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EFFECTS OF INTENSIVE GRAY FOX CONTROL ON POPULATION DYNAMICS OF RODENTS AND SYMPATRIC CARNIVORES

by

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ABSTRACT

The impact of continuously removing gray foxes (*Urocyon cinereoargenteus*) from upland Virginia poultry farms was studied over a 25-month period. Primary study areas were two sets of farm woodlots. Foxes were left undisturbed on one farm, and were intensively controlled for a 14-month period on the other. Demographic analysis of rodent populations and enumeration of sympatric carnivores were performed on both farms before, during, and after the period of fox control. During fox control, weasels (*Mustela frenata*) irrupted to significant ($P < 0.05$) levels; numbers of skunks, opossums, and raccoons remained unchanged. Weasels disappeared upon the reestablishment of foxes during postcontrol. Rodent trapping yielded 631 small mammals, including 331 woodmice (*Peromyscus leucopus*), in 9,042 trapnights. Analysis of woodmouse population dynamics indicated that fox removal (and the resulting weasel irruption) did not affect overall density; however, all other parameters studied showed significant ($P < 0.05$) alteration. On the Reduction Area turnover rate increased, mean longevity fell from 3.10 to 1.68 months, sex ratios shifted toward more females, age structure shifted toward more subadults, and fecundity increased through continuous rather than seasonal breeding. The enlarged weasel population apparently exerted more predatory stress upon woodmice than did the original fox population. This study shows that a sympatric predator can assume the predatory role of a removed species. Implications are that predator removal studies may be invalid where sympatric predators are ignored, or where simple prey density is the only parameter used in assessing predator management.

INTRODUCTION

Predator control has long been a part of wildlife management and agricultural practice. In recent years it has become subject to increasing social and political controversy. Inherent in the phenomenon of predation are cryptic biological complexities which, if understood, might influence management decisions. Therefore, research is needed to identify not only the effects predators have upon prey populations, but also the potential adverse or favorable effects of predator management.

In some Virginia counties foxes have been managed, to a greater or lesser extent, for about 20 years. Control has been practiced in order to circumvent rabies epidemics (Marx and Swink 1963) and to protect livestock, especially poultry. In Rockingham County, Virginia, a professional trapper is employed to remove foxes upon demand by poultrymen or local citizenry. This county supports high populations of both gray foxes (*Urocyon cinereoargenteus*) and red foxes (*Vulpes vulpes*), not only because of prime habitat but also because the area has one of the largest concentrations of domestic turkeys in the world. For about 9 months per year poultrymen keep flocks of turkeys on unprotected open range. In extreme cases there may be more than five flocks of over 5000 birds each, all within an

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area of less than 100 ha. There are some depredations by foxes, usually by family groups which first scavenge poultry carrion and then learn to attack flocks. Control trapping is usually directed toward such nuisance foxes, although some poultrymen demand removal of all foxes on a regular basis.

Since foxes also prey upon small mammals, questions arose concerning the possible impact of fox control on those species which normally serve as staples in the fox diet. Food habits studies by Swink (1952) and Nelson (1933) have shown that both the gray fox and red fox prey heavily on rodents. Because high populations of rodents can also be an agricultural nuisance, it was suggested that fox control might become self-defeating if it resulted in rodent irruptions. Therefore research was undertaken to study the dynamics of rodent populations on an area where foxes were experimentally removed, and on a normal "check" area. It was further decided that the several species of sympatric carnivores should also be studied in case their numbers showed a numerical or functional response following a possible rodent irruption.

The most abundant prey species on the study areas was the woodmouse *(Peromyscus leucopus)*. In food habits studies reviewed by Trapp and Hallberg (1975) for the gray fox, and by Ables (1975) for the red fox, *Peromyscus* spp. was a consistent dietary staple only for the gray. This difference may be because habitat preferences (upland woods) and activity patterns (nocturnal) of woodmice effectively isolate them from red foxes but not from grays. Numerous studies have shown that meadow mice (*Microtus* spp.) are more important in the red fox diet, and meadow mice were virtually absent from upland Virginia when this study began in 1972. With these factors in mind, primary research was performed on dense, brushy woodlots where red foxes did not occur. From the outset, therefore, this study concentrated on the interaction between gray foxes and woodmice.

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MATERIALS AND METHODS

Study Area

Research was performed on two 175 ha poultry farms located in north central Rockingham County near Harrisonburg, Virginia. The farms were 11.5 km apart at closest point. Included on both farms were open turkey range, pasture, croplands, oak-hickory woodlots, and seral brush with slash. Both farms were adjacent to mature forests along Massanutten Mountain. During the summer of 1972, feasibility studies were conducted on the farms to locate woodlots which were closely similar in terms of flora, fauna, slope, exposure, elevation, soil, climatological means, and agricultural useage. Two compatible 8 ha woodlots were selected for primary research. Parts of both lots had been previously logged on one side. Thus, each included about 4 ha of mature oak-hickory woods and a similar amount of dense second growth brush over honeysuckle and debris. Both lots abutted open turkey range. At the start of the study both lots were regularly used by gray foxes, and both supported similar woodmouse populations. To supplement primary data additional information was gathered on nearby fields and other woodlots. A third farm about 16 km to the west, which had no poultry but was similar in all other respects, was also studied to ascertain if the availability of poultry affected the predator-prey relationship.

Predator Enumeration and Removal

The variable in this study was presence or absence of resident gray foxes. On the Reduction Area foxes were removed by trapping during September, 1972. To remove immigrants, trapping continued for one week per month through November, 1973. Thereafter, foxes were allowed to reestablish ranges which included the Reduction woodlot. On each farm approximately 5 hours per month were devoted to calling foxes with a predator call as suggested by Failor (1969). This provided a mechanism to confirm fox presence on the Check farm, and to intensify control on the Reduction farm where responding immigrants were removed by shooting. To further monitor fox activity on the two farms, fox scats were collected weekly from known deposition sites. Scats were frozen and later analyzed as a group using techniques suggested by Korschgen (1971).

Attempts were also made to enumerate other potential mammalian predators which might be affected by fox control. Two-week live trapping programs, employing aluminum and wooden box traps, were initiated on and around each woodlot in the fall of 1972 (precontrol), 1973 (during control), and 1974 (postcontrol). Captured carnivores were identified, marked, and released at capture site.

Supplemental information concerning den sites, home ranges, and feeding habits were recorded during field observations, especially on snow. Snakes and birds of prey were observed, but their populations were not analyzed.

Rodent Studies

On each woodlot two permanent 1 ha grids were established, one in mature woods and one in dense brush. On each grid 49 small (1 x 1 x 2.5 cm) Sherman live traps were placed at intervals of 16m. To maximize the catch, traps were placed at the best location within 3m of a grid point and were elevated where possible. Bait was a mixture of peanut butter, oats, and molasses. On each grid a 6-day trapping period was conducted at bi-monthly intervals from October, 1972, through November, 1973. A final 6-day postcontrol trap-out occurred during August, 1974. All captured mice were identified, sexed, aged, measured, checked for reproductive condition, marked, and then released immediately.

On nearby woodlots and on the third farm, supplemental assessment traplines were established for removal trapping. Each line consisted of 30 snap traps set at intervals of 16m. Traplines were operated for 3-night periods during early fall of 1972, 1973, and 1974. Removed mice were examined as before and then frozen for later study.

Live trapping produced data which permitted a biodemographic analysis of woodmouse populations before, during, and after intensive gray fox control. Computed were raw density per grid, density per adjusted unit area, average movement, longevity, and population structure in terms of sex, age, and reproductivity. Statistical comparisons using these parameters were made among all four grids, and then woodlot means were compared. Tests and confidence limits were G-tests used with 2 x 2 contingency tables and R x C tests of independence (Sokal and Rohlf 1969). The Yates' correction for continuity was used in the predator enumeration where sample sizes were small.

Mice removed through snap-trapping on assessment lines served as a check on the validity of results obtained on the live trapping grids. These mice were further used to compare litter sizes on the two areas. Twenty pregnant or lactating females from each area were dissected under a stereomicroscope. Reproductive tracts were examined in search of unborn young or scars in the uterine horns.

RESULTS

Predator Study

A total of 13 foxes was removed from the Reduction farm during 14 months of trapping and calling. It is believed that foxes were absent from the entire farm for periods of 30-45 days following each trap-out. However, tracks and droppings always began to reappear within 60 days and this generated renewed control efforts. During 14 months of control only 14 gray fox scats were collected on or near the Reduction woodlot, compared to 81 found around the Check woodlot with similar searching effort. During 9 months of postcontrol scat collecting, 70 and 59 scats were found, respectively, indicative of fox reestablishment on the Reduction area. On the Check woodlot foxes were observed often. Tracks were seen and scats were collected in every month. Pups were observed at a rearing den on the woodlot in August, 1973. Thus, although the Reduction Area was occasionally visited by immigrating gray foxes, control efforts reduced fox activity there to a level obviously lower than that on the Check Area.

Observations on the Check woodlot showed that for most of the year a gray fox family unit of three to five animals was utilizing the lot as part of a larger home range. The whole range covered approximately 125 ha, including four additional woodlots and the brushy fencerows connecting them.

Results from analysis of 224 scats are shown in Table 1. The analysis was not extensive, but was performed primarily to determine the importance of woodmice in the fox diet. Scats were picked apart and items from each general category were segregated in the dry condition for determination of percent frequency of occurrence. General categories from the entire sample were then pooled and measured by volume displacement. By frequency the most important general categories on an annual basis were arthropods (64.7%) and fruits (66.0%), although the specific composition of these categories changed drastically with the seasons and no item was a staple. Furthermore, these two categories together comprised only 26.0% of the annual volume. The only dietary staples were determined to be cottontail rabbits (*Sylvilagus* sp.) and rodents. Rabbit remains occurred in 23% of the scats and were the most important item by volume (30.6%). Rodents were eaten more often (38%), but made up less of the volume (12.2%). Approximately 90% of the rodent remains were from woodmice. Poultry remains did not occur often, although they were readily available. It should be noted that 60% of these scats came from a single family unit of foxes, and that dietary analysis of a larger series of scats from many foxes might alter the picture considerably.

Table 1. Gray fox seasonal and annual food habits as revealed by analysis of 224 fecal samples. Seasonal sample sizes are in parentheses.

Food Type	*Seasonal % Frequency of Occurrence*				*Annual % Frequency*	*Annual% Volume*
	M-A-M (42)	*J-J-A (76)*	*S-O-N (49)*	*D-J-F (57)*		
Mammals[a]	76.2	42.1	53.1	75.4	59.4	58.1
. . . Rodents	42.9	22.4	42.8	52.6	38.3	12.2
. . . *Peromyscus*	35.7	21.1	30.6	47.4	32.1	11.8
. . . Lagomorphs	21.4	21.0	32.6	19.3	23.2	30.6
Arthropods	64.3	94.7	77.6	14.0	64.7	10.1
Fruits	33.3	90.8	63.3	59.6	66.0	15.9
Plant Parts	19.0	26.3	16.3	8.8	18.3	6.4
Reptiles, Amphibians	11.9	7.9	4.1	1.7	6.2	1.8
Birds[b]	2.4	2.6	8.2	0.0	3.1	trace
Poultry	4.8	9.2	2.0	0.0	4.4	1.1
Miscellaneous[c]	16.7	21.0	26.5	21.1	21.4	4.7

[a] Includes remains of livestock, probably carrion.
[b] Excluding poultry.
[c] Paper, dirt, metal, and uncategorized material.

Results from three periods of live trapping sympatric carnivores are shown in Table 2. There were no significant changes following fox control in relative numbers of opossums *(Didelphis marsupialis)*, raccoons *(Procyon lotor)*, or striped skunks *(Mephitis mephitis)*, although skunks did increase slightly as revealed by field signs. Among weasels *(Mustela frenata)*, however, the impact of fox control was dramatic. Weasels irrupted to a significant level ($G = 20.69$, $P < 0.01$) on the Reduction woodlot and two nearby lots. This increase was confirmed in several snow sign indices. At first this phenomenon was thought to represent a numerical response to irrupting mice. However, when no corresponding increase was noted among mice, it was decided that weasel numbers probably rose in the absence of competition with (or control by) foxes. In the postcontrol period of August, 1974, after gray foxes had reestablished a population on the Reduction Area, weasels were no longer captured and none of their signs were apparent. It appeared that the returning foxes had eliminated them, although this was never documented. The irruption of weasels invalidated attempts to determine whether or not foxes could control rodents in a density-dependent fashion. However, it added the new dimension of a "replacement" predator assuming the role of a removed species. Hence, rodent population dynamics during fox control were affected not only by a reduction in predatory pressure by foxes, but also by an increase in pressure by weasels. Other predators such as raptors and snakes may also have exerted added pressure, but data on these species was unavailable.

Table 2. Sympatric carnivores captured on or near test woodlots during autumnal predator enumeration in 1972 (precontrol), 1973 (control), and 1974 (postcontrol).

	Reduction Woodlot			*Check Woodlot*		
Total Catch	*1972*	*1973*	*1974*	*1972*	*1973*	*1974*
Striped skunk	1	2	2	1	2	3
Raccoon	0	0	0	2	0	0
Opossum	2	3	3	3	1	3
New York weasel[a]	3[b]	11[c]	0	1	0	2
Total catch	6	16	5	7	3	8

[a] Weasel catch pooled from two additional woodlots to increase sample size.
[b] Includes one least weasel *(Mustela rixosa)*.
[c] Increase significant ($G=20.692$, $P < 0.01$ with Yates' Correction).

Rodent Population Ecology

In a total of 9,042 trapnights of rodent trapping, 631 small mammals were captured on the study areas. During 14 months of demographic study on the woodlots, 417 individual rodents and shrews were captured 1,369 times. On the assessment traplines and in postcontrol grid work 214 small mammals were captured.

The most abundant small mammals on the farms were woodmice and short-tailed shrews *(Blarina brevicauda)*, with 331 and 161 individuals recorded. The shrews usually died in traps. Meadow mice *(Microtus pennsylvanicus)* and pine voles *(M. pinetorum)* were rare in 1972, but increased slightly through 1973 and 1974 on both farms. Chipmunks *(Tamias striatus)*, juvenile gray squirrels *(Sciurus carolinensis)*, and smaller shrews *(Sorex* spp.) were occasionally caught, but small Sherman traps are not efficient for valid sampling of these species. Only woodmouse populations could be effectively analyzed.

It is believed that most all large woodmice on or near each grid were captured in every period because several traps were always available to each mouse, and because mice did not skip periods. Many researchers have reported that all trappable woodmice can be captured within a week (Stickel and Warbach, 1960). Mice were divided into three age classes on the basis of pelage as suggested by Snyder (1956). Very joung juveniles are sometimes too light to activate a trap fulcrum; thus only adults and subadults were included in the analysis of age structure.

Woodmouse density and structural parameters were never significantly different within a woodlot. Density was greatest on the brushy grids during winter, but it was greater in mature woods during the growing seasons of herbaceous ground flora. Therefore results from within each woodlot were pooled for subsequent statistical comparisons.

At the start of the study in October, 1972, woodmouse populations were similar on the two woodlots. Raw estimates were 12.9±4.6 mice per grid on the Check Area and 12.8±7.0 per grid on the Reduction Area (Table 3). The mean movement or "av.D." (Brant 1962) of mice between successive captures was 27.2m on the Check grids and 29.8m on the Reduction grids (Table 4). Previous studies have shown that grid trapping tends to overestimate density because many mice occupy home ranges lying partly outside the grid (Brant 1962). The true or adjusted density was computed after adding a boundary strip equal in width to ½ mean av.D. around the perimeter of each 1 ha grid. This was the effective sampling area. A new av.D. was computed for each period; thus density estimates were not invalidated by seasonal or other changes in range size. Adjusted density at the start was determined to be 7.8 per ha on the Check grids and 7.7 per ha on the Reduction grids (Table 5). Sex and age structures were also similar on the two woodlots at the onset (Table 6).

Table 3. Population estimates of woodmice inhabiting each grid area. Values are Lincoln Index estimates ±2 S.D.

	Check Woodlot		*Reduction Woodlot*	
Trapping Period	*Woods Grid*	*Brush Grid*	*Woods Grid*	*Brush Grid*
October, 1972	12.86±4.64	NA	12.80±7.00	NA
December, 1972	14.67±5.84	NA	11.43±3.02	NA
January, 1973	23.50±7.58	26.83±5.86	8.00±0.00	11.67±3.62[a]
March, 1973	11.67±8.52	16.87±3.98	10.80±3.98	11.00±3.12
May-June, 1973	12.00±6.96	21.64±8.02	13.33±5.44	10.80±3.94
August, 1973	16.33±5.56	18.57±9.54	12.85±5.56	11.20±5.36
November, 1973	13.33±6.88	15.00±4.66	11.25±8.38	10.28±2.76
August, 1974	10.86±5.18	12.80±7.00	11.00±7.80	14.33±8.81

[a] Differences significant at 0.05 level.

Table 4. Mean distance moved by woodmice between three or more successive recapture sites.[a]

Trapping Period	*Check Area (m)*	*Reduction Area (m)*
October, 1972	27.2	29.8[b]
December, 1972	25.8	28.0[b]
January, 1973	18.6	25.5
March, 1973	17.7	31.8
May-June, 1973	13.9	21.9
August, 1973	22.1	30.2
November, 1973	25.9	30.1
August, 1974	25.5	27.5[b]

[a] This is the parameter "av.D." of Brant (1962). A boundary strip equal in width to ½ mean av.D. is added to grid area to find area sampled.
[b] Not significant. These periods represent precontrol and postcontrol.

Table 5. Estimated density per ha of woodmice on the Reduction and Check Area woodlots.[a]

Trapping Period	*Check Area*	*Reduction Area*
October, 1972	7.8	7.7
December, 1972	9.1	6.8
January, 1973	18.2	6.1[b]
March, 1973	10.1	6.5
May-June, 1973	13.4	8.0
August, 1973	11.5	[illegible]
November, 1973	8.7	6.2
August, 1974	7.5	7.1

[a] Estimates derived from raw grid results (Table 3) applied to the parameter av.D. (Table 4).
[b] Significant at 0.05 level.

Table 6. Sex and age structure of woodmouse populations on live-trapping grids.

Trapping Period		Check Area			Reduction Area		
		No. Mice	% Subadults	Sex Ratio	No. Mice	% Subadults	Sex Ratio
O	72	12	50.0	7:5	11	54.5	6:5
D	72	13	53.9	7:6	11	36.4	6:5
J	73	46	49.8	1:1	19	41.5	9:10
M	73	25	09.4	13:12	21	71.4[a]	10:11
M-J	73	29	48.9	14:14	22	68.4[b]	9:13
A	73	32	59.4	17:15	22	72.5[b]	8:14
N	73	27	51.6	14:13	20	65.0[b]	7:13
A	74	23	43.5	10:13	26	46.2	14.12

[a] Significant at 0.01 level.
[b] Significant at 0.05 level.

On the Check lot, woodmouse numbers fluctuated in an annual cycle typical of intermediate latitudes (Stickel and Warbach 1960). Density was greatest in early winter (18.2 per ha) and lowest in autumn (7.8 per ha), with a similar but smaller peak and dip in early summer and spring, respectively (Table 5). Maxima were attributed to two seasonal breeding peaks, one in late summer or fall and one in spring. A majority of adult females were pregnant or lactating only during March, August, and October trapping periods (Table 7).

Table 7. Percentages of females pregnant or lactating during live trapping periods on the woodlot grids.

Trapping Period	Check Area		Reduction Area	
	No. Females	%	No. Females	%
October, 1972[c]	5	80.0	5	60.0
December, 1972	6	0.0	5	20.0
January, 1973	23	4.3	10	50.0[a]
March, 1973[b]	12	75.0	11	81.8
May-June, 1973	14	28.6	13	84.6[a]
August, 1973[c]	15	53.3	14	92.9[a]
November, 1973	13	38.5	13	92.3[a]
August, 1974[c]	13	61.5	12	66.7

[a] Differences significant at 0.05 level.
[b,c] Represent normal breeding seasons of woodmice in upland Virginia ([c]=autumn upsurge, [b]=spring upsurge).

Several woodmouse population parameters were unaffected by fox control; others were altered significantly. The general annual cycle of minima and maxima was similar on both areas, although on the Reduction Area peaks were damped after January, 1973 (Tables 3 and 5). Contrary to original expectations, rodent numbers were reduced in the absence of foxes. Numbers were noticeably lower thoughout the 14-month fox control period. However, density was significantly lower ($G = 3.85$, $P < 0.05$) only during the January, 1973, trapping period when the Check lot population rose to 18.2 per ha compared to only 6.1 per ha on the Reduction lot (Tables 3 and 5). Since this occurred about three months after the initial trap-out of foxes, it is suggested that the initial irruption of weasels probably occurred at this time, bringing heavy predatory pressure on woodmice. Since weasels were not trapped at this time there was no quantitative data to support this conclusion. However, field observations during January snows provided evidence that weasels were more abundant on the Reduction Area than on the Check Area. An increase in weasel signs was also noted on three other woodlots on the Reduction farm. Skunk signs also increased, although trapping results indicated no change in their number.

The major differences between the two areas were noted in demographic measurements. Following the initiation of fox control, significant alterations appeared in reproductivity, sex ratios, age structure, and longevity of woodmice.

On both areas more than half the females of reproductive age were pregnant or lactating during the normal breeding upturns of autumn and early spring. However, a consistently high percentage of females remained in reproductive condition year round on the Reduction woodlot (Table 7). Differences were significant ($P < 0.05$) in all months where mice were normally non-reproductive. Further evidence for this change in reproductivity was observed in the presence of numerous small, gray juveniles on the Reduction woodlot throughout winter. Also, a significantly higher percentage of this population occurred as subadults in all months after January, 1973 (Table 6).

Shifts in the adult sex ratio became apparent in the spring of 1973. Following the initiation of fox control there was a gradual shift toward more females in the population. This could have represented a shift in primary or secondary sex ratios, or it could have resulted from added mortality among males. Differences were not significant (Table 6), although they were apparent.

The most dramatic changes following fox control occurred in age structure and longevity of woodmouse populations. Subsequent to the January, 1973, crash of Reduction Area mice, the population was composed largely of subadults. During the same periods most Check Area mice were adults (Table 6). This measurement, along with year round breeding, suggested that a more rapid population turnover was occurring on the Reduction Area in the absence of fox predation. The best evidence for added predation in the absence of foxes came from longevity calculations, which were prepared following the methods of Snyder (1956). Longevity estimates are often invalid because researchers fail to distinguish between mortality and emigration from the study area. However, the woodlots in this study were "islands" and migration into and out of them was measured (by assessment lines) to be negligible. Therefore disappearance from a woodlot was considered to be synonomous with death. All mice which were in the post-juvenile molt (40-49 days old) at first capture were followed in subsequent trapping periods until they disappeared from the population. Disappearance was assumed to have occurred 30 days (½ interval) prior to the first period of non-recapture. The addition of the 45-day juvenile period to each individual's residency estimate provided mean estimates of cohort life expectancy of 4.60 months on the Check woodlot and 3.38 months on the Reduction woodlot. Residency on the respective lots was 3.10 months and 1.68 months. These estimates apply only to those mice which survived to 45 days (Figure 1). Further evidence was seen in the mean carryover rate (percentage of a period's catch which was recaptured in the next period) which was 49.8% on the Check Area compared to 30.8% on the Reduction Area.

Table 8. Numbers of woodmice captured on removal traplines during autumnal snap-trap assessments in 1972 (precontrol), 1973 (control), and 1974 (postcontrol).

	Reduction Area			*Check Area*			*Poultry-free Area*		
Category	*1972*	*1973*	*1974*	*1972*	*1973*	*1974*	*1972*	*1973*	*1974*
Total catch	15	14	12	16	16	14	13	12	12
No. males	9	6	7	8	9	6	7	6	5
No. females	6	8	5	8	7	8	6	6	7
No. subadults	0	6[a]	1	0	2	2	0	2	1
% subadults	0.0	42.8[a]	0.0	8.3	0.0	12.5	0.0	16.7	8.3

[a] Significant at 0.05 level (RxC test of independence).

Results from the three removal traplines tended to verify measured differences in sex and age structure on the live trapping grids (Table 8). A preponderance of females and subadults following fox removal occurred here also. Confirmed also was the finding that woodmouse density remained essentially unchanged following fox control. Results from the third farm (with no poultry) were similar to the Check Area results in all respects ($P > 0.05$). This suggests that the presence or absence of poultry does not affect the fox-woodmouse interaction, although sample sizes were too small to draw valid conclusions on this point. In dissected reproductive females, litter size (or placental scars) did not vary significantly from 4.1 embryos per female on either area.

In the postcontrol period of woodlot live trapping (August, 1974), all measurements except longevity were made for comparison with 1972 and 1973 values. Although data were available for only one month of postcontrol, all data were derived through time periods and methods which were identical to those used during precontrol and control. Since control and precontrol results were not charted cumulatively, results from the postcontrol month can be justifiably compared with any other month and conclusions can be validly drawn. Following the end of fox control, several parameters returned to near precontrol levels. Significant differences were no longer noted in density (Tables 3 and 5), movement (Table 4), sex and age structures (Table 6), or in any values on the removal traplines (Table 8). It appeared that woodmouse populations had recovered to near normal conditions within 9 months after foxes were allowed to return to the Reduction woodlot.

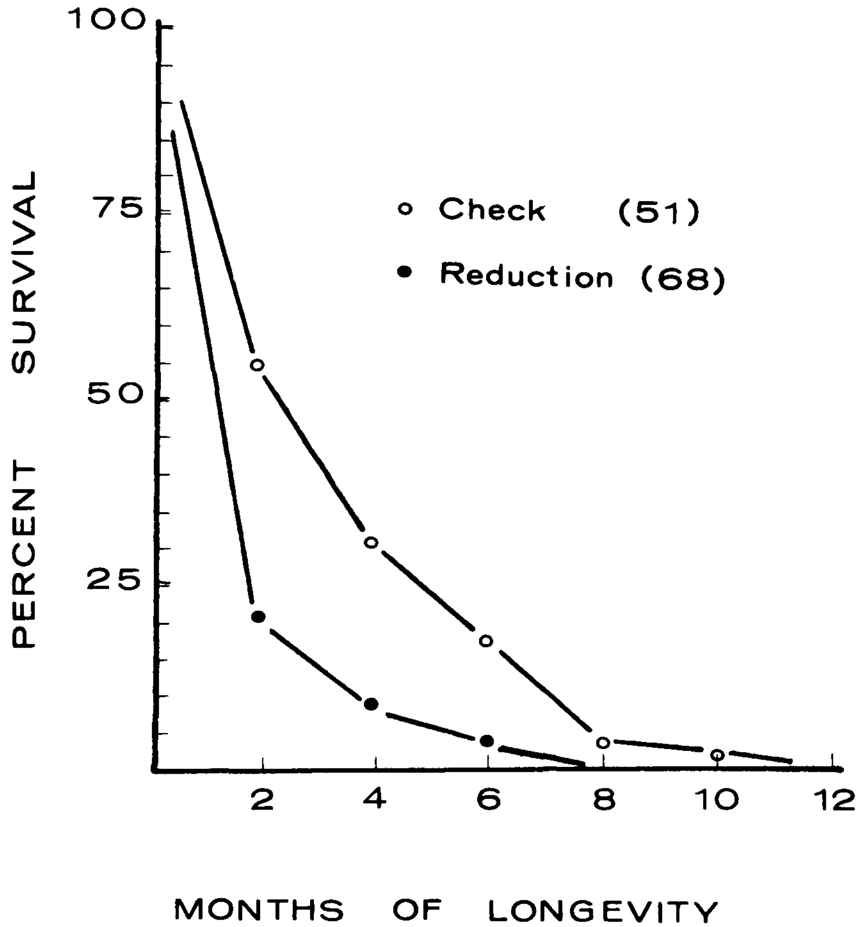

Figure 1. Longevity of woodmice on the Reduction and Control woodlots. All mice used in this calculation were of known age (40-49 days) at initial capture. Numbers in parentheses are sample sizes.

DISCUSSION

This study involved a complex relationship between gray foxes and woodmice, between weasels and woodmice, between foxes and weasels, and possibly between other species which were not captured in numbers sufficient for adequate study.

No evidence was found to indicate any possibility of rodent "explosions" as have been predicted by some writers who advocate an end to predator control. The ultimate effect of fox control on woodmice was to suppress their populations. It would appear that rodent levels should have increased rather than decrease if the gray fox really were a significant predator, especially since scat analysis showed that local woodmice were indeed important food items. A reasonable explanation for such a paradox lies in the observed irruption of weasels which occurred on the Reduction Area after the initiation of intensive fox control measures. The initial time of the irruption is unknown, since sympatric carnivore populations were not remeasured until 9 months of fox control had elapsed. However, circumstantial evidence sets the time at approximately 3 months after the initial trap-out of foxes, just prior to the crash of woodmouse populations on the Reduction Area grids.

Several reserchers have suggested that an antagonistic relationship exists between foxes and weasels. Latham (1952) used Pennsylvania bounty records to show an inverse relationship between numbers of foxes and weasels turned in for bounty over a number of years. He suggested that foxes are able to reduce and control weasels. Several researchers of fox food habits, including Errington (1935, 1967), Scott (1947), and Swink (1952), have reported scattered occurrences of weasel remains in fox stomachs or scats. Scott and Klimstra (1955) found weasel remains, often uneaten, in or around many fox dens. Although weasel remains did not occur in any of the 224 scats examined in this study, an uneaten weasel carcass was found near a rearing den on the Check woodlot. On the Check farm weasel numbers appeared to have remained consistently low in all three years. However, on the Reduction farm their numbers fluctuated from low in 1972 (precontrol), to very high in 1973 (control), to absence in 1974 (postcontrol). It seems likely that foxes were controlling weasels in this study.

There is little in the literature with which to compare the observed weasel irruption. Robinson (1961) determined that there was an increase in numbers of smaller predators following coyote control. During 20 years of predator control, a gradual upward trend was noted among bobcats, skunks, badgers, and raccoons. All these species were unavoidably captured by the coyote removal techniques. Such was not the case in the present study. Neither small Sherman traps nor "dirt-hole" or "scent-post" fox sets allow the efficient capture of weasels, and had not a specific attempt been made to enumerate smaller carnivores, the weasel phenomenon would have gone unnoticed. It is suggested that future research involving predator removal should include attempts to ascertain whether a secondary predator species is assuming any part of the removed predator's role. Otherwise an impact or a lack of impact resulting from predator removal is assumed where it may not really occur.

The woodmouse longevity, carryover, and age structure computations all showed a clearly defined decrease in life expectancy on the area under intensive fox control. This can be explained best by added weasel predation. Year round breeding, which provided for increased fecundity, apparently was the innate mechanism by which the Reduction woodlot population retained its consistent high density. The inordinate stability of wild *Peromyscus* populations has long been an enigma (Terman 1968), and it is suggested that differential fecundity may be largely responsible. The sex ratio shift was probably not an innate mechanism. It was more likely the result of higher male mortality, since males usually have large home ranges and suffer more random encounters with predators.

Several other researchers have studied rodents following predator removal. Byers (1974) removed skunks to measure the effects of nest predation on the nesting success of blue-winged teal. He reported a significant increase in shrews and voles. Beasom (1974) removed various carnivores to see if removal improved reproductive success of game birds and deer. He also trapped mice and reported no significant change in density as a result of control. Trautman, Fredrickson, and Carter (1974) removed foxes in a long term study of predation upon pheasants. They reported no abnormal increase in rodents following control. Turcotte (1947) caused a heavy reduction in a population of red and gray foxes to study possible benefits to quail and rabbits. He performed some rodent trapping and claimed that foxes controlled rodents, but he offered no quantitative evidence. These studies and other similar ones have employed extensive and valid techniques to analyze populations of predators and game prey. However, to analyze rodent populations they have employed only brief censusses which provide no more than an estimate of simple density. In terms of rodent density, those previous studies were mostly in agreement with the present one in that rodent numbers were not altered by fox control. However, this brings up another point concerning interpretation. In the present study, woodmouse population dynamics were greatly affected by the removal of foxes, in spite of the fact that density remained essentially unchanged. This effect was measured as significantly altered sex and age structures, longevity, and reproductivity. This exposes an important and often overlooked fallacy inherent in measuring only the density parameter.

Apparently weasels are more efficient as mousers than are foxes. This seems logical in that weasels can pursue woodmice into hiding places, and in the fact that their hunting efforts are more concentrated in space and time. If weasel irruptions are documented on other fox control areas in future studies, the phenomenon should be integrated into management considerations. Large numbers of weasels might prove to be desirable in situations where rodents cause heavy economic loss. However, on farms where weasels could gain access to young poultry, farmers might expect to suffer greater losses to weasels than to foxes.

CONCLUSIONS

Limited food habits data suggest that gray foxes are significant predators upon woodmice. Importance of major food categories in order of decreasing volume was mammals (especially rabbits and woodmice), fruits, arthropods, and parts of green plants. All other categories, including poultry, were of negligible importance.

In apparent response to the intensive control of gray foxes, weasel numbers increased significantly ($P < 0.05$). No rodent irruptions were measured in the interim. In apparent response to increased predatory pressure by weasels, several aspects of woodmouse population ecology were significantly altered. Density fell sharply ($P < 0.05$) and then quickly recovered to near normal levels, remaining consistently high for the duration of the study. Average movement of mice increased slightly, carryover rate between trapping periods decreased ($P < 0.05$), mean longevity of mice was reduced markedly ($P < 0.05$), adult and subadult sex ratios shifted toward a greater percentage of females, age ratios shifted toward a greater percentage of subadults ($P < 0.05$), and a much larger percentage of females remained reproductive year round compared to normal seasonal breeding. Demographic analysis of the woodmouse populations indicated that the enlarged weasel population exerted more predatory stress upon woodmice than did the original fox population. This study apparently represents the first documented case wherein a sympatric predator species has assumed the predatory role of a removed species. Management implications are that predator removal studies may be invalid where sympatric carnivores are ignored or where simple prey density is the only parameter utilized in determining the impact of predator management.

Although this study was not designed to reach a judgment concerning the merits of predator management, several of the following conclusions bear on the question. There was no evidence that fox control affected rodent numbers, although the general dynamics of rodent populations appeared to have been altered as an indirect result. There was good evidence that fox control measures were responsible for a significant increase in at least one species of sympatric carnivore. Apparently, mammalian population dynamics in upland Virginia woodlots are sufficiently complex so as to absorb these alterations with minimal obvious impact. Changes in numbers of sympatric carnivores can be considered beneficial or unfavorable, depending upon local conditions.

This study was deficient in that it was limited in duration and in replications. As such it is primarily adequate only for formulation of hypotheses. It is suggested that other such studies be initiated. Future research, where funds permit, should employ stronger baseline data, more replications, and a longer time period.

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