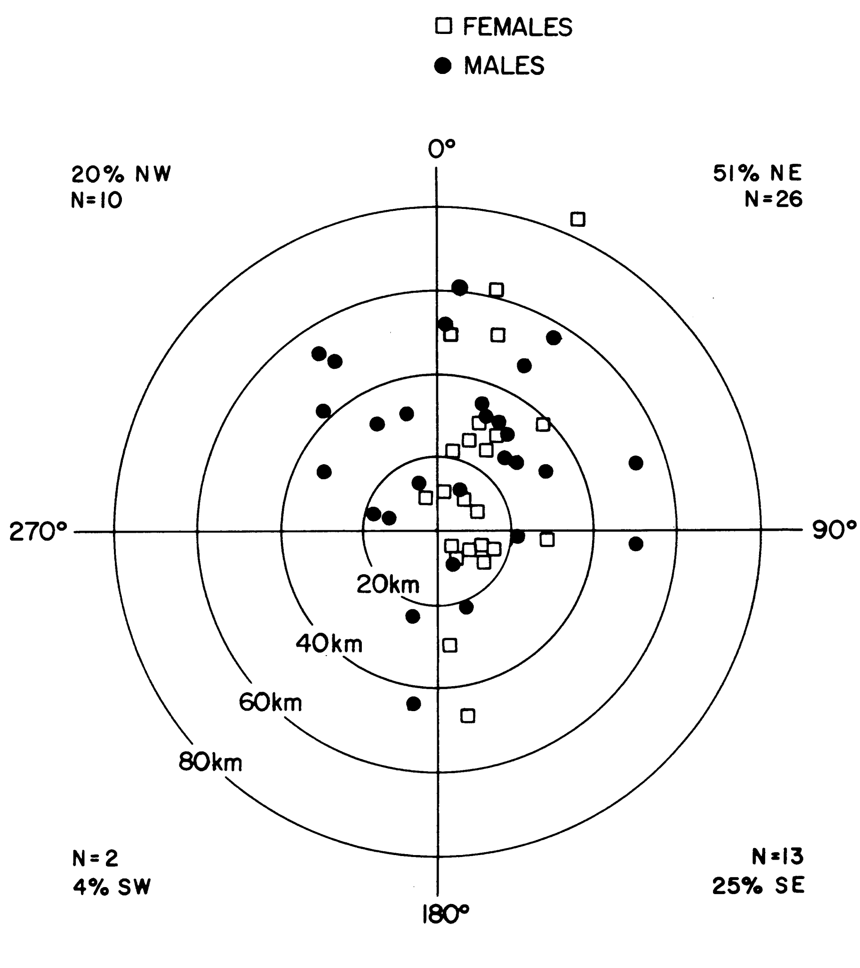


FIGURE 9. *Comparative pattern of dispersal for male and female foxes from October through May. (Male and female symbols are placed according to direction of travel. Center of circle represents tagging site.)*

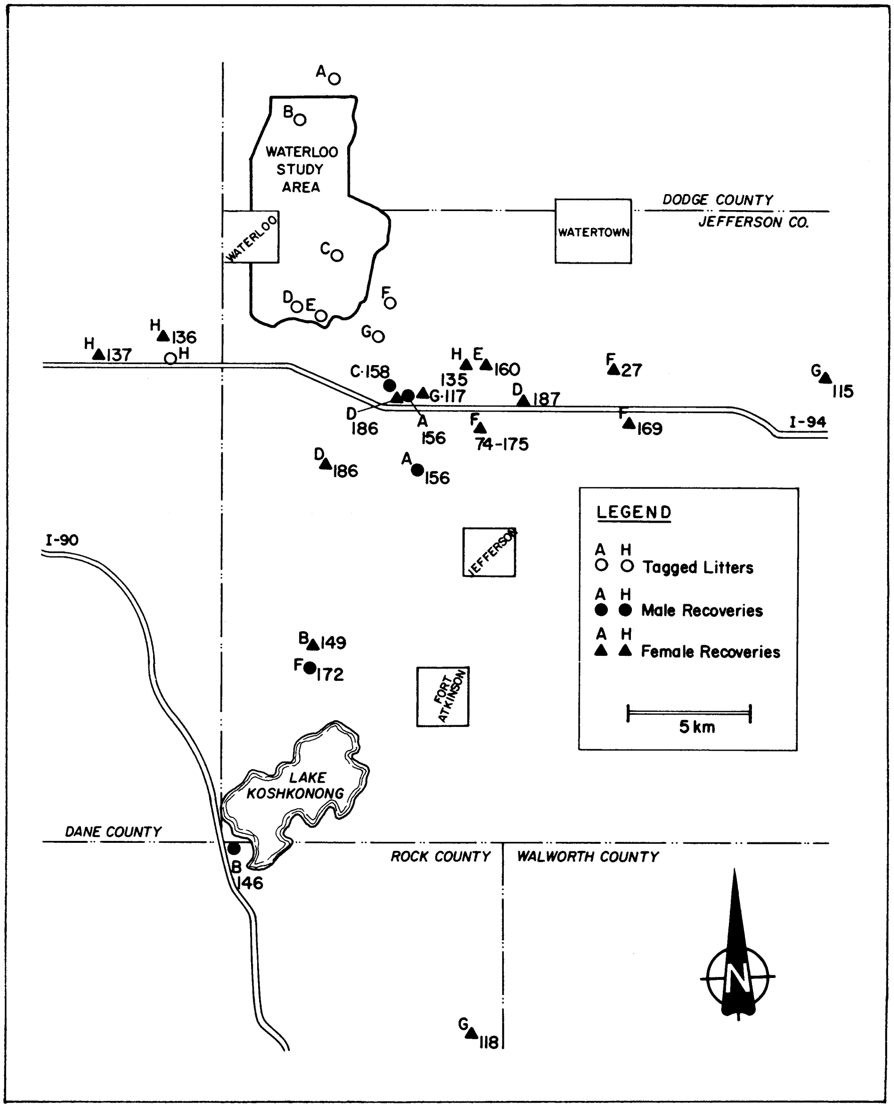


FIGURE 10. *Distribution map of fox recoveries south of the Waterloo Study Area, 1974-76. Dot and letter indicates den site of tagged litter. Recovery locations are indicated by sex and den origin.*

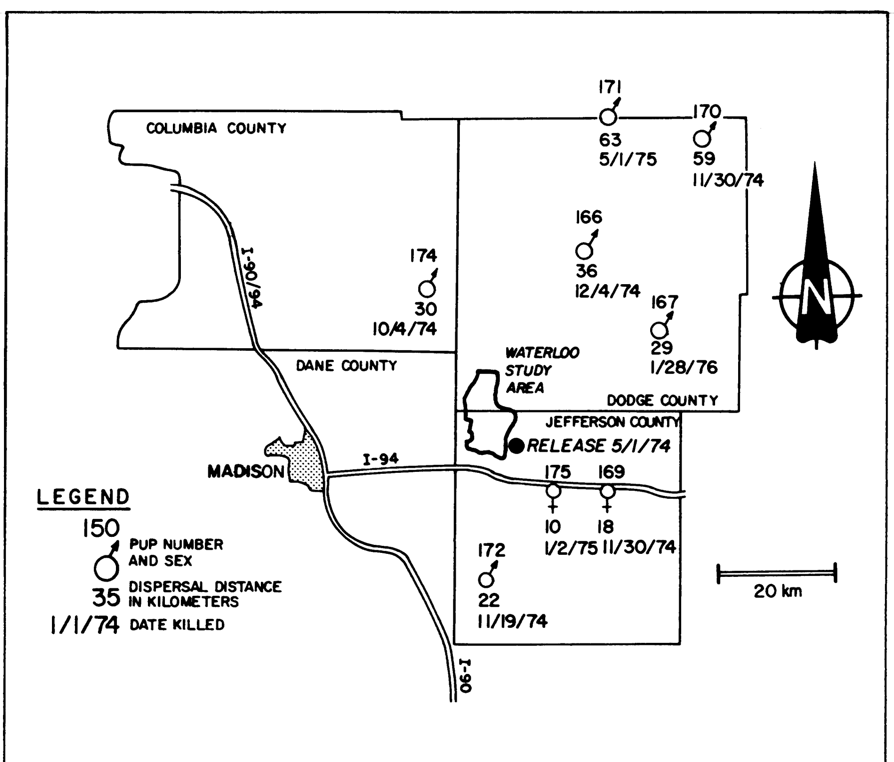


FIGURE 11. *Recoveries of 8 red foxes tagged in a southern Wisconsin communal den on 1 May 1974.*

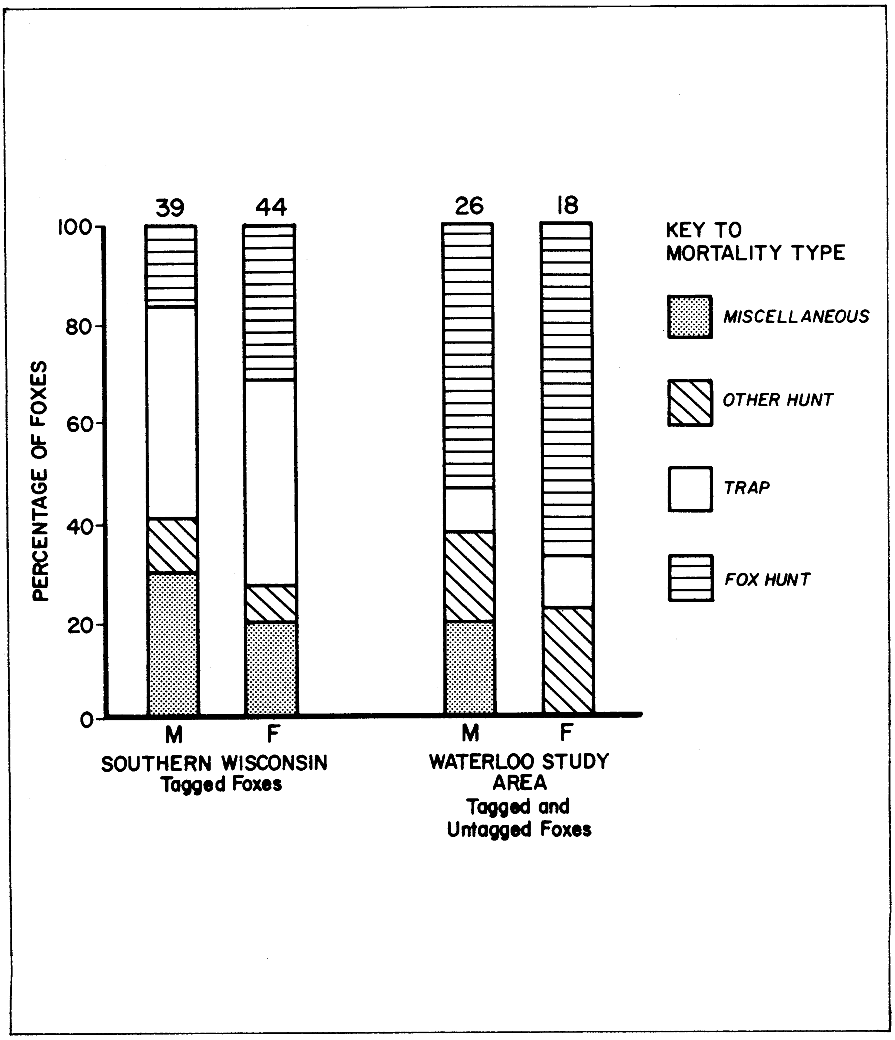


FIGURE 12. *Causes of deaths of tagged foxes recovered in southern Wisconsin from 1973-77 and from foxes killed on the Waterloo Study Area from 1973-76. The number above each bar represents sample size.*

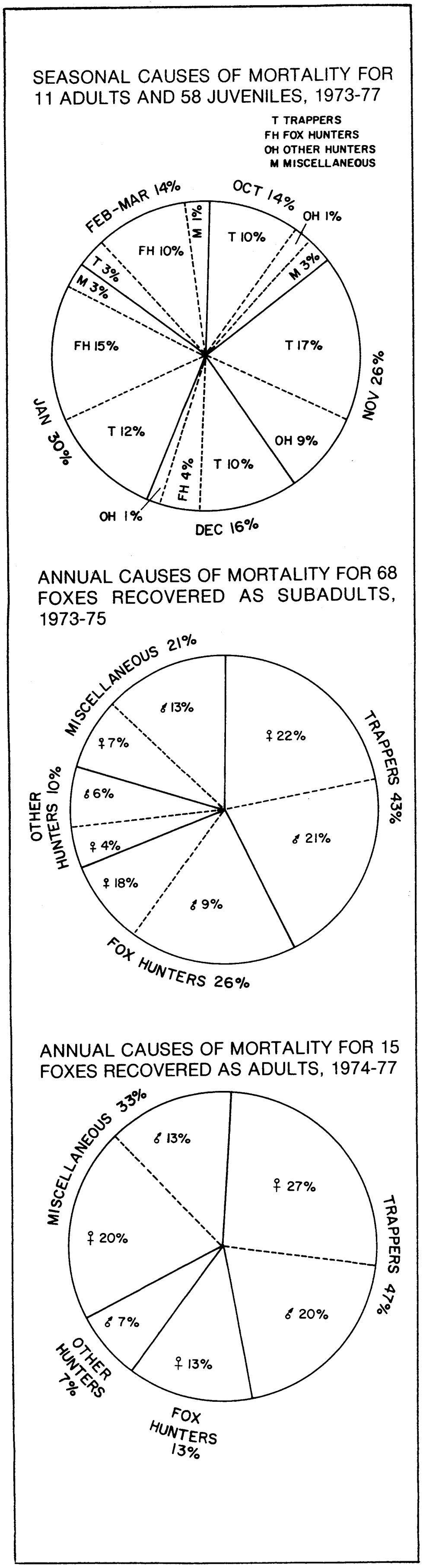


FIGURE 13. *Causes of death of red foxes tagged as pups and recovered in southern Wisconsin, 1973-77.*

TABLE 15. *Monthly mortality categories on the Waterloo Study Area, 1971-75.*

Month	Shot While Hunting: Pheasants	Shot While Hunting: Deer	Shot While Hunting: Fox	Trapped	Miscellaneous*
October	4	0	0	0	1
November	0	5	0	0	2
December	1	0	3	3	1
January	0	0	18	1	0
February	0	0	6	0	1
Totals (percent)	5(11)	5(11)	27(59)	4(9)	5(11)

*Includes 5 foxes that were seen by landowners and shot shortly thereafter.

TABLE 16. *Results of the 1974-75 and 1975-76 Wisconsin fur-buyer's statewide questionnaire on red fox.*

Pelt Data	1974-75 Number	1974-75 Percent	1975-76 Number	1975-76 Percent
Type of harvest				
Trap	15,167	70	8,061	64
Fox hunt	5,448	25	3,908	31
Other*	964	4	549	4
Month(s) of harvest				
October-November	8,329	42	4,041	34
December-January	8,521	43	6,157	52
February-March	3,107	16	1,655	13
Number of mangy foxes reported	1,484	7	655	4
Numbers of buyers reporting mange:				
More than previous year	19	23	15	18
Less	27	32	36	43
Same	38	45	32	39
Population estimates from buyer's reports:				
More than previous year	10	9	3	3
Less	74	68	64	67
Same	38	45	28	30
Total replies	123	63**	118	56**

*Car kills, bird hunters, deer hunters and unknown causes.
**Percent of total furbuyers reporting.

Mangy fox trapped during November 1973.

Miscellaneous causes of death for 14 tagged foxes recovered as juveniles were mange (7), vehicle-kills (5), dog (1), and unknown (1). Eleven of these 14 juveniles were predispersal mortalities, recovered between June and September. The 5 recoveries of tagged adults included 4 vehicle-deaths and 1 mange death, recovered during January (2), May (2) and June (1). Vehicle kills during these months were probably underestimated because of lower pelt values and because some carcasses may have been concealed by vegetation. Mortality due to mange was also likely underestimated because of the difficulty in finding carcasses; therefore, we suggest that losses from this disease are much higher than the 7% and 4% figures reported by Wisconsin furbuyers (Table 16). Trainer and Hale (1969) indicated that mange can be a severe mortality factor over a large area of Wisconsin area. Stone et al. (1972) inferred that most cases of sarcoptic manage in wild red foxes are fatal; however, Storm et al. (1976:50) documented several cases of recovery. Tullar et al. (1976) theorized that mange could be readily spread through communal denning, resulting in heavy spring mortality. Although in some of the following cases mortality ultimately resulted from injuries inflicted by dog and man, mange was considered as the primary cause of death. Nine of our tagged foxes which appeared healthy when tagged, were known to have contracted mange prior to recovery. Eight of these were juveniles that moved less than 2.5 km. Two mangy pups from the same litter were killed while in a weakened state by a dog, which in turn was infected by the disease. Four mangy pups from a litter of 8 were recovered after 2 were found dead in the field and 2 juveniles were shot in a farmyard. The only mangy, tagged adult (2.5 years old) that was recovered was clubbed to death after straying into a farmyard 47.5 km from its tagging site.

Recovery Rates

Analysis of recovery rates must primarily consider tag losses. By using the method of Fairley (1969) to determine tag losses in 60 marked pups with complete tag information out of 82 recoveries, we found that only 0.5% of our tagged foxes would likely have lost both ear tags. Therefore, tag loss was not an important bias when calculating recovery rates and subsequent survival rates.

Data for 154 tagged pups included recoveries through 1 March 1977, two years after the last juvenile fox was marked (Table 17). At this time any

TABLE 17. *Number of foxes recovered 1-4 years after tagging in southern Wisconsin through 1 March 1977.*

Year of Tagging	Number Tagged	Year of Return*			
		1973	1974	1975	1976
1973	30	13	2	1	1
1974	66		29	6	1
1975	58			26	4

*Return years started in May of designated year and extended through April of the succeeding year, e.g. 1973 = 1 May 73 - 30 April 74.

Year (i)	Number Tagged and Released (Ni) - (Ri)	Number of Tags Recovered: In Designated Year (Mi)	Relative to Year of Release (Di)	From Release in Designated Year (Vi)	After Designated Release From Prior Releases (Zi)	Total Recoveries After Designated Release (Ti)
1	30	13	68	17	0	17
2	66	31	12	36	4	40
3	58	33	2	30	9	39
4		6	1		6	6

animals tagged in 1973 would have been three years old.

Fifty-four percent of all foxes tagged at the dens were recovered; 96% of those recovered were reported during the first or second year after tagging. Only 2 foxes were recovered during the third year, while 1 was recovered during the fourth year. These recovery rates correspond almost exactly to the results in Storm et al. (1976:54).

Survivorship of Tagged Foxes

The objectives of our analysis of fox population survivorship rates obtained from tag recovery data were to determine whether: (1) tag recoveries represent a sample of the living (l_x) or dying (d_x) series, (2) recovery data relate to fox populations as a whole, (3) mortality rates can be stratified by age or year, (4) there is any bias to a particular age class, and (5) there are any implications of the demographic parameters which we have estimated.

We tested our first two objectives by comparing the results of two models. Model 1 considered survival and recovery rates as a function of the year recovered, independent of age. Table 18

TABLE 18. *Survival and recovery rates as a function of year and independent of age.*

MODEL 1

Year (i)	(Tag Recovered After Designated Year of Release) $\hat{\theta}_i = V_i/R_i$	(Tag Recovered in Year Designated-- 1 Animal Alive at Beginning of Year) $\hat{B}_i = \hat{\theta}_i M_i/T_i$	(Survivorship) $\hat{\phi}_i = \frac{Z_i+1}{T_i} \cdot \frac{\hat{\theta}_i}{\hat{\theta}_{i+1}}$	Recovery Rate $\hat{\lambda}_i = \frac{\hat{B}}{(1-\hat{\phi}_i)}$
1(1973)	.567	.434	.245	.575
2(1974)	.545	.422	.213	.536
3(1975)	.517	.437	.161	.521

MODEL 2

Year	$1-\phi_i$	ϕ_i	$\hat{B}_i = \lambda(1-\hat{\phi}_i)$
1973	.765	.235	.415
1974	.775	.225	.421
1975	.846	.154	.459

TABLE 19. *Survivorship and recovery rate estimates incorporating survival and recovery rates as a function of year and independent of age.*

Year	$\hat{\emptyset}$	Survivorship Estimates $V(\emptyset_i)$	$S(\emptyset_i)$	$C(\emptyset_i)$	95% C. I. $(\hat{\emptyset}_i \pm 2\hat{S})$
1973	.245	.0138	.1175	.467	(.010-.480)
1974	.213	.0052	.0722	.339	(.069-.357)

Year	$\hat{\lambda}_i$	Recovery Rate Estimates $V(\lambda_i)$	$S(\lambda_i)$	$C(\lambda_i)$	95% C.I. $(\hat{\lambda}_i \pm 2\hat{S})$
1973	.575	.0152	.123	.214	(.329-.821)
1974	.536	.0062	.079	.147	(.378-.694)

TABLE 20. *Population matrix of a hypothetical red fox population of 1,000 females based on previous calculations of survivorship*, pregnancy rates**, litter size*[1] and fecundity[2].

$$\begin{bmatrix} .33 & 1.0 & 1.5 \\ .10 & 0 & 0 \\ 0 & .20 & .30 \end{bmatrix} \begin{bmatrix} 1000 \\ 0 \\ 0 \end{bmatrix} = \begin{bmatrix} 330 \\ 100 \\ 0 \end{bmatrix} = \begin{bmatrix} 209 \\ 33 \\ 20 \end{bmatrix} =$$

Year 0 Year 1(430) Year 2(259)

$$\begin{bmatrix} 132 \\ 21 \\ 13 \end{bmatrix} = \begin{bmatrix} 84 \\ 13 \\ 8 \end{bmatrix} = \begin{bmatrix} 51 \\ 8 \\ 5 \end{bmatrix} = \begin{bmatrix} 33 \\ 5 \\ 3 \end{bmatrix}$$

Year 3(166) Year 4 (105) Year 5(64) Year 6(41)

*Survivorship: juvenile ~.10
yearling ~.20
adult ~.30

**Pregnancy rate: yearling = .59
adult = .89

[1]Litter size = 5.6

[2]Fecundity: juvenile = .33
yearling = 1.00
adult = 1.50

summarizes tag recovery information and includes the last tagged fox that we recovered, which was harvested on 19 February 1977. When tag recovery rates were calculated using the techniques of Seber (1973), they were constant, ranging from 0.575 during the first year to 0.521 during year 3, averaging 0.54. These recovery rates were among the highest recorded in the red fox literature, implicating hunting and trapping as the major mortality factors. Therefore, the tag recoveries represent a sample of the dying (d_x). When our recovery data were analyzed according to an age-specific life table (Seber 1973), survivorship ($\hat{\emptyset}_i$) decreased from 1973 to 1975 (Table 18). Average pelt values increased from \$28.06 to \$40.79 during the same period, indicating a direct relationship between pelt value and mortality. When expected recoveries (Seber 1973) calculated under the estimated parameters of Model 1 were compared by a Chi-square test with actual recoveries from Table 18, no significant departure was noted ($P > 0.05$, 3 d.f.). These results indicate that Model 1 is a very good fit to the actual recovery data, even though confidence intervals are large (Table 19).

In Model 2, we assumed that recovery rates were constant, while survivorship rates were a function of year only and were independent of age (Seber 1973:245). In this Model, we assumed that $\theta_i = \lambda$, thus we have three estimates of θ_i from Table 18; which gave us a mean $\hat{\theta}_i$ ($\hat{\lambda}$) of .543. The survivorship can be estimated by $1 - \emptyset_i = \hat{B}_i / \theta_i = M_i / T_i$. Thus, our estimates of survivorship ($\emptyset_i$) and tags recovered in the year designated with one animal alive at the beginning of year ($\hat{B}_i$) from Table 18 are comparable to Model 1. When a Chi-square test of the expected recoveries calculated under the estimated parameters of Model 2 were compared with the actual recoveries from Table 18, a value of 0.19 was produced which was not significantly different ($P > 0.05$, 3 d.f.). Therefore, the results of both Model 1 and 2 are well-fitted to the actual recovery data. Both indicate that survivorship has steadily decreased from 1973 to 1975, probably in an inverse relationship to increased pelt prices during the same period (Table 17).

Objectives (3) and (4) were determined by the following calculations. When survivorship was analyzed by an age-specific (life-table) method, we determined that there undoubtedly was a change in mortality rates from pups to adults. By creating a simple d_x series from the D_i column from Table 17, we found that survivorship increases with age in the following progression; juveniles (.18), 1.5 years (.17), 2.5 years (.5), and 3.5 years

(1.00). However, there is no possibility of estimating juvenile survivorship from our d_x data, but it has to be less than 0.18. Therefore, results from our year-specific (Models 1 and 2) and age-specific data indicate that both year and age influence survival, but juvenile survival, which is of the greatest importance in red fox population dynamics, cannot be estimated. By substituting an approximate juvenile survivorship value of .10, we create a perfect life table incorporating both number of foxes marked and eventual returns:

Age	l_x	d_x
.5	154	68+(70)
1.5	16	12
2.5	4	3
3.5	1	1

According to this life table, 50% of juvenile mortality, due to factors such as mange, unknown predation and diseases, is unreported, where as approximately 100% of adult mortality from causes such as hunting, trapping, and vehicle mortality is reported.

Population Matrix

Authors such as Nellis and Keith (1976) and Henny et al. (1970) have used life equations and population matricies to predict the stability of a particular population after factors such as survivorship (ø), pregnancy rates (pr), litter sizes (Ls) and fecundity (F) have been determined ($F = ø \times pr \times Ls$). From our previous discussion, we determined that juvenile survivorship was unknown but was estimated to be approximately .10; yearling survivorship was roughly .20 and adult survivorship was approximately .30. When other previously estimated data such as pregnancy rates (Table 8) and litter size (Table 9) were incorporated into a population matrix used by Henny et al. (1970), the population decreased from 430 foxes in year 1 to 41 foxes in year 6 (Table 20). We resolved objective (5) by finding that age-specific survival rates determined from our tag recovery imply a strong exponential decline in the southern Wisconsin fox population. Therefore, stabilization of the population could only occur with an increase in productivity or a decline in harvest mortality.

TABLE 21. *Comparative age structure of 37 foxes killed on the Waterloo Study Area (WSA) and 232 foxes harvested in 6 southern Wisconsin counties (SW) *, 1972-75.*

	Shot While Hunting:						Miscellaneous Kill	
	Fox		Deer-Pheasants		Trapped			
Age	WSA	SW	WSA	SW	WSA	SW	WSA	SW
0.5	9	38	5	16	2	89	0	1
1.5	10	20	1	2	1	17	1	1
2.5	2	10	0	0	0	9	0	0
3.5	2	9	0	1	0	6	1	1
4.5	1	4	1	1	0	1	0	1
5.5-8.5	1	3	0	0	0	2	0	0
Totals	25	84	7	20	3	124	2	4

*Includes Dodge, Jefferson, Fond du Lac, Marquette, Dane and Columbia Counties.

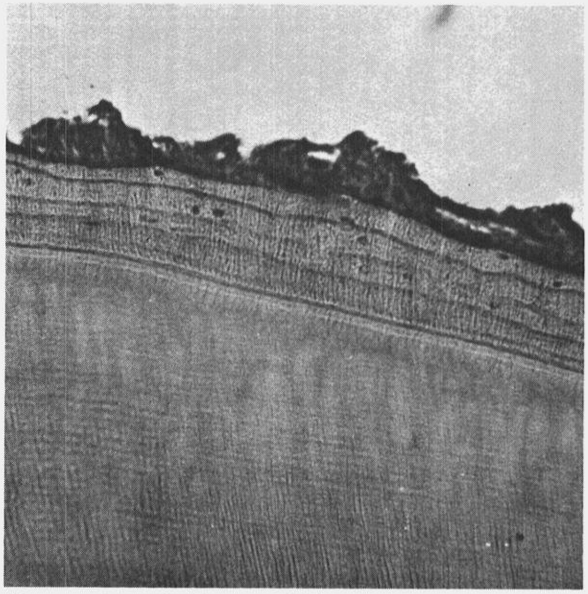
TABLE 22. *Juvenile:adult ratios and survival rates for red foxes collected in southern Wisconsin and on the Waterloo Study Area, 1971-75.*

Untagged Southern Wisconsin Foxes	No. of Foxes	Juv:Adult Ratio	Survival Rates Year 1	Year 2	Year 3
Trapped					
Females	64	1.46	0.41	0.46	0.37
Males	60	5.67	0.15	0.67	0.54
Combined	124	2.54	0.28	0.51	0.44
Hunted					
Females	39	0.63	0.62	0.58	0.48
Males	45	1.04	0.49	0.55	0.52
Combined	84	0.83	0.55	0.57	0.50
Combined total	208	1.57	0.39	0.54	0.48
Water Study Area Foxes					
Males	20	0.82	0.55	0.45	0.58
Females	15	0.67	0.60	0.22	0.33
Combined	35	0.75	0.57	0.35	0.53

TABLE 23. *Chi-square tests of age ratios of hunted versus trapped red foxes from the Waterloo Study Area and southern Wisconsin, 1971-75.*

Southern Wisconsin Foxes		X^2
Trapped females vs.	Hunted females	3.44*
Trapped males	Hunted males	12.61[1]
Total trapped	Total hunted	13.73[1]
Trapped females	Trapped males	8.81[1]
Southern Wisconsin (SW) and WSA Foxes		
Hunted and trapped WSA males vs.	Trapped SW males	10.75[1]
Hunted and trapped WSA males	Trapped and hunted SW males	3.81**
Hunted and trapped WSA males and females	Trapped and hunted SW males and females	3.37*
Hunted and trapped WSA males and females	Trapped SW males and females	8.85[1]

*P <.10, 1 d.f.
**P <.05, 1 d.f.
[1]P <.01, 1 d.f.



Four and one-half year old fox aged by cementum annuli.

Age Structure of Southern Wisconsin Foxes

Only 2% of the sample of 232 aged red foxes collected in southern Wisconsin were 5.5 years or older, which corresponded to the WSA age structure (Table 21). Our results were comparable to the ranges of fox longevity indicated by Storm et al. (1976:54). Red foxes that survive beyond the 3.5 year class probably become adept at avoiding trappers and hunters. As a result, they may not be represented proportionally in a collection of hunted and trapped foxes.

Survival Rates of Southern Wisconsin Foxes

Several authors, including Nellis and Keith (1976), found that lower survival rates are prevalent during the first year of life. Storm et al. (1976:56-57) computed survival rates for foxes tagged as juveniles and as adults and found that survival was lower in juveniles. Only 10 adult-sized foxes were tagged during our research, while one recovery was made. Therefore, we could not compare survival between adults and juveniles. We prepared a time-specific life table (Geis and Taber 1963:285) to estimate survival rates of untagged southern Wisconsin and WSA foxes. This was done by computing the l_x, d_x, q_x and s_x (survival rate or the number surviving during each age interval divided by the number alive at the start of the interval) values for the various age classes of the southern Wisconsin and WSA males and females. The resulting survival rates (s_x) were presented as those found in Year 1 (foxes aged at 0.5 year), Year 2 (1.5 years) and Year 3-6 (2.5 to 5.5 years) along with juvenile:adult ratios (Table 22). Therefore, juvenile:adult ratios and survival rates were sex-, time- and source-specific.

Trapping (excluding the WSA) was the main source of mortality for southern Wisconsin foxes during October and November (Fig. 13). As a result, trappers took a large number of juveniles, leaving a higher proportion of adults to survive until the first of January, when hunting intensified. Therefore, trapped juvenile:adult ratios from southern Wisconsin were substantially higher than ratios obtained by hunting (Table 22). Significant differences were found between the age ratios of hunted and trapped males and females killed both on and off the WSA (Table 23). The WSA juvenile:adult age ratio was lower than the southern Wisconsin sample due to 3 factors: (1) Juveniles produced on the WSA dispersed off the area, while trapping outside the WSA resulted in substantial mortality of ingressing juveniles. (2) Heavy pheasant and deer hunting pressure during late October and November may have forced dispersing foxes off the study area that had temporarily settled at Waterloo. (3) Pheasant and deer hunters shot a larger number of juveniles as compared to adults that remained at Waterloo (Table 21).

Southern Wisconsin males trapped during year 1 exhibited the lowest survival of any segment within the sample. Conversely, during the second year, trapped males displayed the highest rates of survival. Survival rates compiled for foxes hunted later in the season were higher partially because of generally poorer snow conditions. Waterloo data in particular mirrors these latter two conditions. Fewer juveniles were available for WSA hunters by 1 January. Therefore what appears to be a high Waterloo juvenile survival rate in an area that is heavily hunted, is a consequence of prior trapping mortality resulting in a low juvenile:adult ratio.

PREDATOR-PREY RELATIONSHIPS

Our purpose within this section is to analyze the impact of red fox predation on its principal prey species, particularly ring-necked pheasants and cottontails, through a close scrutiny of red fox food habits. Southern Wisconsin fox scats, stomach contents, food items at dens, and food items found while winter tracking used for this analysis were primarily collected on the WSA. Evidence of pheasant predation was compared with the findings of Dumke and Pils (1973). All food habits data were used to compare the combined seasonal diet of red foxes. Food items found at dens were used to compute spring predation rates.

Prey Populations

Ring-necked pheasants. Winter and spring pheasant populations on the WSA were compared from 1968-75 in order to place into perspective available pheasant densities from the Dumke and Pils (1973) investigation as well as the current study (Table 24). Winter pheasant populations were derived from calculations of posthunt populations and represented a composite date of 5 December. This figure was expanded to represent the ensuing 1 January population. For example, the 1 January 1970 winter population estimate actually represented the 7 December 1969 posthunt population of 1,147 (Table 24). Spring populations were derived from crowing cock counts and winter sex-ratio observations and represented pheasant densities on 1 April. The 1975 population estimated by Woehler (pers. comm.) was the lowest spring population observed on the study area since the 1968 counts. Neither the 1968-71 winter or spring population means differed significantly ($P > 0.05$) from those of 1972-75.

Small mammals. All small mammal population trends were expressed in captures per 1,000 trap nights (Petersen in press). Populations appeared to build from March through September with peaks probably being higher in August than September. Small mammal numbers held fairly well from October through November, then dropped rapidly from December to January, reaching their lowest point in March-April, just prior to the spring reproductive period (Fig. 14). Some rodent and insectivore species are reproductively active all year but the best reproductive success undoubtedly occurs during the summer months (F. Iwen pers. comm.).

TABLE 24. *Ring-necked pheasant populations on the Waterloo Study Area, 1968-75.*

	Winter		Spring	
Year	Pheasant Population On 1 January	Pheasants Per km^2	Pheasant Population on 1 April	Pheasants Per km^2
1968	--	--	757	9.0
1969	1,393	16.6	867	10.3
1970	1,147	13.7	602	7.2
1971	1,481	17.7	841	10.0
1972	1,190	14.2	860	10.3
1973	1,295	15.5	695	8.3
1974	1,270	15.2	747	8.9
1975	867	10.4	527	6.3
Mean 1968-71 ± S.E.	1,340 ± 99.9	16.0	767	9.1
Mean 1972-75 ± S.E.	1.156 ± 98.7	13.8	707	8.5

TABLE 25. *Percentage of small mammal species trapped in six cover types, Waterloo Study Area, 1972-75.*

	Uplands			Lowlands		
Species	Hardwoods	Grassland	Corn	Hardwoods	Tamarack	Shrub-Carr
Deer mice	16	7	20	25	23	9
Meadow voles	T	39	2	3	13	42
Jumping mice	T	54	12	8	12	15
House mice		12	80	3	T	4
Cinereous shrews	1	23	1	17	25	33
Tricolor shrews	--	5	--	T	16	77
Short-tailed shrews	2	36	3	12	13	34
Other species	24	22	39	5	10	--

TABLE 26. *Cottontails per hectare derived from live-trapping three areas on the Waterloo Study Area, 1971-75.*

Date	Quarry	Faultersack	Kerl	Total No./ha
Fall 1971	8.7	--	--	8.7
Winter 1972	--	6.8	--	6.8
Fall 1972	7.3	14.7	--	11.0
Winter 1973	10.2	12.0	6.3	9.5
Fall 1973	5.7	8.2	--	7.0
Winter 1974	3.2	--	4.4	3.8
Fall 1974	4.0	--	2.9	3.4
Winter 1975	1.9	--	4.4	3.1

Mean fall density = 7.4
Mean winter density = 7.0

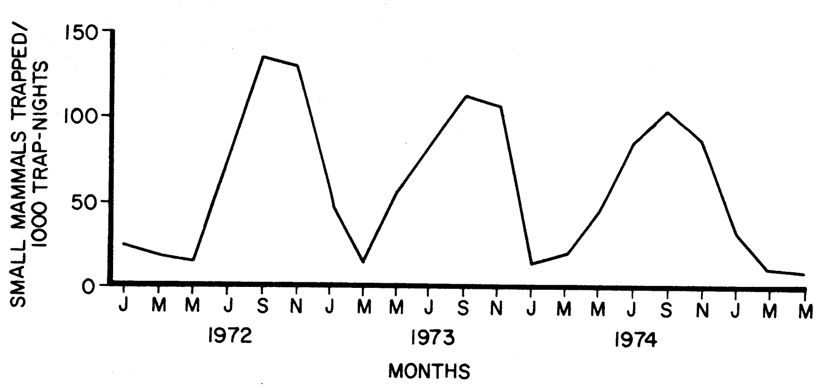


FIGURE 14. *Indexes to relative abundance of small mammals on the Waterloo Study Area from bimonthly snap-trapping, 1972-75.*

Table 25 lists the percentage of the principal small mammals trapped at the six major cover types on the WSA. Petersen (in press) discusses small mammal abundance cycles and rodent-insectivore cover type preference in more detail.

Cottontails. Live-trapping cottontails provided the best index for estimating rabbit abundance at Waterloo (Table 26). Cottontail trapping was conducted in selected areas where cottontail densities were sufficiently high to derive statistically reliable population estimates using the regression analysis technique of Edwards and Eberhardt (1967).

Cottontails were trapped during eight fall and winter periods from October 1971 to January 1975. Data on 331 individual cottontails, plus 724 recaptures were obtained during 17,432 trap nights. Cottontail densities on the WSA trapping sites varied from 1.9 to 14.7 cottontails per hectare; mean fall and winter densities were similar (Table 26). Upland hardwoods with a brushy understory contained high cottontail numbers, but constituted only 4.5% of the total WSA cover types. The mean fall density of cottontails trapped in WSA upland woodlots was 8.1 rabbits per hectare as compared to 8.9 cottontails per hectare taken during the fall at a 34.6 ha woodlot in southwestern Wisconsin (Trent and Rongstad 1974:459). Most of the WSA cover types were cultivated lands, marsh, and pasture (Table 1) that contained low cottontail densities. A downward trend in cottontail population was indicated for the 1971-75 period.

Red Fox Food Habits

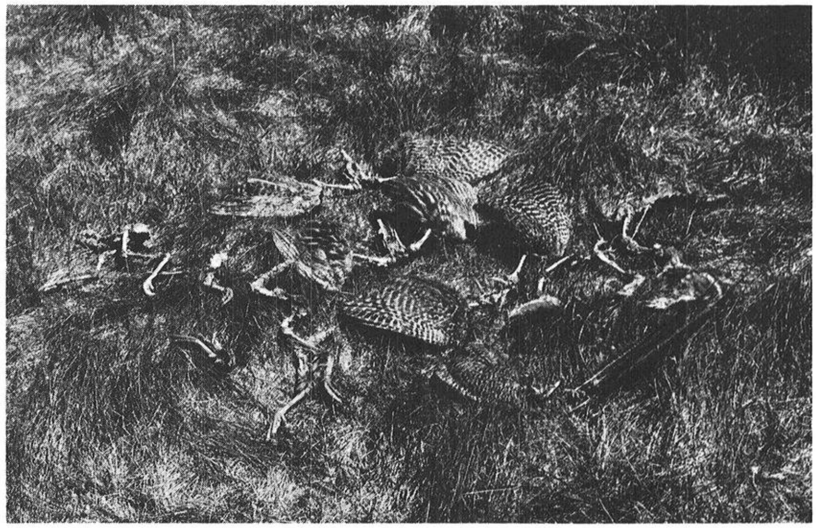
Interpretation Problems. The proper analysis and interpretation of red fox food habits is a serious problem facing predator research and management. Latham (1951:8-20) discussed many of the problems encountered in food habits studies. The three most common sources of error were: (1) faulty sampling; (2) inadequate presentation of data; and (3) insufficient ecological information for proper interpretation. Richards and Hine (1953:44) suggested that the fox's reputation as a game killer must be evaluated not only in terms of the foods eaten and their availability, but also with respect to the population trends of the prey species. Besadny (1966:5) examined the contents from 1,737 Wisconsin red fox stomachs and listed the problems inherent in the identification of food items due to varying digestion rates. Englund (1965:386-390) further discussed the importance of volume and weight interpretations, when analyzing stomach contents.

Scat Analysis. Table 27 summarizes the dates and areas in which scats were collected. The month of defecation was difficult to determine for old adult scats, especially those found away from dens under melting snow. Pup and adult scats found at dens represented fresher samples and were more indicative of the month in which found. Important food items in these samples were small mammals, cottontails and unknown birds (Table 27).

Small mammals occurred more frequently than any other food item in scats collected away from dens, but were surpassed in terms of biomass by cottontails (Table 27). The high cottontail biomass in scats found away from dens possibly indicated higher predation on cottontails during the winter months; later winter tracking data also indicated that foxes fed largely on cottontails. Cottontails may be more susceptible during the winter, when voles and deer mice are not as numerous (Fig. 14) or are under snow cover and are less vulnerable.

Pheasants were infrequently identified in scats, but may have been represented in the unknown bird category, due to the difficulty in identifying pheasant feather fragments. Birds, plants and insects were found more frequently in scats at denning sites than in those away from dens (Table 27). These prey items probably were more available during the warmer denning season.

Stomach Contents. Results from analysis of stomach contents were similar to the scat analysis (Table 28). Cottontails represented 49 to 66% of the total biomass and small rodents occurred in 38 to 57% of all stomachs sampled. Again, availability probably determined the quantity and fre-



Pheasant and cottontail remains found at a Waterloo den in mid-May.

quency of the time consumed. Bird identifications were not as difficult as in the scat analysis because other anatomical structures were present with the feathers. Domestic fowl represented 9 to 15% of the total biomass. Many southern Wisconsin farmers dispose of their chickens with manure spreaders and thus make the fowl readily available for foxes. Scott and Klimstra (1955:45-46) recognized scavenging as a red fox dietary trait resulting in the consumption of large mammals such as pigs, cows and sheep. Pheasants were found in relatively low percentages for both frequency of occurrence and quantity. These lower occurrences may have been a reflection of the milder winters encountered by pheasants during the current study, as compared to the previous severe winters documented by Dumke and Pils (1973). Fox hunting habits may also have been influenced by mild winters, i.e. more small mammals available. Opossums constituted 11% biomass in stomach contents from the WSA. The annual WSA mammal survey indicated that opossums were commonly observed by Waterloo landowners. These slow-moving marsupials may have been obtained by foxes as vehicle-killed carrion.

Food Items at Dens. Remains found at fox dens gave the most visible and highly identifiable food items. Although 58 dens were investigated for food items and scats, several dens were visited more than once, resulting in a total of 90 visits (Table 29). Almost 80% of the checks were made during April and May, the months of peak fox family activity.

Cottontails were the most important food item by both percent frequency of occurrence and biomass, a finding similar to the conclusions of Scott and Klimstra (1955:42-43). Cottontail densities were probably higher during the fox denning months of April and May than any other two-month

TABLE 27. *Food items taken from 1,020 scat samples collected at and away from dens on the Waterloo Study Area, 1972-75.*

Food Item*	Away From Den (392 Scats) Percent Frequency of Occurrence	Away From Den (392 Scats) Percent Biomass	At Den (628 Scats) Percent Frequency of Occurrence	At Den (628 Scats) Percent Biomass
Mammals				
Small mammals**	40	3	26	2
Cottontails	25	66	13	44
Unknown mammals	2	8	5	28
Muskrats	T	T	T	1
Skunks	T	2	0	0
Opossums	T	4	0	0
	67	83	44	75
Birds				
Unknown birds	11	9	21	22
Pheasants	1	2	1	3
Domestic fowl	2	5	0	0
Meadowlarks	0	1	1	T
	14	17	23	25
Insects				
Unknown insects	1	T	9	T
Beetles	0	0	2	T
Grasshoppers	0	0	1	T
	1	T	12	T
Plants				
Unknown plants	8	T	16	T
Grass	3	T	2	T
Corn	2	T	1	0
Apples	1	T	0	0
Soybeans	1	T	0	0
	15	T	19	T
Totals	97	100	98	100

*Month Collected	Total Scats Collected Away From Den	Total Scats Collected At Den
January	32	
February	48	
March	203	
April	32	145
May	6	271
June	1	170
July	7	42
November	6	
December	57	

**Predominantly voles and deer mice.

period, and thus rabbits were readily available. Pheasants were the second most important food item at dens. Hens were especially prone to predation during the 23-day incubation period primarily spent on the nest (Dumke and Pils 1973). Ninety percent of the 39 sex-determined pheasants found at the dens were hens. The combined spring sex ratio (1972-74) on the WSA was 6.7 hens per cock, therefore more hens than cocks were available for foxes during the spring. The largest numbers of small mammal carcasses were ususally found at dens in late March and early April. Meadow voles and short-tailed shrews were the small mammals most frequently encountered. A more diverse selection of food items appeared as spring progressed. For example, ground nesting passerines such as meadowlarks were frequently found during late April and early May. Tree-roosting and tree-nesting passerines such as bluejays, robins and warblers were also found at dens (Table 29). We were not able to determine how foxes preyed upon these birds, unless they were scavenged. Domestic fowl (chickens and ducks) were regularly found at dens (Table 29); chickens constituted the third most important food source encountered at dens. Fowl discovered at dens probably represented scavenging, although one Columbia County farmer requested that DNR personnel move a fox family that had been extensively preying on his poorly penned friers that were nearby. Another WSA farmer regularly deposited dead or dying chickens at an active fox den on his property.

A crucial factor associated with interpretation of food remains at fox dens during the denning season, which has generally been ignored (except by Johnson and Sargeant 1977), is the number of food items that are overlooked because they are located below ground in burrows. Errington (1937:54), for example, relied only on scats and food items collected at the den surface to evaluate the food habits of Iowa red foxes during a drought summer. Richards and Hine (1953:44-45) used a fishwire probe to remove items from within the den; however, they were aware that some items were missed by this technique.

Foods found at dens from 1973 to 1975 were separated into remains collected either inside or outside of burrows. The difficulty encountered with this technique was making an accurate specimen count for each category. For example, when a left wing and foot from a hen pheasant were found inside the den and a right wing from a hen was found outside the den, only one hen was counted as present at the den. Whole mice and rats were found at each of the 58 dens. Table 30 shows that a sizeable number of food items were located below the surfaces of active fox dens. The ratios of specimens found outside active fox dens compared to inside for the three major food items were: Cottontails 1:2.6; meadow voles 1:6.7; hen pheasants 1:1.4; and cock pheasants 1:2. Only 33% of the total food items were discovered outside the den. As a result, the total numbers of game species represented at dens (Errington 1937) probably has been conservatively estimated in the past.

Cached food items represent another source of data that have been minimized when evaluating the impact of red fox predation on game species during the denning season. Red foxes commonly cache kills for later use (Dumke and Pils 1973:28). Mallard mortality studies incorporating radiotelemetry in North Dakota (Johnson and Sargeant 1977) have shown that during the April to June period, only 77 of 285 ducks killed by foxes were found at the denning site. The remaining 208 mallards, which could not be identified in den food remains, were consumed or cached. Although we could not determine the number of prey items cached away from dens as compared to foods found at active dens, Dumke and Pils (1973) indicated that practically all of the pheasant kills found during the fox denning season were cached away from active

TABLE 28. *Food items taken from 132 fox stomachs collected both on and off the Waterloo Study Area, 1972-75.*

Food Item*	On the WSA (47 stomachs**) Percent Frequency of Occurrence	On the WSA Percent Biomass	Off the WSA (85 stomachs[1]) Percent Frequency of Occurrence	Off the WSA Percent Biomass
Mammals				
Small mammals	57	4	38	2
Cottontails	16	49	27	66
Opossums	1	11	0	0
Skunk	1	7	0	0
Jumping mouse	1	T	0	0
Unknown mammals	0	0	3	10
Pig	0	0	1	1
	76	71	69	79
Bird				
Domestic fowl	5	15	3	9
Pheasant	1	3	4	8
Unknown birds	9	8	5	4
	15	26	12	21
Plants				
Grass	2	T	13	T
Corn	1	T	0	0
Unknown	5	T	3	T
	8	T	16	T
Totals	99	97	97	100

*Monthly Number of Stomachs Collected	On WSA	Off WSA
June		1
July	1	
September		1
October	3	33
November	4	3
December	7	9
January	17	20
February	15	18
Total	47	85

**13 Empty
[1]17 Empty

TABLE 29. *Food items found at 58 dens* from March to July, 1972-75** in southern Wisconsin.*

Food Item	Mean Food Item Weight(g)	Percent Frequency of Occurrence	Percent Biomass
Small Mammals			
Meadow vole	46	8.3	T
Deer mouse	22	1.2	T
Short-tailed shrew	24	2.0	T
Norway rat	358	1.0	T
Striped ground squirrel	110	T	T
Cinereous shrew	5	T	T
Tricolor shrew	9	T	T
Mid-sized Mammals			
Cottontail	1,300	26.4	34.6
Muskrat	1,200	4.3	5.3
Fox squirrel	765	2.7	2.1
Unknown mammal	2,000	1.0	2.1
Domestic rabbit	3,632	1.5	5.4
Opossum	4,082	1.0	3.1
Raccoon	9,080	1.0	6.9
Long-tailed weasel	150	1.0	T
Gray squirrel	625	T	T
Least weasel	40	T	T
Mink	908	T	T
Skunk	2,495	T	T
Woodchuck	3,632	T	T
Cat	2,724	T	T
Large Mammals			
Pig	454	3.1	1.4
White-tailed deer	454	1.0	T
Cow	454	T	T
Reptiles			
Garter snake	20	T	T
Fish			
Carp	800	T	T
Birds			
Unknown bird	70	4.9	T
Grackle	100	3.6	T
Red-winged blackbird	70	2.2	T
Meadowlark	120	1.9	T
Robin	80	1.0	T
Warbler	30	T	T
Blue jay	95	T	T
Crow	330	T	T
Catbird	75	T	T
Mourning dove	120	T	T
Upland sandpiper	200	T	T
Great horned owl	1,200	T	T
Unknown egg	35	T	T
Yellow-shafted flicker	135	T	T
Game Birds			
Ring-necked pheasant	1,150	14.8	17.2
Mallard	1,150	T	1.0
Blue-winged teal	425	T	T
American coot	400	T	T
Hooded merganser	450	T	T
Pheasant egg	30	T	T
Domestic Fowl			
Chicken	1,360	8.2	11.3
Duck	1,400	2.2	3.2
Goose	4,540	T	1.4
Guinea fowl	1,816	T	T
Duck egg	40	T	T
Total		94.3	96.0

TABLE 29. *Continued.*

*1972 - 15 dens
1973 - 15 dens
1974 - 13 dens
1975 - 15 dens

**Food items were collected from dens during the following number of visits:

	March	April	May	June	July
1972	2	6	10	4	1
1973	2	3	12	4	
1974		6	10	1	2
1975		6	9	2	
Total	4	21	51	11	3

TABLE 30. *Comparison of food items found inside and outside dens, southern Wisconsin, 1973-75.*

Food Item	Number of Den Food Items			Percent Found Outside Den
	Inside	Outside	Total*	
Mammals				
Cottontals	85	33	111	30
Muskrats	10	4	12	33
Fox squirrel	4	6	10	60
Pig	10	6	13	46
Meadow voles	47	7	54	13
Long-tailed weasels	1	2	3	66
Norway rats	6	0	6	0
Deer mice	4	0	4	0
Birds				
Female pheasants	23	17	35	49
Male pheasants	2	4	4	100
Meadowlark	6	1	7	14
Red-winged blackbird	9	4	12	33
Wild duck	4	1	5	20
Chicken	10	10	16	63
Total and Average	221	95	292	33

*Total food items, whether found inside or outside of den.

dens. Therefore, knowledge of cached game species could conceivably have changed the conclusions of previous research based on prey remains found at dens. For example Richards and Hine (1953:46) found only four grouse and two pheasants which probably represented a minimal count of prey remains at 33 red fox dens in southwestern Wisconsin. If additional cached grouse and pheasants had been found the actual number of predated game birds may have been considerably higher.

Winter Tracking. Table 31 summarizes by cover type the number of kills and carrion foods encountered. Tracks in retired cropland and marsh were followed for the greatest distances and the two cover types contained the most evidence of kills and carrion. Retired cropland, which was significantly preferred in excess of abundance, may have been used by foxes as hunting cover because it contained high winter populations of small mammals (Petersen in press). Evidence of foxes feeding on larger animals such as raccoons, pigs and deer, probably represented scavenging. Farmers frequently dumped pig carcasses in their fields where they were fed upon by many animals, including foxes. Smaller carrion such as cottontails, skunks and opossums may have been killed earlier by foxes and exhumed for a later feeding. The most unusual fox kill found was a great horned owl (Pils 1975:158).

Food items found while snow tracking are summarized in terms of occurrence and biomass (Table 32). Carrion

TABLE 31. *Winter hunting and feeding summary from tracking red foxes 182.6 km on the Waterloo Study Area, 1972-75.*

Land Use	Small Mammal Attempted Kills	Small Mammal Kills	Number of Kills: Cottontail	Number of Kills: Other	Number of Carrion Items: Cottontail	Number of Carrion Items: Pheasant	Number of Carrion Items: Pig	Number of Carrion Items: Other
Retired cropland	33	6	2	Passerine	1			Skunk, Deer Small mammal
Marsh								
Shrub-carr	26	9	3	Passerine	1		4	Opossum Raccoon
Lowland herbaceous	19	2	1	Pheasant	1	1		
Wet pasture	1	1						
Canary	14	1		Great horned owl				
Upland hardwoods	7	1	3					
Lowland hardwoods	1							
Cultivated lands								
Hay	22	4			1			
Corn	8	4	1				1	
Plowing	3							
Pasture	5	2	1			1	1	
Strip cover								
Ditchbank	4	1			1			
Farm lane	4							
Fenceline								2 Raccoons
Multiflora rose	1							
Miscellaneous								
Gravel pit	5						1	
Conifer plantation				Mourning dove				
Sod farm	4							
Wood edge	2							
TOTAL	159	31	11	5	5	2	7	7

TABLE 32. *Frequency of kills based on winter tracking red foxes on the Waterloo Study Area, 1972-75.*

Food Item	Number of Kills	Percent Frequency of Occurrence	Percent Biomass
Small mammals	31	66.1	4.5
Cottontail	11	23.4	80.8
Pheasant	1	2.1	6.5
Unknown passerine	2	4.2	.8
Great horned owl	1	2.1	6.7
Mourning dove	1	2.1	.7
Totals	47	100	100

not cached represented food items assumed not to have been killed by foxes. Therefore, only "known" kills were used to calculate percent biomass and percent frequency of occurrence. We recognized that carrion may possibly represent an important source of winter food that could be gathered with little expenditure of energy. However, we felt that the inclusion of carrion was not compatible with later predation rate calculations. Only portions of scavenged pigs were noted at dens, but entire carcasses, averaging approximately 20 kg apiece, were fed upon by foxes during the winter. A small portion of a deer was scavenged on one occasion. Pheasants consumed by tracked foxes were found as carrion in three of four instances. Arnold (1956:27) found evidence of only three pheasant kills while tracking foxes 928 km during five winters in southern Michigan. Mice and shrews were the

Evidence of foxes and other scavengers feeding on dead pigs.

chief prey items found by Schofield (1960:432-433) while following 1,784 km of fox trails in central Michigan; he also found 19 ruffed grouse previously killed by other predators. Arnold (1956:18) stated that "except under unusual circumstances pheasants and other birds are ignored by foxes during the winter"; however, Arnold did not define "unusual circumstances". Dumke and Pils (1973) found that foxes preyed heavily on pheasants during severe winters at Waterloo. Our experience in tracking foxes tends to agree with Huff's (1964:45-46) suggestion that foxes meander through a variety of habitats and use very little persistent effort in hunting a specific prey animal.

Burrows (1968:58) theorized that although smell is the most vital single sense a fox possesses, its nose is not used extensively while hunting. The type of animal normally eaten is more easily detected by either sight or sound or both combined. Smell is most importantly utilized for locating carrion, detecting enemies and for social information (Burrows 1968:58-59). We estimated mousing success at Waterloo by noting the times small mammal blood, carcasses or hair was found after an apparent "pounce" in the snow. Waterloo foxes were successful only about 20% of their attempts to catch small mammals. The earlier Waterloo studies proved that foxes can be extremely efficient pheasant stalkers under severe winter conditions (Dumke and Pils 1973). Stanley (1963:13) was able to use winter tracking data to deduce that rabbits were not caught by foxes once the former had left cover.

Combined Food Habits. All food item collections (Table 33) were fitted into five of the six seasonal periods developed by Dumke and Pils (1973:18). The post-brood-rearing period (28 August - 15 October) was not used due to lack of food habits data. The bulk of our fox dietary data was obtained during the pheasant nesting period (15 April to 28 June). Cottontails were the most important food item consumed by both percent frequency of occurrence and biomass during the five seasons. Most cottontails were taken during the hunting (16 October - 14 December) period, although the number of food items obtained was lower than for any of the other periods. The snow cover period (15 December - 18 February) was the second highest period for cottontail prey items, possibly due to the reduced availability of escape cover. Small mammals and meadow voles frequently occurred in the red fox diet during the snow cover season, possibly also due to the lack of adequate cover.

Pheasants were noted most frequently and in greatest quantities during the nesting season (15 April — 28 June). Although Dumke and Pils (1973:27) noted that foxes preyed more heavily on pheasants during the snow cover season, the nesting period was the second most vulnerable period for WSA pheasants. Unknown bird remains were found in large quantities during the nesting season. Utilization of domestic fowl as carrion was reflected by its usage as a food throughout the hunting, snow cover and late winter seasons. Greater numbers of chickens and ducks were probably available as free-roaming live prey during the spring on southern Wisconsin farms. During our study, we observed several farms that allowed chickens to roam considerable distances from farmsteads.

The omnivorous nature of the red fox was apparent by its ingestion of plants during all of the five seasonal periods (Table 34). Corn and grass were the most evident items. Various grasses were not chewed thoroughly due to the nature of canid dentition (Pils 1965:10).

Quantifying Predation

The major objective of our food habits study was to determine the impact of fox predation on game populations. From the analysis of stomach contents Richards and Hine (1953:53-55) estimated numbers of species taken by foxes. Korschgen (1959:174), by combining food item information from 1,170 red fox stomachs with an estimate of daily food requirements of foxes, estimated that 6,000 rabbits were eaten each year by 100 red foxes. However, this type of analysis requires qualifications in order to properly evaluate results. The occurrence of a particular food item in the diet may represent carrion which cannot be distinguished from prey. Deer, pigs and cattle that appear in this analysis usually may be safely assumed to represent carrion. On the other hand smaller species such as rabbits or pheasants are not as easily classified.

Raptor researchers such as Craighead and Craighead (1956), have also used predation rates (the precentage of a prey population taken by a predator) to quantitatively describe the impact of predation on various prey species. This technique was refined by Luttich et al. (1970) and McInvaille and Keith (1974). Computation of prey biomass killed by red-tailed hawks on a study area required: (1) a knowledge of changes in redtail numbers over time; (2) species compo-

TABLE 33. *Red fox food habits summary by seasonal periods, 1972-75, taken from analyses of food items from dens, scats, stomach contents and winter tracking. Seasonal periods are taken from Dumke and Pils (1973:19).*

	Seasonal Periods									
	Hunting (16 Oct-14 Dec)		Snow Cover (15 Dec-18 Feb)		Late Winter (19 Feb-14 Apr)		Nesting (15 Apr-28 Jun)		Brood Rearing (29 Jun-27 Aug)	
Food Items	Freq. of Occurr.	Percent Biomass	Freq. of Occurr.	Percent Biomass	Freq. of Occurr.	Percent Biomass	Freq. of Occurr.	Percent Biomass	Freq. of Occurr.	Percent Biomass
Small Mammals										
Meadow vole	19	1	11	T	14	1	5	T	2	T
Short-tailed shrew			1	T			1	T	1	T
Deer mouse			T	T	1	T	1	T		
Norway rat							T	T		
Striped ground squirrel							T	T		
Cinereous shrew			1	T			T	T		
Tricolor shrew							T	T		
Jumping mouse			T	T					1	T
Long-tailed weasel							T	T		
Least weasel							T	T		
Unknown small mammal	26	1	32	2	26	2	15	T	16	2
Mid-sized mammals										
Cottontail	33	72	28	57	22	58	15	37	5	21
Fox squirrel					T	T	1	1	1	2
Gray squirrel							T	T		
Muskrat			1	1	T	T	1	3		
Skunk			1	3	1	4	T	T		
Opossum			T	2	1	5	T	1		
Domestic rabbit							1	T		
Domestic cat							T	T		
Raccoon			1	15			T	5		
Mink					T	T	T	T		
Woodchuck							T	T		
Unknown mammal	4	12	1	4	2	10	4	16	7	44
Large mammals										
Pig			1	T			1	T		
Cow							T	T		
White-tailed deer			T	T			T	T		
Reptiles										
Garter snake							T	T	1	T
Fish										
Carp							T	T		
Birds										
Red-winged blackbird							T	T		
Grackle							1	T		
Meadowlark							1	T		
Warbler							T	T		
Robin							T	T		
Yellow-shafted flicker							T	T		
Blue jay							T	T		
Catbird							T	T		
Unknown passerine							1	T		
Game Birds										
Ring-necked pheasant	2	4	2	4	1	2	5	10	1	2
Mallard							T	T		
Blue-winged teal							T	T		
American coot							T	T		
Hooded merganser							T	T		
Pheasant egg							T	T		
Duck egg							T	T		
Domestic fowl	2	4	1	3	3	7				
Chicken							3	7	1	5
Duck							1	3		
Goose							T	T		
Guinea fowl							T	2		
Other Birds										
Crow							T	T		
Upland sandpiper							T	T		
Mourning dove							T	T		
Great horned owl							T	T		
Unknown egg							T	T		
Unknown bird							14	11		

TABLE 33. *Continued.*

Food Items	Seasonal Periods Hunting (16 Oct-14 Dec) Freq. of Occurr.	Percent Biomass	Snow Cover (15 Dec-18 Feb) Freq. of Occurr.	Percent Biomass	Late Winter (19 Feb-14 Apr) Freq. of Occurr.	Percent Biomass	Nesting (15 Apr-28 Jun) Freq. of Occurr.	Percent Biomass	Brood Rearing (29 Jun-27 Aug) Freq. of Occurr.	Percent Biomass
Plants										
Grass	2	T	T	T	2	T	2	T	2	T
Corn			1	T	2	T	2	T	2	T
Oats					1	T			5	T
Unknown plant			5	T	11	T	12	T	13	T
Insects							11	T	28	T
TOTAL	99	99	97	97	99	98	98	93	104	101

sition of the redtail kill expressed in percent biomass; and (3) average daily biomass of food taken or required by adult and young redtails (Luttich et al. 1970:194).

The calculation of red fox predation rates on pheasants at Waterloo utilized the first two prerequisites from Luttich et al. (1970:194). Predation rates on cottontails were not determined, because total WSA rabbit populations were not known. Instead, total numbers of cottontails killed during the spring were calculated. Pheasant and cottontail remains encountered at dens during the spring (April-June), the only season in which food habits data were sufficiently represented for the estimation of numbers killed, were all assumed to be prey. This assumption is based upon the low number of vehicle-killed pheasants available as carrion during the Dumke and Pils (1973) study and the low number of vehicle-killed cottontails and pheasants observed during our investigation.

Spring predation rates were determined from examination of food items collected at active dens. An estimate was made of the den-days or the number of days a den was used on the WSA during April-June. Den-days were derived by: (1) Assuming that by 1 April, pups 3-4 weeks of age were eating solid foods; mean birth date was 8 March (Table 7). (2) All dens that were excavated or were known to be active during April were considered to have been occupied by fox families since at least 1 April. (3) Weekly observations were made of all potential fox dens during the spring. Thus giving us information on how many days fox families used these dens prior to excavation (den days). (4) The total number of days of den use at Waterloo by fox families (total den-days) was calculated by multiplying the number of fox families by 91, the number of days in the spring season. This figure represented the expansion of den usage for the entire spring season, after dens were excavated or checked for the last time.

The rate of pheasant consumption at the den (days per pheasant eaten) was obtained by dividing den-days by the number of pheasants found at dens. The total number of pheasants killed on the WSA throughout the spring was obtained by dividing total den-days by days per pheasant eaten. The total number of pheasants available during the spring was taken from Table 24. For example, during 1972 (Table 34), 10 fox families collectively occupied dens for 398 days (den-days). When den use was expanded for the 1972 spring season 10 families were multiplied by 91 days to obtain 910 total den days. Ten days per pheasant eaten for 1972 was obtained by dividing den-days (398) by the total number of pheasants found at the den (40). Total spring mortality was calculated by dividing total den-days (910) by days per pheasant eaten (10) to obtain 91 pheasants killed.

Predation rates were based on two types of expanded data: (1) pheasants found at dens were expanded to total pheasants killed, and (2) our estimation of den-days was expanded to total den-days for the 91 day period. Predation rates represented total pheasants estimated to be killed divided by total pheasants thought to be available on the study area; e.g., 1972 predation rates were 91 pheasants killed divided by 860 pheasants available, or a predation rate of 10.6%. Total cottontails killed by foxes were computed in the same manner.

It should be stressed that the numbers of cottontails and pheasants computed as prey taken by red foxes were only crude estimates. Spring predation rates computed for the WSA may have underestimated the numbers of game species killed because of the caching behavior of foxes. Johnson and Sargeant (1977) documented that foxes only brought 33 % of preyed mallards back to dens. Based on considerable field observations, we felt that domestic fowl were more available as carrion during the spring than were carcasses of pheasants or cottontails (Table 29). Therefore, the amount of pheasant or cottontail carrion we may have included as fresh kills was more than offset by cached individuals not included in the spring predation rate analysis.

The impact of red fox predation on cottontails and pheasants during the winter was calculated in a manner different than that for spring predation rates. The number of pheasant and cottontail occurrences found by examining 29 stomach contents, 283 scats and carcasses found during 133 km of winter tracking were used to assess predation during the winter season (Table 35). Based on data from Arnold (1956), WSA foxes were assumed to travel 8 km per night, thus our winter tracking data represented approximately 17 nights of hunting by a fox. The number of fox-days for each winter was calculated by multiplying the number of male and female foxes found on the WSA during the ensuring spring times 90, the number of days during the winter season, plus the number of days that other foxes remained on the WSA before they were harvested. For example, if a fox was shot on 10 January, it was thought to be on the area 10 fox-days. A total of 4,946 fox-days were calculated for the 1973-75 winters. This figure provides an index of total fox activity present on Waterloo during the winters studied and gives perspective to the incidence

TABLE 34. *The impact of predation by red foxes on pheasants and cottontails during the spring on the Waterloo Study Area, 1972-75.*

	1972	1973	1974	1975	Mean 1972-75
Foxes					
Den-days	398	432	254	213	324
Total den-days	910	819	546	546	710
Pheasants					
Pheasant found at dens	40	26	27	24	29
Days per pheasant eaten	10	16.7	9.6	9.0	11.1
Total pheasants available	860	695	747	527	707
Total pheasants killed	91	49	57	61	64
Predation Rate	10.6	7.1	7.6	11.6	9.1
Cottontails					
Cottontails found at dens	65	37	52	52	52
Days per cottontail eaten	6.1	11.7	4.9	4.1	6.2
Total cottontails killed	149	70	111	133	115

of prey found. Pheasants occurred infrequently in all three of the dietary analyses, suggesting a lower rate of predation than was found during the spring. Cottontails were noted as prey items more frequently than pheasants in scats, stomachs and during winter tracking, suggesting that winter predation may have been higher than spring predation.

Cottontails constituted the most important single food item in the winter and spring at Waterloo in terms of percent biomass (Table 33). Richards and Hine (1953), Scott and Klimstra (1955) and Korschgen (1959) also found that the cottontail was the chief fox food item by frequency of occurrence. While winter fox predation at Waterloo may have been more severe on cottontails, spring predation was greater for pheasants. Scott and Klimstra (1955:44) reported that a general decline in cottontail population during their Iowa study was not accompanied by a corresponding decline in the proportion of cottontails in the diet of foxes. Spring rabbit densities were not determined at the WSA and a comparison of spring fox diets and cottontail numbers was not possible. Cottontails were likely the most important buffer against heavy pheasant predation by foxes. Weather acts as a modifying factor. Darrow (1944:33-34) reported that many foxes on an area may have less of an effect on grouse abundance when buffer species (rabbits and mice) are numerous, than would fewer foxes with buffers scarce. Small mammals were commonly taken at Waterloo as buffer species during the winter and spring but remained low in terms of percent biomass consumed.

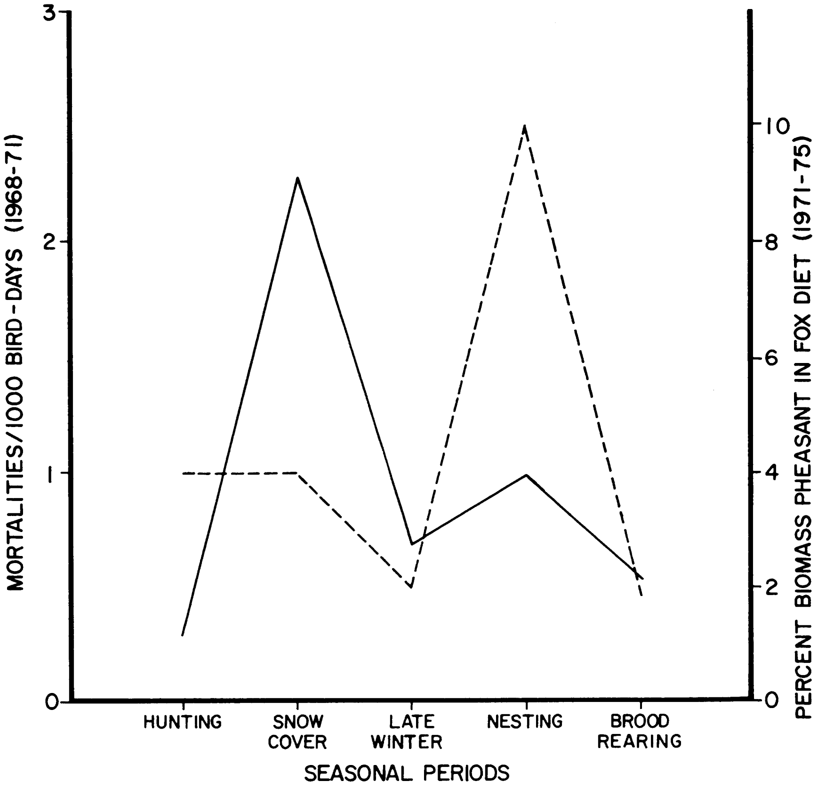


FIGURE 15. *Comparison of seasonal mortality between 1968-71 (Dumke and Pils 1973) and 1971-75.*

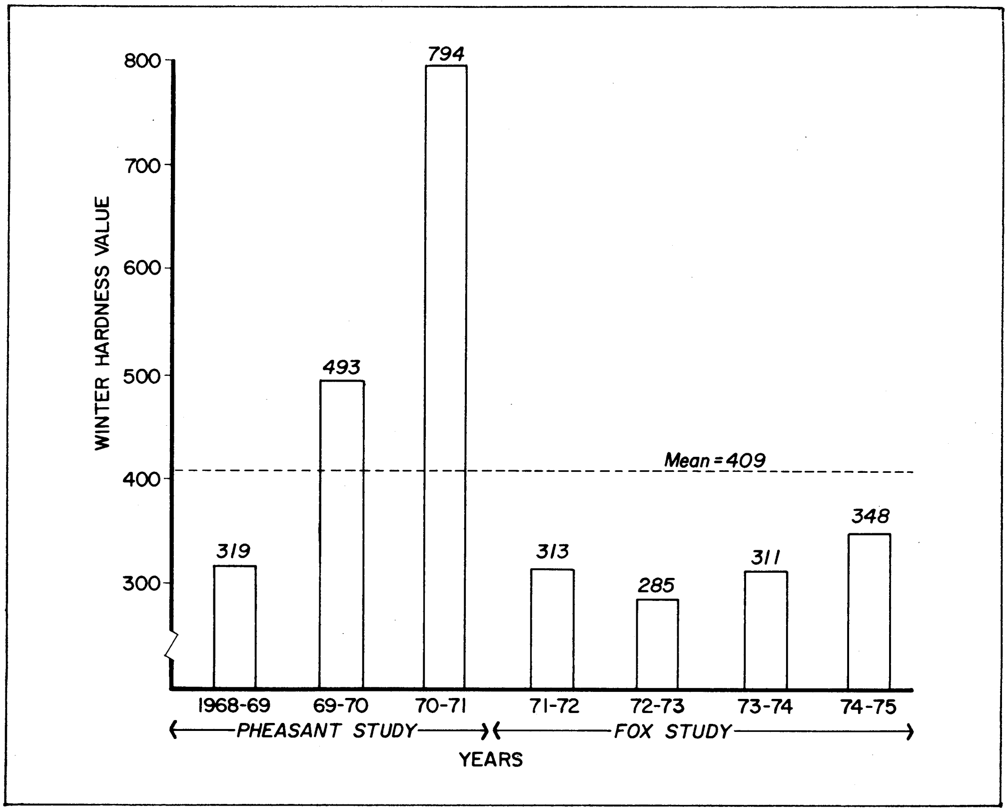


FIGURE 16. *Winter hardness index for the Waterloo Study Area, 1968-75.*

A comparison of the seasonal pattern of fox predation on pheasants between the Dumke and Pils (1973) study and our investigation (Fig. 15) indicated differences in severity of predation between the seasons. Weather is believed to have been the major factor responsible for the heavy fox predation on pheasants during the 1968-71 snow covered periods. Extensive snow accumulation, coupled with low temperatures during 1968-71, reduced adequate food and cover which may have stressed the pheasant population, making it highly susceptible to fox predation. Both Besadny (1966) and Gates (1971:747) cited evidence of increased pheasant predation during periods of severe winter weather. A winter hardness index (Fig. 16), derived from combining snow depth and temperature data (Dumke and Pils 1973:37-38), illustrates the severity of the 1969-71 winters. By comparison, the 1971-75 winters were relatively mild and low in snow cover.

In addition, higher fox populations during the 1968-71 pheasant mortality study (Table 4) exerted greater predation pressure on WSA pheasants. It is not clear why the lower 1971-75 spring red fox populations preyed more extensively on Waterloo hen pheasants when compared to the 1968-71 spring when more foxes were available. One possible explanation was a gradual loss of retired cropland (suitable for nesting) from 1971 to 1975, coupled with excessive spring precipitation from 1973 to 1975. Dumke and Pils (Unpubl.) found that retired cropland held the largest complement of nests and had the best hatching success during 1968-71. All retired cropland fields, including those adjacent to wetlands were converted to croplands from 1971 to 1975. Dumke and Pils (1973:38) noted that mortality during nesting was low in years of little spring precipitation and high in years with heavy May and June rainfall. May was the principal month for the onset of egg-laying at Waterloo from 1968-71 (Dumke and Pils unpubl.). Heavy precipitation exceeding the normal mean for May (1973-75) by 1.8 cm may have also forced nesting hens out of flooded wetlands, which ranked third in nesting preference (Dumke and Pils unpubl.). Foxes probably used strip cover as travel lanes in the spring when large areas were planted as row crops. Therefore, contacts should have increased between foxes and hen pheasants during the current study, resulting in relatively higher nesting period predation.

Modes of Fox Predation

In order to understand all consequences of red fox predation on game species, more insight is needed into the manner with which predators select and kill prey. Basically, carnivores that depend on their speed to capture and kill quarry select either old, weak or crippled prey. Conversely, stalkers such as red foxes would select both weak and strong individuals as potential victims. Few studies have documented the hunting techniques employed by foxes in capturing prey. The majority of these investigations have described small mammal hunting habits outlined in the snow while winter tracking foxes (Huff 1964). Sargeant and Eberhardt (1975:109) utilized a 4 ha enclosure to observe death feigning by ducks in response to red fox predation and Phillips (1971:36) observed feeding behavior of pups on beetles within a 5.3 ha pen. However, detailed descriptions of actual red fox predation on game species in the wild have not been published.

The red fox's penchant for taking easily available foods such as carrion (Arnold 1956), fleshy fruits (Scott and Klimstra 1955) and incapacitated prey (Errington 1937) has been documented. However, the ability of red foxes to take normal, healthy prey species by stalking has not been extensively studied under field conditions. Errington (1967:29-30) noted that red foxes are capable of stealthy approaches and sudden dashes; through astuteness and agility they may take formidably sized prey, such as snapping turtles. Storm et al. (1976:37) showed through the use of radio telemetry, that red fox activity periods were primarily nocturnal. Highly skilled stalkers such as red foxes are apparently quite capable of taking healthy, ground roosting pheasants at night. Similarly, pheasants attempting to hatch a clutch of eggs, especially late in incubation when attachment to the nest site is strongest, might easily be killed by hunting foxes at day or night, regardless of the hen's physical condition.

TABLE 35. *The impact of predation by red foxes* on pheasants and cottontails during the winter on the Waterloo Study Area, 1973-75.*

	Stomach Contents	Scats	Winter Tracking
Number examined	29	283	133 km**
Number of pheasant occurrences	0	2	1
Number of cottontail occurrences	12	121	8

*4,946 total fox-days.
**Distance tracked during 1974 and 1975.

Impact of Predation

Red fox predation on pheasants and cottontails, two of the most highly sought small game species by southern Wisconsin hunters, is an irrevocable fact. Large numbers of voles, deer mice and shrews are also killed by foxes. Mammalian predation is especially difficult to analyze because both functional and numerical response are complicated by buffering, territoriality and learning (Keith 1974:25). Although the magnitude of predation at Waterloo appears to be primarily influenced by severity of winter temperatures combined with snow depth (Dumke and Pils 1973:38) it is also affected by changes in habitat (causing prey vulnerability to vary) and sizes of predator and prey populations. Perhaps the key factor barring a fuller understanding of the forces limiting prey populations is the complexity of southern Wisconsin ecosystems. Waterloo pheasants, cottontails and small mammals are being taken by red foxes, gray foxes, raccoons, skunks, and weasels. Red-tailed hawks and great horned owls, the primary avian predators, are also responsible for a segment of mortality for these three prey groupings (Petersen in press).

Pheasants. Intensive research incorporating 3 separate studies designed either directly or indirectly to benefit pheasant populations have been conducted at Waterloo from 1966 through 1975. Frank and Woehler (1969:802) attempted to increase pheasant numbers by habitat manipulation, Dumke and Pils (1973:2) identified the causes and assessed the importance of hen mortality and the current study evaluated red fox diet and control. Frank and Woehler (1969:802) concluded that Waterloo pheasant numbers and hunting success remained constant from 1966-68 in spite of habitat manipulation. Dumke and Pils (1973:42) indicted the red fox, the great-horned owl, and the red-tailed hawk as chief predators of fully grown hen pheasants from 1968-71. The results of our study confirmed that predation by red foxes, other mammals and raptors (Petersen in press) apparently prevented increases in Waterloo pheasant populations over a seven-year period (Table 24). The consequences of weather also induced increased susceptibility and greater predation. Foxes preyed heavily upon pheasants during wet springs (1973-75) and severe winters (1968-71), when climatic conditions had narrowed the suitable habitat and made pheasants more vulnerable.

Although fox reduction was deleted as an objective for our current study, the lower fox densities noted from 1971-75 as compared to 1968-71 gave us an opportunity to observe what effect fewer foxes would have on the WSA pheasant population. Predation on pheasants from the lower fox densities still resulted in a loss of 9.1% of the spring pheasant population (Table 35). However, raptor predation on pheasants at Waterloo was 35% (Petersen in press), surpassing the fox predation rate by 26% during the same season. Raptor food habit data from the other seasons strongly suggested that raptor predation exceeded fox predation on pheasants during 1971-75. Wagner et al. (1965:113) felt that predation was more pronounced in marginal pheasant range than in better habitat. However, Waterloo data (1971-75) imply that when fox populations are low and prey less, raptors and mammalian predators compensate by limiting pheasant densities in an area of good pheasant habitat.

Cottontails. Fox predation on cottontails during our investigations (Table 34) limited cottontail abundance at Waterloo to an unknown extent. Unlike pheasant populations, total WSA cottontail densities could not be calculated; therefore, the total estimated predatory effect could not be estimated. Cottontail densities at Waterloo remained fairly constant during the 4-year trapping period (Table 26). The high degree of cottontail predation probably buffered the level of pheasant mortality by foxes, especially during the winter (Table 35). We felt that cottontail predation was tempered by the condition of the habitat and by weather. Trent and Rongstad (1974) found that foxes inflicted heavy mortality on radio-tagged cottontails in southwestern Wisconsin; they concluded that cottontail survival appeared to be related to exposure in secure cover. Because no data were gathered during 1968-71 on levels of cottontail predation, the amount of buffering from the former study could not be compared with evidence gathered from our research.

Small Mammals. The relative abundance of small mammals apparently was not affected by fox predation at Waterloo. Bi-monthly fluctuations in small mammal abundance remained similar at Waterloo from 1972-74 in spite of heavy predation from raptors and mammals (Fig. 14). Small mammals also buffered pheasant predation to an unknown extent, because small mammal densities were not calculated. Trautman et al. (1974:247) reported that when only foxes were controlled at a South Dakota study area from 1965-

69, small rodents increased by only 15%. Therefore, we felt that small mammal populations were density independent of fox predation at Waterloo.

MANAGEMENT

BACKGROUND

Sound management techniques are probably the least documented aspect of red fox ecology in the eastern half of the United States. Prior to 1965, management of the red fox was primarily concerned with denouncing bounties (Arnold 1956) and debating the tenets of predator control (Richards and Hine 1953). The Wisconsin Conservation Department promoted the use of trapping to control foxes during the late 1950's (Keener 1959). Several authors, including Arnold (1956:47), offered suggestions to dispel public misconceptions about red foxes, including the concept of wise use and appreciation rather than control. Stanley (1963:29) indicated that red foxes may be under intensive pressure by trappers when pelt prices are high, but offered no alternatives for alleviating fox exploitation through management strategies. Scott (1955:14) listed five steps to improve the economic position of foxes, including the cropping of surplus animals by game managers in areas where adequate harvesting had not been accomplished by hunters. Two management practices mentioned by Scott and Klimstra (1955:98) were the planting of trees with fruit palatable to foxes which would tend to reduce utilization of other prey, and proper poultry husbandry practices which would reduce the vulnerability of chickens. Seagears (1944:84) recommended an educational program designed to interest people in efficient methods of hunting and trapping. Latham (1951:24-67) discussed "predator management" by listing the benefits and deficits of predation, rather than listing specific management techniques.

The most intensive positive management practices encountered in the literature were the construction of artificial dens and propagation of red foxes for release in low density areas (Everett 1952). Storm et al. (1976) concluded that red foxes should be considered a valuable carnivore and an important furbearer, but did not make specific management recommendations. Montague (1975) suggested a rearrangement of Indiana fox season dates to maximize hunting and trapping recreation.

Thus, management of the red fox in states other than Wisconsin has been primarily designed to increase densities of target species such as pheasants by reducing fox predation. Herein lies the problem of designing Wisconsin management guidelines: Should management be directed at reducing fox predation through control of fox numbers, or at increasing fox numbers because of their economic and recreational values? The following information concerning bounties, predator control, fur values and factors motivating hunters and trappers attempts to put the question of priorities into perspective before management possibilities are explored.

Bounties

State bounties have been intermittently used in Wisconsin since their enactment by the state legislature in 1923 at $2.00 per fox. This bounty was repealed in 1931, but was reintroduced in 1946 at $2.50 per fox. It was dropped during 1957-58 and was then re-enacted during 1959-64. State bounties were finally terminated after 15 September 1963 (Pils 1977). Bounties were sometimes utilized to "control" foxes during periods of low or declining pelt values; for example state bounties were offered when mean pelt prices remained under $1.00 from 1946-47 to 1958-59. Richards and Hine (1953:68) methodically dismantled the logic of employing bounties to regulate fox harvest. Some state money still went to counties for payment of bounties until 1975, when bounties were made ineligible projects for county conservation project funding. As a result, only Waukesha County (7 out of 13 townships) still pays fox bounties. No further discussion will be made of bounties, because they are not a potential future management tool.

Predator Control

One of the original objectives of our current investigation, which was never implemented, was to evaluate techniques of experimental red fox control on the WSA. We originally planned to reduce the Waterloo fox population, beginning in December, 1973 for the purpose of significantly increasing the WSA pheasant population. Trautman et al. (1974) increased pheasant numbers by 19%, after reducing carnivores for a 4-year period. Our predator control efforts were to have been concentrated at spring dens, when fox families were most vulnerable. Supplementary steel-trapping was to aid our control efforts. After 2.5 years of field experience with other phases of the study, we excluded experimental predator control for the following reasons:

(1) Landowner Attitude. We found through the results of a questionnaire that most landowners would not allow us to remove foxes at dens on their lands. We felt that complete landowner cooperation was necessary for effective fox control.

(2) Rising Pelt Prices. Increasing fur prices made foxes a highly sought after furbearer.

(3) Establishment of a Red Fox Season. Landowners became concerned that the DNR was proposing a reduction in numbers of a game species which was economically and recreationally valuable to them. We feared

TABLE 36. *Wisconsin red fox fur values, bounties and estimated purchases, 1950-76.*

Year	Mean Fur Value($)	Mean Adjusted Value($)	Number of Estimated Purchases	Number Bountied ($2.50 Each)	Total Pelt Value($)
1950-51*	0.98	1.26	--	17,417	--
1951-52	0.66	0.83	--	23,646	--
1952-53	0.61	0.76	--	30,548	--
1953-54	0.43	0.53	--	21,890	--
1954-55	0.40	0.50	--	33,535	--
$\bar{x} \pm$ S.E.	0.62 ± 0.10	0.78 ± 0.14	--	25,407 ± 2,930	--
1955-56	0.62	0.76	--	29,285	--
1956-57	0.36	0.43	--	33,944	--
1957-58	0.47	0.54	--	No bounty	--
1958-59	0.55	0.63	--	No bounty	--
1959-60	1.08	1.22	3,800	58,139	4,104
$\bar{x} \pm$ S.E.	0.62 ± 0.12	0.72 ± 0.14	--	40,456 ± 8,943	--
1960-61	1.32	1.47	7,688	54,090	10,148
1961-62	1.50	1.66	4,364	47,342	6,546
1962-63	1.91	2.08	10,876	50,315	20,773
1963-64	1.89	2.03	10,000	5,284	18,900
1964-65	2.32	2.46	12,000	**	27,840
$\bar{x} \pm$ S.E.	1.79 ± 0.17	1.94 ± 0.17	8,986 ± 1,355	39,257 ± 5,284	16,841
1965-66	6.57	6.76	31,321	--	205,779
1966-67	3.43	3.43	43,405	--	148,879
1967-68	3.81	3.66	25,192	--	95,981
1968-69	8.03	7.31	35,989	--	288,991
1969-70	6.43	5.53	34,818	--	223,880
$\bar{x} \pm$ S.E.	5.65 ± 0.88	5.34 ± 0.79	34,145 ± 2,981	--	192,702
1970-71	6.57	5.42	29,960	--	196,837
1971-72	10.65	8.50	26,373	--	280,872
1972-73	20.65	15.51	25,386	--	524,221
1973-74	28.06	19.00	33,766	--	947,474
1974-75	23.61	14.65	25,662	--	605,880
$\bar{x} \pm$ S.E.	17.91 ± 4.03	12.62 ± 2.47	28,229 ± 2,342	--	511,057
1975-76	40.79	22.66	23,364	--	953,018

*Fur harvest estimates from 1950-51 to 1958-59; estimated purchases calculated thereafter.
**Bounty discontinued 15 Sep 63.

that they would not allow us to trespass on their property for other phases of the study.

(4) Mobility of Foxes. Our dispersal results showed that less than 10% of the pups tagged on the WSA remained after 1 October. Therefore, the long-term effectiveness of removing pups from dens was questionable.

(5) Interference by Non-target Species. Only 14 foxes were taken during more than 1,000 steel trap-nights in attempts to capture foxes for radio-tracking. This was primarily due to interference by dogs, raccoons and opossums. Injury of the dogs encountered in traps during our field research would have created severe public relations problems.

For these reasons, we concluded that the control of red foxes at Waterloo for the benefit of pheasants was not justified; therefore, predator control was omitted as a management tool (Pils 1977).

Relationship Between Pelt Value and Estimated Purchases

Richards and Hine (1953:27) concluded that there was little evidence in Wisconsin to support the apparent relation between take and pelt price found by Seagears (1944) in New York. Seagears (1944:44) reasoned that annual fox harvests are not a true index of fox abundance, because they

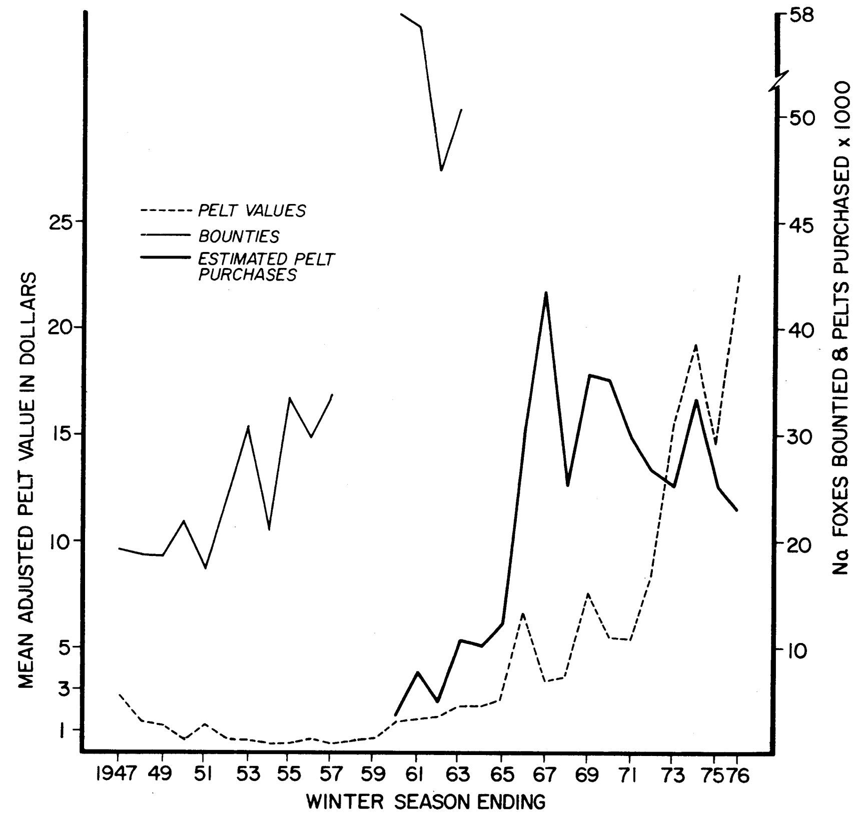


FIGURE 17. *Comparison of mean adjusted red fox pelt values, incorporating the consumer price index, with bounties (1946-47 to 1956-57) and estimated pelt purchases (1959-60 to 1975-76).*

are strongly modified by pelt prices. The possibility that red fox populations are cyclic, based on Canadian fur records, is an alternative explanation of fox abundance offered by Seagears (1944:45). Keith (1974:35) offered considerable data to substantiate his theories that Canadian red foxes undergo a 3-5 year cycle on the tundra and an 8-11 year cycle within the boreal forests. However, available data from the United States do not support any cyclic tendencies.

Table 36 summarizes red fox fur values, estimated purchases and bounty data available since Richards and Hine (1953). We were aware of the errors made by licensed fur buyers when reporting numbers of fox pelts purchased during the fox season (Append. D). These errors consisted of reporting out-of-state purchases, pelts bought from other dealers and the general public, red foxes reported as grays, and vice versa, and inconsistent harvest figures for various other DNR surveys, resulting in an inflated harvest index (Petersen et al. 1977). We felt that a comparison could still be made between pelt value and estimated purchases after taking these factors into consideration. To fully evaluate any possible relationships between fur value and harvest, adjusted pelt values were incorporated into Table 36 and Fig. 17. Adjustments were made using the consumer price index from 1967 for urban wage earners and clerical workers as a base year (U.S. Department of Labor, Bureau of Labor Statistics). Price indexes reflect the purchasing price of the dollar, are inversely related to price changes, and are computed by dividing the consumer price index number for the period in which the dollar's value is expressed as $1.00, by the index number for a particular period, and expressing the result in dollars and cents.

We felt that the adjusted fur values fully incorporated the effects of inflation and made a meaningful comparison of fur prices from 1947 to 1976 possible. From 1930-31 to 1958-59, estimates of fur harvest were derived by sampling less than 85% of the hunting and trapping records and projecting the results to obtain a 100% correction factor. The percentage of records sampled varied from 75-80% during the 1930's, to only 10-15% during the mid-1950's (F. Zimmerman pers. comm.). From 1959-60, through 1975-76, the DNR estimates of furs purchased were based on an average return of 91% of the licensed fur buyer's purchase questionnaire (Append. D). Bounty data were used from 1946-47 to 1956-57, when estimated fur purchase data were not available. The highest number of estimated purchases ever recorded in Wisconsin

Southern Wisconsin fur trapper with partial catch from the 1975-76 season.

was 43,405 in 1966-67, while the highest adjusted fur value was $22.66 in 1975-76 (Table 36).

The use of bounties and estimated purchases to gauge harvest has obscured the relationship between pelt prices and estimated harvest or purchases since the findings of Richards and Hine (1953). Bounty data were relied upon from 1951-52 to 1956-57 to supplement our 30-year perspective of fur take (Fig. 17). From 1959-60 to 1962-63, estimated purchases could be compared with bounty data for the first time. Bounty data were available for only a portion of 1963-64; therefore, data from this period were not compared. As a result of low pelt prices during this period ($\bar{x}$ = $1.45), more foxes were annually bountied ($\bar{x}$ = 52,471) than were sold to fur dealers ($\bar{x}$ = 6,682). Richards and Hine (1953) used bounty data to estimate fur taken from 1946-47 and 1950-51. If estimated purchases from fur dealers had been used to calculate take during this period of low pelt values (annual $\bar{x}$ = $1.08), the calculated take would probably have been much lower.

When a regression analysis was made between the number of estimated fur purchases made by licensed dealers in Wisconsin and pelt price (incorporating adjusted fur values) from 1959-60 to 1975-76, no significant correlation was noted ($P>0.05$). Prior years were not examined because of the lack of uniform (estimated harvest) data. Petersen et al. (1977) found a significant correlation ($P<0.01$) between pelt prices and estimated purchases for gray foxes during the same period. The primary reason for the lack of a direct relationship between red fox purchases and pelt price is the incidence of sarcoptic mange, which readily infests red foxes (Stone et al. 1972), but only occurs at a negligible rate in gray foxes (Trainer and Hale 1969). For the last two years, from 4-7% of the total red fox pelts reported by licensed fur buyers were mangy (Table 16). The figure is probably a conservative estimate of the statewide effect of mange for three reasons: (1) Mangy foxes brought to fur dealers were probably slightly affected animals whose pelt was still worth a premium, albeit reduced; (2) harvested foxes exhibiting severe mange were worthless and abandoned without being reported to fur buyers; and (3) mangy foxes harvested during the fall and winter represented foxes from only two seasons during the year; many mangy foxes could have died before the hunting season and were not available for harvesting. Additional foxes probably died during the fox season without being harvested or reported. Therefore, proportionally more mange-free gray foxes were available for harvest than were red foxes.

From 1973-74 to 1975-76, the number of estimated purchases had declined in spite of an increase in average fur values from $28.06 to $40.79 (Table 36). This recent trend may indicate that state fox populations are declining and are yielding lower fur returns in spite of high hunting and trapping pressure. Therefore, this type of trend clearly suggests a relationship between pelt prices and estimated purchases. Increasing pelt prices and resultant intensive harvest may be overtaxing a valuable fur resource.

Factors Motivating Fox Hunters and Trappers

Hunting and trapping are leading causes of red fox mortality in Wisconsin. Extensive field contacts made on the WSA as well as knowledge gained from contact with many southern Wisconsin trappers and hunters, has led us to the conclusion that different factors motivate each group. We found that the majority of southern Wisconsin fox hunters are more inclined to hunt foxes for the camaraderie and sporting qualities of the hunt itself; profit considerations are less important. Fox hunters living on the WSA illustrated this contention by hunting with approximately the same intensity from 1967 to 1975, regardless of the pelt price. The only factor limiting their hunting was insufficient snow cover. Contacts with fox hunters in other areas further support this belief. Waterloo fox hunters usually hunted in groups. Only after mean pelt prices exceeded $20 did we receive reports of solitary hunters pursuing foxes, probably for the monetary return.

Fox trappers, on the other hand, were more strongly motivated to harvest foxes for profit, although the sporting qualities of trapping were also part of their decision. Trappers in southern Wisconsin generally maintained their traplines alone and usually were much more efficient in harvesting foxes than were fox hunters. Experienced trappers were especially effective at catching foxes, especially during adverse weather when inexperienced trappers caught very little or stopped trapping completely.

CONSIDERATIONS

The status of the red fox as a game species and furbearer changed dramatically in Wisconsin from 1971 to 1976; bounties nearly disappeared, a harvest season was established, and pelt prices greatly increased (Pils 1977). Planning and policy guidelines were also modified accordingly. For example, a 1965 Wisconsin Conservation Department planning report advocated the reduction of overpopulated foxes in order to alleviate excessive property damage or destructive effects on other species. An annual harvest goal of 35,000 red and gray foxes was projected for 1980. These objectives were never realized after 1970, as a result of the general decline of the state fox population.

The initiation of a fox season also changed management priorities after 1965. The DNR policy (Wis. Adm. Code NR 1.16) for furbearers adopted in 1977 states that when foxes depresss the population of other species, management activities on DNR lands should be designed to achieve a desirable balance between predator and prey species. Results from our investigation illustrate methods for applying this policy.

Transplants

Andrews et al. (1973:72) reported that 1 to 2-month-old juvenile red foxes were successfully transplanted and adopted by foster parents in Iowa; and that pups transplanted immediately after capture had the best chance of survival. Sargeant and Allen (pers. comm.) also found that pups transplanted in North Dakota were accepted by foster parents.

We transplanted three litters (12 pups) plus 2 pups from separate litters to alternate red fox families during 1975. One communal litter consisted of 4 foxes aged at 38 days and 2 juveniles aged at 46 days. All 6 pups were moved during 15 April to an active den 16 km northeast from the original den. Tagged and unmarked pups were seen playing with each other at the new den on 4 occasions during the following 2 weeks. Two of the pups were recovered during July and October, proving that at least one-third of the transplants survived at least for the remainder of the denning season.

A third litter of 6 pups was moved on 15 May to two WSA dens located 14 km apart, after being taken from a den 62 km east of Waterloo. Three pups transplanted to the northern den were all trapped during the following fall. The remaining 3 foxes were observed twice during June and July at the southern WSA den, while a male pup was shot and reported the following January. These data indicate that adoption of this litter was successful.

We suggest that this technique be considered to alleviate depredation problems associated with domestic fowl. Adults could be caught at the den using steel traps. Another possible application would include the steel-trapping and relocation of foxes threatening wildlife species on state lands. The public relation benefits from such a practice would far exceed the costs incurred. Local, experienced trappers could be contracted to do the trapping, similar to arrangements made for trapping problem beaver.

Harvest Regulation Changes

The DNR wildlife management policy calls for the creation of regulations to make optimum use of furbearers from a biological, recreational and economic standpoint. The code also asserts that every effort should be made to design regulations on as uniform a basis as possible and yet maintain desirable population levels from year to year.

A recurring management proposal associated with explorations of red fox natural history concerns the encouragement of hunting (Scott 1955:14) and trapping (Seagears 1944:84) as a means of utilizing the harvestable surplus. Yet we have not reviewed any publication that has objectively designed the framework of a season to achieve a sustained harvest of foxes. Since there are no known cost-effective ways to manage red fox populations through habitat alterations, the most practical fox management technique consists of designing flexible and biologically efficient harvest regulations that are based on accurate fox abundance indexes. A sampling of 14 states (Table 37), including 11 from the midwest, revealed that only Missouri and Illinois have had a fox season for many years. Foxes can still be taken in 8 of the 14 states at any time during the calendar year. The catalyst for the relatively recent initiation of fox seasons in the midwest has been the sharp ascent of pelt prices, which started about 1971, accompanied by declining fox populations.

Wisconsin's initial fox season, which began on 14 October 1972, offered individual counties the option of a season running from the first Saturday in mid-October through the end of February, or a completely open season. The introductory 4½ month season selected by 31 counties in 1972-73 increased to 45 of the 72 counties by 1975-76. In 1976-77, the county option was removed and a statewide fox season was established running from 16 October to 28 February (136 days). An initial 1978-79 regulation proposal called for shortening the season by approximately 43 days; the revised season would run from 1 November through 31 January.

The primary objective of these alterations was to reduce mortality for current Wisconsin fox populations by eliminating February from the season. Approximately 14% of our tagged fox harvest occurred during February (Fig. 13). Eliminating February from the season should also decrease the harvest of rubbed or poorer quality pelts. Our investiagion revealed that the mean conception date for southern Wisconsin vixens was 14 January (Table 7). By February, pairs of foxes were spending longer amounts of time at dens in preparation for birth. If the season ended on 31 January, the practice of shooting or trapping foxes at the denning site should be reduced.

Conclusions from our analysis of red fox mortality indicate that WSA populations are declining and southern Wisconsin densities are low. Wisconsin fur-buyer surveys (Table 16) suggested that statewide red fox populations are also declining. Our data indicated that restricting the trapping season from about the first of November to 31 December would eliminate a sizeable segment of fox mortality. Trappers could not legally shoot foxes caught in steel traps. Approximately 12% of our tagged fox harvest from trapping occurred in January (Fig. 13). Other mammalian predators such as skunks and raccoons might compensate for lower fox densities by increasing their level of predation on eggs or young of ground-nesting species. Waterloo data suggested that small mammal populations were independent of fox predation and would not greatly increase if the fox season were shortened. In addition, opening the fox trapping season concurrently with muskrats and mink could help reduce the trapping of nontarget furbearers. (Petersen et al. 1977).

Our data implied that the fox hunting season be further shortened to run from 1 December to 31 January. Data from returns of tagged foxes indicated that pheasant and deer hunters (Fig. 12) took 11% of the annual fox kill in southeastern Wisconsin. The Wisconsin deer season ends before 1 December; the pheasant season extends into the first or second week in December, although December pheasant hunting pressure is less severe than during the first half of the season (E. Woehler pers. comm.). Therefore, fox mortality should be diminished by closing November to hunting, although some illegal kill would undoubtedly occur by pheasant and deer hunters.

Another potential fox mortality factor associated with deer and pheasant hunting is crippling loss. A considerable number of wounded foxes may be lost before adequate snow tracking cover is on the ground. This problem would be greatly lessened with a 1 December opening. Finally, by staggering the opening of trapping and hunting seasons, the difference in views between fox hunters and trappers should be minimized. Each faction believes the other group is harvesting too many red foxes (Petersen et al. 1977).

Accurate fox abundance indexes can lead to the design of an equitable season. The only current index to fox numbers in Wisconsin is the DNR annual fur harvest report, which is based on data supplied by licensed fur buyers. However, since the accuracy of the

TABLE 37. *Comparative summary of red fox season structure, harvest, fur values and populations at the conclusion of the 1975-76 season in 14 states.*

State	Number Past Seasons	Seasons Separate?	Length (Days)	Dates Start-End	Estimated Purchases	Mean Pelt Value ($)	Current Population Level Compared With Previous Year
Minnesota	0	--*	--	--	43,000	50.00	Down
Michigan	0	--	--	--	--	25.00	Down
Iowa	6	Yes	Hunt-83 Trap-23	8 Nov-31 Jan 8 Nov-30 Nov	25,000	40.00	Down
Illinois	62	No	76	8 Nov-15 Jan-N. 8 Nov-23 Jan-S.	11,000	33.00	Down
Wisconsin	4	No	141	16 Oct-28 Feb	23,364	40.79	Down
Ohio	Season in 1976-77	No	122	15 Oct-1 Feb	19,374	37.04	Same
Indiana	2	Yes	Hunt-136 Trap-108	15 Oct-28 Feb 15 Oct-31 Jan	14,516	34.26	Same
Missouri	62	Yes	Hunt-65 Trap-46	10 Nov-15 Jan 1 Dec-15 Jan	3,337	29.50	Down
North Dakota	9	Yes	121	1 Oct-31 Jan	35,000	35.00	--
South Dakota	0	--	--	--	28,100	35.50	Same
Nebraska	0	--	--	--	--	--	Same
Texas	0	--	--	--	1,745	25.00	Up
California	Protected fur bearer since 1974			--	--	--	Very Low
New York	Season in 1976-77	--	--	--	± 7,000	35.00	--
*No Data						$\bar{x}$ 35.00	

buyers' reports is questionable, some consideration should be given for a tighter harvest recording system. Such a system should include mandatory fox pelt tagging in the same manner that bobcats, otter and beaver are now recorded, and a mandatory, more detailed and standardized fur buyers report. These modifications would provide a more accurate statewide fox harvest estimate.

Consideration should also be given to instituting some form of separate licensing for all fox hunters and fox trappers so that access will be provided to all persons pursuing foxes, thereby enabling better estimates of trapping and hunting effort. Such data would be a valuable supplement to the other fur harvest reports.

If current high pelt prices continue without curtailment of harvest seasons, we feel that statewide red fox populations will become precariously low. Other states have taken drastic steps to protect low fox populations. California prohibited the harvest of red fox for commerical purposes in 1974 (Gray 1975:3). Missouri has closed seasons until pelt prices return to a normal level (Sampson 1977:3). We do not feel that reducing the length of fox seasons would have an adverse economic effect on hunters and trappers. The Wisconsin Trappers Association and several fox hunting clubs have endorsed this view. In addition, the current DNR furbearer management policy endorses this viewpoint by stating that when high pelt prices depress fox populations, both recreational and biological considerations shall be accorded primary consideration in the establishment of harvest regulations.

Other Recreational Activities

Although most red fox management considers only hunting and trapping, a much larger number of potential recreation-hours are available throughout the year for other recreational users of Wisconsin outdoors. An under-utilized type of recreation, especially on state wildlife areas, is the observation and photography of predators. Such activities can be done year around and can result in a high level of aesthetic pleasure. For example, observing and photographing active fox dens requires skill and patience and is extremely rewarding. Following fox trails in the snow also stimulates one's environmental awareness by observing signs of the red fox's daily activities, which is the framework for Wisconsin red fox life history. Combined with photography, this pursuit will permanently record moments of extremely satisfying and memorable outdoor activities. We believe that this form of recreation is vastly underemphasized and should receive greater promotion.

SUMMARY

From 1971 to 1975, we analyzed red fox population trends, movements, dispersal, diet, productivity, and age structure primarily on the 8,097 ha Waterloo Study Area (WSA) located in Dodge and Jefferson counties. Similar data was also gathered in six adjacent southern Wisconsin counties. Numbers of foxes and active dens observed by WSA residents declined from 1971-74. Spring fox families at Waterloo decreased from 10 to 1972 to 6 in 1975. The mean annual WSA harvest of 72 foxes from 1968-71 decreased significantly to an average of 21 during 1971-75.

The most important factors influencing den site selection were cover type, human disturbance, water and length of use. The mean southern Wisconsin birth date for 35 litters was 8 March. Pregnancy rates for 48, 1-7 year old vixens were 59% for juveniles and 89% for adults. Mean WSA litter size was 5.6.

From 1 to 283 radio-locations were made of 8 pups and 5 adult vixens from 1972-74. Three radioed females, whose home range averaged 598 ha, were most frequently located in cultivated lands, pasture and marsh. Foxes were snow-tracked primarily in retired cropland, marsh and upland hardwood for a total of 182 km. Of the 73 recoveries, 81% dispersed after 1 October; males dispersed almost twice the mean distance of females. Significantly, more foxes dispersed into the northeast quadrant. Interstate highways may have impeded southerly dispersal.

Trapping (primarily on private lands), followed by hunting on private and state-owned wildlife areas constituted the major source of mortality for 127 tagged and unmarked southern Wisconsin foxes. The majority of trapping harvest occurred from October to December, while fox hunting predominated during January and February. The following percentages of WSA fox mortality were attributed to: fox hunters 59, deer and pheasant hunters 22, foxes accidently spotted and shot 11, and trappers 9. Fifty-four percent of the foxes tagged at dens were recovered; 96% were returned during the first or second year.

Analysis of survivorship from tag returns indicated a steady decrease from 1973 to 1975, which was inversely related to pelt prices. Both year of kill and fox age influenced survival. Population matrix analyses implied a strong exponential decline in the southern Wisconsin population. Stabilization of the fox population could occur only with an increase in productivity or a decline in harvest mortality.

A higher proportion of southern Wisconsin juvenile foxes were taken by trappers than by hunters in January and February, when fewer juveniles were available. Significant differences were found between hunted and trapped fox age ratios both on and off the WSA.

Mean spring and fall pheasant populations did not vary significantly between 1968-71 and 1972-75. Mean fall WSA rabbit densities were 7.4 per ha versus 7.0 per ha in the winter. Cottontails, small mammals and pheasants were the most important food items taken by foxes from 1972-75, based on analysis of 1,020 scat samples, 132 stomach contents, food items from 58 dens and foods collected from 182 km of snow tracking. Nine percent of the available spring pheasant population and an annual average of 115 cottontails at Waterloo were taken by foxes during 1973-75; cottontails were killed at a higher rate than pheasants during the winter and acted as a buffer against pheasant predation by foxes. Predation by red foxes, other mammals, and raptors at Waterloo apparently prevented increases in pheasant and cottontail abundance but did not affect small mammal densities.

Predator control was deleted from our study because of landowner attitude, rising pelt prices, establishment of a fox season, mobility of foxes and interference by nontarget species. Six percent of Wisconsin red foxes purchased during 1974-75 and 1975-76 were mangy. Errors in reporting red fox purchases, Wisconsin's only estimate of fox abundance, has duplicated and inflated results of past harvests. Management considerations include (1) a shortened trapping season opening concurrently with the muskrat and mink season; (2) a hunting season running from 1 December to 31 January; (3) mandatory registration of pelts; and (4) a special license for all trappers to serve as a source for contacting trappers.

APPENDIX A:
Scientific Names of Plants and Animals Used in the Text

Scientific names of plants from Fernald (1950); birds, Gromme (1963); domestic mammals, Jackson (1961) and Hoffmeister and Mohr (1957); exotic mammals, Walker (1964); reptiles, Smith (1961); fish, Hubbs and Lagler (1958) and insects, Borror and DeLong (1954).

PLANTS

Apples, *Pyrus* sp.
Corn, *Zea mays*
Grass, Graminae
Oats, *Avena* sp.
Soybeans, *Glycine* sp.
Tamarack, *Larix laricina*

MAMMALS

Badger, *Taxidea taxus*
Beaver, *Castor canadensis*
Bobcat, *Lynx rufus*
Cinereus shrew, *Sorex cinereus*
Cow, *Bos taurus*
Cottontail rabbit, *Sylvilagus floridanus*
Deer mouse, *Peromyscus maniculatus*
Domestic cat, *Felis domestica*
Domestic dog, *Canis familiaris*
Domestic rabbit, *Oryctolagus cuniculus*
Fox squirrel, *Sciurus niger*
Gray fox, *Urocyon cinereoargenteus*
Gray squirrel, *Sciurus carolinensis*
Jumping mouse, *Zapus hudsonius*
Least weasel, *Mustela rixosa*
Long-tailed weasel, *Mustela frenata*
Meadow vole, *Microtus pennsylvanicus*
Mink, *Mustela vison*
Muskrat, *Ondatra zibethicus*
Norway rat, *Rattus norvegicus*
Opossum, *Didelphis marsupialis*
Otter, *Lutra canadensis*
Pig, *Sus scrofa*
Red fox, *Vulpes vulpes*
Raccoon, *Procyon lotor*
Short-tailed shrew, *Blarina brevicauda*
Skunk, *Mephitis mephitis*
Striped ground squirrel, *Citellus tridecemlineatus*
Tricolor shrew, *Sorex arcticus*
White-tailed deer, *Odocoileus virginianus*
Woodchuck, *Marmota monax*

BIRDS

Blue jay, *Cyanocitta cristata*
Blue-winged teal, *Anas discors*
Chicken, *Gallus gallus*
Coot, *Fulica americana*
Crow, *Corvus brachyrhynchos*
Catbird, *Dumetella carolinensis*
Domestic duck, *Anatinae*
Domestic goose, *Anserinae*
Grackle, *Quiscalus quiscula*
Great horned owl, *Bubo virginianus*
Guinea fowl, *Acryllium* sp.
Hooded merganser, *Lophodytes cucullatus*
Mallard, *Anas platyrhynchos*
Meadowlark, *Sturnella*, spp.
Mourning dove, *Zenaidura macroura*
Red-tailed hawk, *Buteo jamaicensis*
Red-winged blackbird, *Agelaius phoeniceus*
Ring-necked pheasant, *Phasianus colchicus*
Robin, *Turdus migratorius*
Ruffed grouse, *Bonasa umbellus*
Upland sandpiper, *Bartramia longicauda*
Warbler, *Parulidae*
Yellow-shafted flicker, *Colaptes auratus*

REPTILES

Garter snake, *Thamnophis sirtalis*

FISH

Carp, *Cyprinus carpio*

INSECTS

Grasshoppers, Orthoptera
Beetles, Coleoptera

APPENDIX B:
Wisconsin Fur Buyer Questionnaire

The Wisconsin Department of Natural Resources has been conducting a study of the Biology of Red Fox in Southern Wisconsin for the past four years. I would like you to answer the following questions in order to give us more information to better manage this valuable fur resource.

Thank you.

Charles M. Pils
Research Biologist

CMP:jg

----

1. Approximate number of red fox bought from the public from the fall of 1974 to the spring of 1975 ________________________.

2. Of the red fox you bought, approximately what numbers were taken by

   _____________ trappers

   _____________ fox hunters

   _____________ others (car kills, bird hunters, etc.)

3. Of the red fox that you bought, approximately how many were killed

   _____________ During October-November, 1974

   _____________ During December-January, 1974

   _____________ During February-March, 1975

4. Approximately how many mangy red fox were brought in to you this year? _____ How does this compare to last year?

   _____________ More _____________ Less _____________ About the same

5. Do you think the red fox population at this time is ______ up ________ down ________ about the same as last year at this time?

6. Would you like to see the red fox season for the whole state open and close at the same time, OR would you be in favor of having the state broken into 2 or 3 zones with different opening and closing dates?

   ____

   ____

NAME OF FUR-BUYER ________________________________ COUNTY _______________

APPENDIX C:

Annual Mammal Inquiry Form Used to Interview WSA Residents from 1971-74

ANNUAL MAMMAL INQUIRY - 197_

I. FOXES ON YOUR FARM - 197_

1. Have you seen any foxes on your farm during 197_? YES NO
2. Do you have any active fox dens on your farm? YES NO
3. Do you know of any fox litters raised on your farm during 197_? YES NO
   How many litters did you see on your land in 197_? ______ (number)
4. Were any foxes trapped on your farm this year? YES NO
   How many were trapped? ______ (number)
5. Did hunters shoot any foxes on your farm this year? YES NO
   If yes, how many were shot? ______ (number)

6.* Would you be willing to have foxes removed from your land at any time of the year by trapping, shooting or by digging up dens and removing young pups? YES NO

II. SKUNKS ON YOUR FARM - 197_

1. Have you seen any skunks on your farm during 197_? YES NO
   How many skunks did you see during 197_? ______ (number)

III. BADGERS ON YOUR FARM - 197_

1. Have you seen any badgers on your farm during 197_? YES NO
   How many badgers did you see during 197_? ______ (number)

IV. RACCOONS ON YOUR FARM - 197_

1. Have you seen any raccoons on your farm during 197_? YES NO
   How many did you see during 197_? ______ (number)

V. OPOSSUMS ON YOUR FARM - 197_

1. Have you seen any opossums on your farm during 197_? ______ (number)

VI. DOGS AND CATS ON YOUR FARM - 197_

1. How many dogs on your farm during 197_? ______
2. How many cats on your farm during 197_? ______ (number)

---

*Used only during January, 1974 interview.

APPENDIX D:
Current Wisconsin Fur Buyer Survey Form

Department of Natural Resources
State Game Farm
Poynette, Wisconsin 53955

May 1976 IN REPLY REFER TO 2310

Dear Fur Buyer:

To enable us to better manage the fur resources of Wisconsin, it is important that we obtain an accurate and quick estimate of the fur harvest each year.

We would again like to ask for your cooperation in making this survey. You can do this simply by filling in the numbers of each type of fur that you purchased directly from Wisconsin trappers.

These figures are used only to obtain an estimate of the harvest of each species and the average pelt price. All information is confidential.

Do not include fur purchased out of state or that from other Wisconsin fur buyers.

Your assistance in helping us to obtain this information is appreciated. Please return your report before May 24, 1976.

Sincerely,

N. E. Damaske, Supv.
Game Farms & Shooting Preserves

NED:cn
Enc. - 1 return envelope

. . . .

1. How many of each of the following furs have you bought directly from Wisconsin trappers in the current season?

Species	Number	Estimated Value Per Pelt	Species	Number	Estimated Value Per Pelt
Muskrat	______	$____________	Gray Fox	______	$____________
Mink	______	____________	Red Fox	______	____________
Raccoon	______	____________	Coyote	______	____________
Skunk	______	____________	Bobcat	______	____________
Weasel	______	____________	Beaver	______	____________
Opossum	______	____________	Otter	______	____________

2. Cross out or add license numbers included in this report: ____________

3. Licensee's Name ____________________ City ____________________

4. County ____________________

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