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The Effect of Exploitation on Some Parameters of Coyote Populations

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THE EFFECT OF EXPLOITATION
ON
SOME PARAMETERS OF COYOTE POPULATIONS

by

Robert P. Davison

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Wildlife Science

Utah State University
Logan, Utah

1980

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Robert P. Davison

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ABSTRACT

The Effect of Exploitation on Some Parameters of Coyote Populations

by

Robert P. Davison, Doctor of Philosophy
Utah State University, 1980

Major Professor: Dr. Frederick F. Knowlton
Department: Wildlife Science

The study was conducted to examine the effect of exploitation on population parameters of coyotes (*Canis latrans*). Hypotheses tested were: (1) Substantial levels of exploitation do not change spring and fall coyote densities significantly; (2) Coyote recruitment (reproduction and immigration) rates are unaffected by substantial levels of exploitation; (3) Annual coyote survival rates are not related to intensity of harvest rates; (4) Coyote emigration rates remain unchanged by substantial levels of exploitation. Coyote demographic parameters were measured from 1975 to 1978 for a treatment population subject to substantial exploitation (Curlew Valley, Utah and Idaho), and for an unexploited to lightly exploited control population (Idaho National Engineering Laboratory, INEL). Treatment and control populations were about 100 km apart on environmentally similar areas. Availability and utilization of prey also were similar for the two populations, with the major difference being in the type of lagomorph consumed.

Relative spring densities, estimated by scent station indices, increased for both populations over the study period. Relative fall densities in the two areas were estimated by scent station lines, scat indices, and catch-effort indices and increased from 1975 to 1976, but were relatively constant thereafter. Estimates of absolute fall density from isotope labeling of feces also were similar within each area for 1977 and 1978. Neither spring nor fall density estimates were significantly different between areas in any given year or overall.

Recruitment rates, as estimated from spring to fall increase in scent station visitation rates generally decreased over the study period, while estimates from age and sex structure of coyotes trapped in the fall increased for both populations over the study period. Estimated recruitment to fall populations (P_f) was consistently greater in Curlew Valley each of the four years, and overall was significantly greater than recruitment at the INEL. Spring to fall change in scent station indices was greater for Curlew Valley for all years except 1975.

Annual survival rates were estimated for adults and juveniles marked with transmitters and/or ear tags using methods of statistical inference from band recovery data. Estimated survival rates for adults and juveniles were constant over the study period for each population and did not differ significantly between populations. Estimates of adult and juvenile survival and/or recovery (mortality) rates were significantly different within the Curlew Valley and INEL populations.

Estimated hunting mortality rates for adults and juveniles remaining in the treatment population were 56 and 350 percent higher than similar estimates for the control population. Significantly higher in situ juvenile hunting mortality rates were associated with significantly lower nonhunting mortality and emigration rates. Emigration was not only greater from the control population, but it was distributed more evenly over the fall and winter.

The following conclusions resulted from the study. Exploitation (kill) rates were substantially higher in the treatment population as expected. Observed differences in fall-winter adult and juvenile in situ kill rates did not produce significant differences in spring or fall densities, or in annual survival rates. Recruitment rates were related directly to hunting mortality rates, while emigration rates were related inversely.

(153 pages)

INTRODUCTION

The dynamics of populations may be affected by a variety of influences. Most commonly these have been categorized as either extrinsic or intrinsic factors. Extrinsic climatic factors such as seasonal change in temperature, rainfall, and daily photoperiod produce effects on populations independent of density. Other extrinsic influences such as food supply, predation, and interspecific competition more commonly have been assumed to be related to density. Intrinsic influences include density-dependent mechanisms of behavior, physiologic stress, and genetics. Assessments of the relative importance of these factors (both extrinsic and intrinsic) have varied by species and circumstances.

Evidence of density-independent extrinsic influences has come chiefly from insect ecologists (Andrewartha and Birch 1954, Ehrlich and Birch 1967, Varley et al. 1973). They have found weather affects insects independently of density and may determine, but not regulate, population change (Varley et al. 1973).

It has been difficult to demonstrate the effect of the dynamics of one species on the dynamics of another. Frequently, evidence of exclusion is assumed to be an indication that one species has produced enough individuals to prevent the population of another species from increasing. Connell (1961) provided a well-documented example of the influence of interspecific competition in causing exclusion among several species of barnacles. Among coexisting species there is evidence that the densities of coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are inversely related (Robinson 1961, Linhart and Robinson 1972).

Intraspecific factors (extrinsic and intrinsic) that have been shown or proposed to influence the dynamics of populations include nutritional and behavioral mechanisms, physiological stress, and genetic changes. Lack (1954, 1966) suggested most birds, carnivorous mammals, and certain rodents were limited in numbers by food resources. Schultz (1964) found that fluctuations in primary production, forage quality, and decomposition rates were correlated with the lemming cycle. Keith (1974) and Keith and Windberg (1978) hypothesized that depletion of food resources by snowshoe hares (*Lepus americanus*) at high densities resulted in increased mortality rates and subsequent declines in density. Similar density-dependent responses to food supply have been shown for large ungulates (Sinclair 1974). Clark (1972) and Gier (1968) reported a positive relationship between food supply and reproductive performance in coyotes.

Wynne-Edwards (1962) has contended that populations are maintained within some upper and lower bounds in relation to available resources through behavior-induced dispersion. Communal displays and other social behavior were suggested as the means by which populations assessed their numbers relative to available resources. Adjustments in density were accomplished most expediently by dispersal.

Christian (1950) has proposed generally that mammalian density is influenced by a combination of behavioral and physiological changes. Christian and Davis (1964) found increased adrenal activity, and associated mortality and decreased reproduction in high density microtine populations. The important behavioral factor affecting adrenal function was the number of interactions between individuals, which presumably increased with density.

Chitty (1960) and others (Krebs et al. 1973) also assumed that intraspecific interactions increased as population densities increased, but that the associated mutual antagonism at high densities caused selective pressures (rather than phenotypic modification) for a change in the behavior and physiology of individuals. Several studies of genotypic differences in voles are consistent with the hypothesis that a behavioral polymorphism is an important influence in the dynamics of microtine populations (Tamarin and Krebs 1969, Gaines and Krebs 1971, Kohn and Tamarin 1978). Although large changes in gene frequency at certain loci occurred in association with population changes, the mechan-mechanism of the association remains unclear.

More generally, Brown (1975) has noted that agonistic behavior may influence the dynamics of populations through the effects of exclusion or subordination. Exclusion effects are most commonly caused by territoriality. Territorial behavior has been shown to play a role in maintaining stability of breeding bird populations (Brown 1969). Subordination effects may be physiological, as proposed by Christian (1970), or may result in dispersal as has been well documented for voles (cf Krebs and Myers 1974).

The evidence for the influence of predation on prey population levels is conflicting. Errington's (1956) work with territorial species such as bobwhite quail (*Colinus virginianus*) and muskrats (*Ondrata zibethicus*) led him to believe that much of predation is incidental to the dynamics of prey populations. The "doomed surplus" or "wastage parts" of a population created by the exclusion effects of territoriality were those portions with poor life expectancies irrespective of the level of predation. Thus, to Errington death from predation may be nullified largely by reduced losses to other causes or by accelerated reproductive output.

Errington (1963) did realize that species such as white-tailed deer "have social intolerances too weak to be much of a self-limiting factor" and may have population levels suppressed by predators. Mech (1977) and Hirst (1969) have demonstrated such suppression of ungulate populations by large predators, but Pimlott (1967) and Hornocker (1970) found large carnivore populations were unable to prevent their chief ungulate prey from increasing.

The role of predation in the population dynamics of lagomorphs and microtines apparently differs from the above cases. Wagner and Stoddart (1972) found that coyote predation had the greatest impact on low to moderate densities of black-tailed jackrabbit (*Lepus californicus*) populations, i.e., an inverse density-dependent relationship. Similar findings have been presented for snowshoe hare (Keith 1974) and voles (Pearson 1966). Factors other than predation were suggested by Wagner and Stoddart (1972) as being necessary to reduce jackrabbit populations at peak densities, although Stoddart (1978:33) more recently has reported that the "general trend of the observed jackrabbit 'cycle' can be accounted for by coyote predation."

The influences of exploitation and predation on the dynamics of populations are closely related (Anderson and Burnham 1976).

Errington (1956) noted that the impact of predatory man may be more severe than that of other predators.

Perhaps the most prevalent hypothesis regarding the effect of exploitation involves the concept of compensation. Errington (1945) generally is credited with being one of the first to propose the components of the compensatory hypothesis, which were discussed briefly above in regard to the influence of predation. Basically, Errington suggested that exploitation may affect birth processes (inversity) and death processes (compensating mortalities). Populations were considered to produce animals in excess of a carrying capacity (threshold of security) that operated primarily during the winter. Because these excess individuals could not be crowded within the security threshold, spring population levels tended to be constant and independent of previous fall density. Exploitation during the period in which the population exceeded the security threshold merely took animals that would have died of other causes (compensating mortalities).

Anderson and Burnham (1976:5) have stated an hypothesis of completely compensatory natural mortality as follows:

> Below a certain level of exploitation, populations are 'resilient' and exploitation does not decrease the annual survival rate of the population, i.e., nonhunting mortality rate decreased, thereby compensating for increased hunting mortality. Beyond this level, exploitation has a marked effect on annual survival.

Evidence that exploitation does not decrease annual survival rate has been provided for a variety of birds and small mammals, including woodchucks (*Marmota marmox*)--Davis et al. (1964), gray squirrels (*Sciurus carolinensis*)--Mosby (1969), scaled quail (*Callipepla squamata*)--

Campbell et al. (1973), mallards (*Anas platyrhynchos*)--Anderson and Burnham (1976), and bobwhite quail (Roseberry 1979).

Errington's (1945) principle of inversity is basically that of density-dependent production rates. Spring to fall gains were inversely related to spring densities. As a result, exploitation above a certain level may reduce survival and spring density but result in increased production rates. Evidence of compensatory natural mortality and inversity in wolves (*Canus lupus*) has been summarized by Mech (1970). Density-dependent responses in production as a response to exploitation also have been shown for coyotes (Knowlton 1972).

That the above hypothesized influences of exploitation may not be universal has been suggested for pheasants (*Phasianus colchicus*) by Wagner and Stokes (1968). While their findings supported the principle of inversity, they found that reduced fall populations resulted in lower densities the following spring, and that the effects of exploitation may be greater than hypothesized by Errington. Unfortunately, Eberhardt (1970) has raised serious questions about the validity of these findings. Nevertheless, in contrast to the annual surplus-inversity concept of exploitation, Wagner (1969) proposed a sigmoid hypothesis in which adjustments in mortality and/or production rates are unable to compensate completely for hunting losses within the same year those losses occur. Moreover, evidence that deaths due to hunting represent an additional component to the natural mortality of female elk (*Cervus canadensis*) has been presented by Kimball and Wolfe (1974, 1979). They found that the female mortality rate decreased with a decrease in the female harvest rate, and that population trends were correlated with the level of female harvest. Similar evidence of additive hunting mortality has been suggested for suppression of population size in marine mammals (Fowler, pers. comm).[1] Clearly, examples of additive hunting mortality may represent the effects of exploitation levels that exceed the resiliency of populations as defined by Anderson and Burnham (1976).

Undoubtedly, it would be incorrect to imply that any of the influences on population dynamics discussed above is alone responsible for significant demographic events. It seems likely that the degree to which population parameters and dynamics are affected by a given factor may vary, and that there may be considerable interaction among factors. The challenge in assessing the effect of any given influence, such as exploitation, is to isolate that influence from other environmental factors. The relative paucity of field studies directed toward this problem testifies to the difficulty of the challenge.

---

[1] Dr. Charles W. Fowler, National Marine Mammals Lab, Seattle, WA.

OBJECTIVES AND APPROACH

The overall objective of this study was to examine the effect of exploitation on population parameters of coyotes. A direct approach to this question requires monitoring density, natality and immigration, and mortality and emigration under different exploitation intensities (Connolly 1978).

To date the demographics of coyote populations have been studied independently over a wide geographic area under varying, but usually moderate to high, intensities of exploitation (Gier 1968, Clark 1972, Knowlton 1972, Knudsen 1976, Nellis and Keith 1976, Tzilkowski 1980). Although Knowlton (1972) was able to document population responses, particularly in reproduction, to varying intensities of control in Texas, often temporal, spatial, and methodological disparities among coyote demographic studies have hindered comparisons in which the effect of exploitation could be isolated from other environmental factors. The difficulties inherent in assessing the impact of exploitation on coyote populations from existing demographic studies have led several workers to approach the problem through the use of simulation models (cf Connolly 1978). However, estimates of parameters and of relationships among parameters in these models have been based on insufficient data, and emigration has not been considered.

As Hornocker (1972) and Wagner (1972, 1975) have pointed out, many of the present difficulties have resulted from the absence of a systematic approach in which specific hypotheses regarding the effects of exploitation are tested with an appropriate experimental design. This study represents such a systematic approach.

Formulation of Hypotheses

Numerous demographic analyses of coyote populations have reported high annual mortality rates despite environmental differences and varying intensities of exploitation (U. S. Fish and Wildlife Service 1978). Moreover, Knowlton (1972) and Robinson (1956) have shown coyote reproductive rates increase with the level of exploitation. It follows from these observations that exploitation may not reduce coyote densities for any appreciable length of time due to intercompensatory trends in rates of population gains and losses (Errington 1967). An initial null hypothesis tested by this study was as follows:

H1: Substantial levels of exploitation do not change spring and fall coyote densities significantly.

Density is the outcome of environmental factors (including exploitation) operating on rates of reproduction, immigration, mortality, and emigration. Because maintenance of a given density only requires recruitment and loss to be balanced on an annual basis, exploitation may influence coyote populations in ways that may or may not be apparent as changes in density. Whether coyote density is changed by exploitation probably depends on the compensatory capabilities within or between rates of recruitment and loss.

One possibility is increased mortality from exploitation may reduce populations and trigger density-dependent increases in reproduction and/or immigration. Such increases may or may not be of sufficient magnitude and immediacy to result in rapid return to original density. This possibility forms a second hypothesis tested by this study in conjunction with H1:

H2: Coyote recruitment (reproduction and immigration) rates are not changed by substantial levels of exploitation.

A second possibility is losses due to exploitation may merely supplant mortality that would have resulted from other causes (Wagner 1975). In this case, the hypothesis tested by this study is as follows:

H3: Annual coyote survival rates are not related to intensity of harvest rates.

Finally, if emigration rates are directly related to density, as suggested by Christian (1970), Krebs and Myers (1974), Lidicker (1975), and others, then temporary reductions in density due to losses from exploitation may result in decreased emigration. The corresponding null hypothesis was tested:

H4: Coyote emigration rates remain unchanged by substantial levels of exploitation.

Hypotheses H2, H3, and H4 test whether compensatory changes occur in rates of recruitment and loss as a result of exploitation. Hypothesis H1 tests whether these compensatory changes, if any, are of sufficient immediacy and magnitude to result in density remaining unchanged by exploitation.

Experimental Design

Coyote demographic parameters were measured for a treatment population subject to moderate to high exploitation, and for an unexploited to lightly exploited control population. The two populations were far enough apart (100 km) to be independent of one another, yet be found on environmentally similar areas (see study area descriptions).

Numerous studies have identified food as an important or even predominant factor in the regulation of coyote populations (Murie 1940, Robinson 1956, Gier 1968, Clark 1972, Nellis and Keith 1976). As a result, the density of rodents and lagomorphs as well as coyote feeding patterns were estimated for the control and treatment areas. Such estimates allowed for reasonable isolation of the effects of exploitation.

Tests of hypotheses H1-H4 were accomplished in part by specifying the following field objectives for comparison of the treatment and control populations:

1. Estimate relative coyote densities and trends semi-annually and absolute densities annually.
2. Estimate recruitment rates.
3. Estimate causes and annual distribution of mortality, and annual survival rates.
4. Estimate annual rates and timing of emigration.

The 10 percent significance level ($P = 0.10$) was used as the criterion for rejection of hypotheses H1-H4 as well as other related hypotheses.

METHODS

Study Areas

Curlew Valley

The Curlew Valley study area is located in Box Elder County, Utah and Oneida and Cassia Counties, Idaho (Fig. 1). The area comprises approximately 1650 km^2 and is nearly equally divided between Idaho and Utah. Hoffman (1979) has provided a detailed description of physiography, climate, vegetation, and vertebrate fauna. Similar descriptions also have been provided by Gross et al. (1974) and Knudsen (1976).

Briefly, about 60 percent of the study area lies within a semi-arid intermountain basin. Elevations within this basin range from 1280 m in the south to 1585 m in the north. The remaining portion of the study area includes the foothill regions of the Black Pine Mountains (maximum elevation 2680 m) to the west and the Subletts (maximum elevation 1947 m) to the north. Annual precipitation ranges from 180 to 420 mm. Snow depth usually does not exceed 30 cm within the basin, but may reach 80 cm in the foothill regions. Mean monthly temperatures range from -7°C to 23°C for January and July, respectively.

Vegetation is typical of the Northern Shrub Desert Biome. Hoffman (1979) has classified plant communities into eight habitat types. Approximately one-half of the study area is comprised of sage-annuals, with big sagebrush (*Artemisia tridentata*) as the dominant shrub.

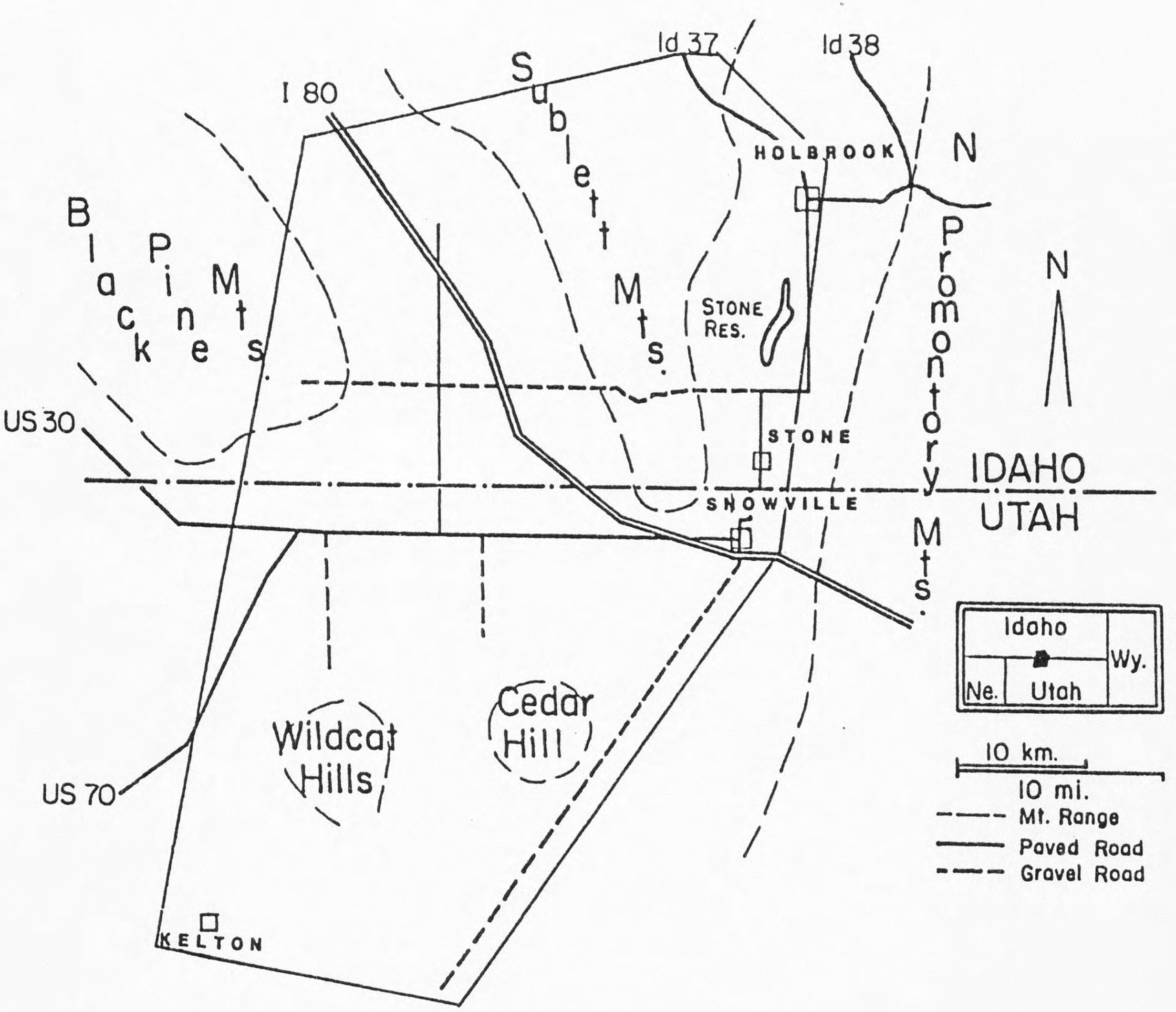

Figure 1. Map of the 1650 km^2 Curlew Valley study area, Utah and Idaho.

Over one-quarter of the area consists of crested wheatgrass (*Agropyron desertorum*), cultivated grains, and alfalfa. Juniper (*Juniperus osteosperma*) occupies approximately 10 percent of the area, with sagebrush-bunchgrass and shadscale types accounting for the remainder.

The principal mammalian fauna of the study area include blacktailed jackrabbit, mountain and pygmy cottontails (*Sylvilagus nuttalli* and *S. idahoensis*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), badger (*Taxidea taxus*), bobcat, and at least 20 species of rodents. Hoffman (1979) found that of the latter the deer mouse (*Peromyscus maniculatus*), pocket mouse (*Perognathus parvus*), least chipmunk (*Eutamias minimus*), and Ord's kangaroo rat (*Dipodomys ordii*) comprised more than 90 percent of the rodents caught in snap traps.

Roughly 57 percent (450 km^2) of the Utah portion of Curlew Valley is in private ownership. Private holdings in the Idaho portion of the valley constitute approximately 30 percent of the area under study. The remainder of the study area is public land administered by the Bureau of Land Management, with some minor holdings belonging to the state of Utah. Nearly 30 percent of the entire study area (Utah and Idaho) is subject to tilled agriculture. Much of the remaining area is grazed by cattle year-around and by sheep during winter (Utah) and spring (Idaho).

Aerial hunting of coyotes is conducted on public lands by the U. S. Fish and Wildlife Service to control depredations to livestock. In Utah, aerial hunting is conducted on private lands by private individuals with permission of the landowner and a permit from the Utah Department of Agriculture. In addition, various forms of sport hunting as well as trapping occur on public and private lands in Utah and Idaho. Neither activity is regulated by Utah nor Idaho.

INEL

The Idaho National Engineering Laboratory (INEL) National Environmental Research Park (NERP) is located in Bingham, Bonneville, Butte, Clark, and Jefferson Counties, Idaho, approximately 56 km northwest of the city of Idaho Falls. The study area comprises roughly 53 percent (1225 km^2) of the total area of the 2300 km^2 INEL site (Fig. 2). There have been several previous detailed descriptions of the site, including those describing flora (Atwood 1970), vegetation patterns (Harniss and West 1973), and more recently vegetation types and surface soils (McBride et al. 1978). Information on numerous ecological studies at the INEL also is available (cf Markham 1978).

The INEL site is located on the northern half of the Snake River Plain, along the foothills of the Lemhi and Lost River mountain ranges (maximum elevation 3147 m). Predominant physiographic features of the site include flows of relatively unweathered basalt 10,000 to 2,000,000 years old, and two buttes which originated from volcanic activity that rise 488 m (East Butte) and 427 m (Middle Butte) above the average elevation of 1524 m. Average annual precipitation is 18-20 cm. Precipitation occurs mainly in winter as snow and in early spring as rain. Mean annual temperature is approximately 5.5°C, but ranges from -16°C in January to 31°C in July.

Based on the classification scheme of McBride et al. (1978), the predominant plant associations of the study area are 1) *Artemisia*

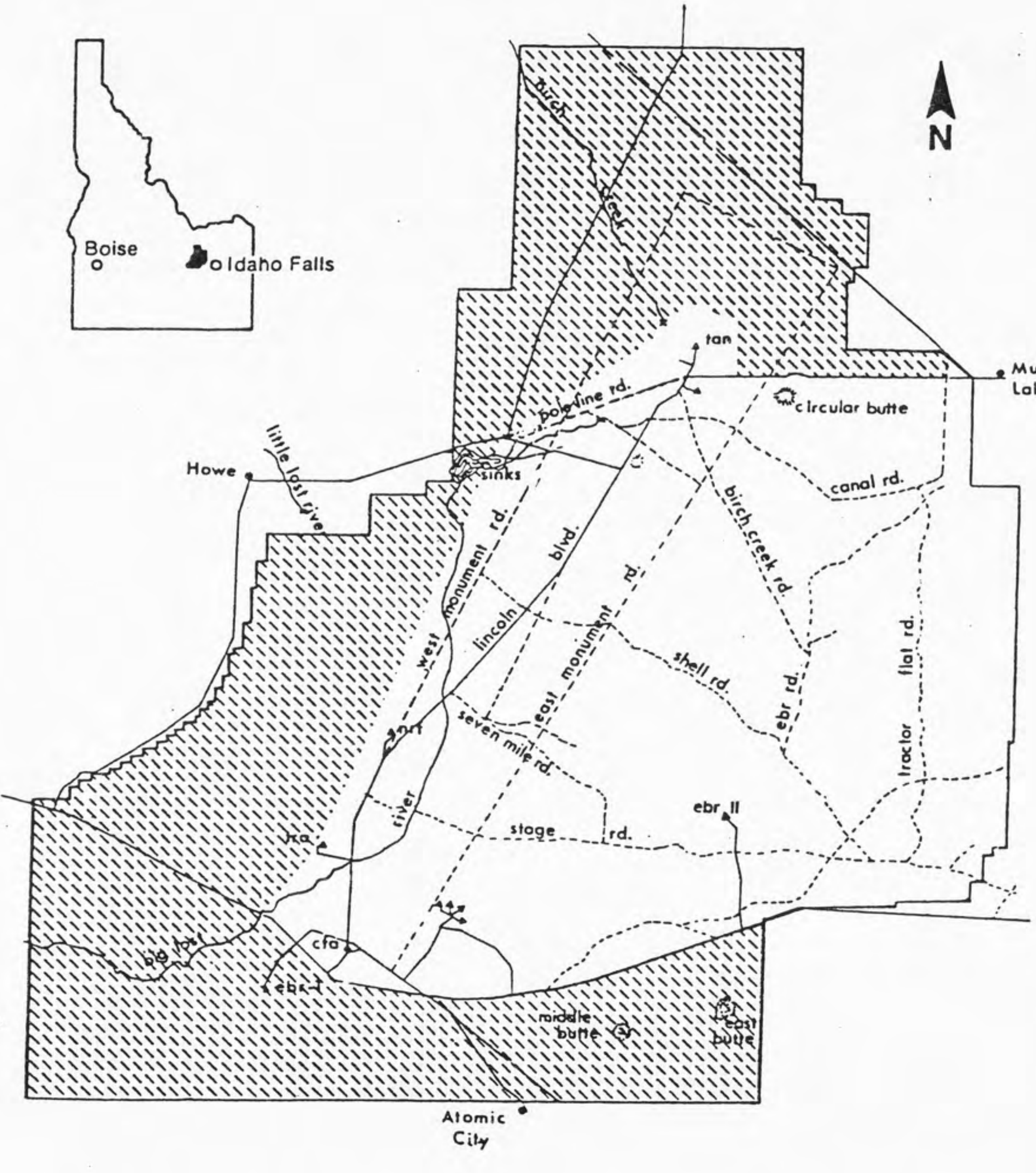

Figure 2. Map of the 1225 km^2 study area (unshaded) within the Idaho National Engineering Laboratory (INEL).

tridentata-Oryzopsis hymenoides-Stipa comata (35 percent), 2) *A. tridentata-Chrysothamnis viscidiflorus-Sitanion hystrix* (32 percent), 3) *A. tridentata-Agropyron dasystachum-S. comata* (13 percent), 4) *C. viscidiflorus-A. tridentata*-grass (10 percent). None of the study area is under cultivation, and perhaps 1 percent has been seeded to crested wheatgrass.

The principal mammalian fauna of the study area include black-tailed jackrabbit, pygmy and mountain cottontails, pronghorn, mule deer, badger, bobcat, and approximately 17 species of rodents. Using snap traps, Stoddart (1978) found the deer mouse, least chipmunk, Great Basin pocket mouse, Ord's kangaroo rat, and Townsend's ground squirrel (*Spermophilus townsendii*) were the five most abundant, or at least most easily trapped, rodent species. Sehman and Linder (1978) have provided information on the reptilian fauna of the INEL site.

Approximately 38 percent (460 km^2) of the INEL study area is subject to limited and infrequent aerial hunting by the U. S. Fish and Wildlife Service to control depredations by coyotes. Another 950 km^2 of the site adjacent to the study area on the west and southwest is grazed by sheep and cattle. Coyote removal to control depredations on this portion of the INEL site is somewhat more intensive, although still limited, and includes shooting, trapping, and aerial hunting. Individuals who graze livestock on the site also are permitted to take coyotes by shooting or trapping. As a National Environmental Research Park, the site is closed not only to aerial hunting, shooting, and trapping by the general public, but also to trespassing.

Estimation of Density

Relative Density

Scent Station Lines. Indices of relative abundance of coyotes on the two study areas were estimated by means of scent station lines as described by Linhart and Knowlton (1975) with some modifications. The unavailability of the standard fermented egg powder attractant (FEP) after 1975 necessitated the selection of a new standard attractant by the U. S. Fish and Wildlife Service (Roughton 1976). In accordance with this change in procedure, all scent station lines in this study run during 1976-1978 used a scent (FAS) synthesized from fatty acids found in the fermented egg attractant. Roughton (1976) reported this scent drew 9 percent more visits than the original standard. As a result, scent station visitation rates for 1975 were adjusted upward by 9 percent to permit comparison with subsequent years.

A second modification of the standard scent station lines resulted in stations being run for only one night. Analysis of scent station data from previous years indicated little information was gained after the first night (Davison unpublished data). In addition, it seemed likely the visits were not independent from night to night on a given line. Running scent stations for only one night also allowed more stations to be used at the INEL study area.

A final modification of the technique of Linhart and Knowlton (1975) was an increase in the density of stations. In the Curlew Valley study area (1650 km^2), 400 stations were run each of the four years of the study (1975-1978). In order to facilitate data collection, the stations were organized into eight lines located systematically along dirt roads in the area (Fig. 3). The 50 stations within each line were spaced at 0.5 km intervals. In 1975 and spring of 1976, 300 stations were run on the 1225 km^2 INEL study area. Thereafter, 500 stations were run at the INEL. As in Curlew Valley, the stations were grouped into six, and later ten, lines located systematically along dirt roads within the study area with stations placed 0.5 km apart (Fig. 4).

The scent stations in the two study areas were run concurrently, or as nearly so as possible. Estimates of relative abundance during the spring were obtained in May and early June (2 May to 6 June). Fall estimates were obtained in late August or early September (27 August to 5 September), with one exception (Curlew Valley, 17 October to 13 November 1975).

For purposes of analysis, each of the scent station lines run in Curlew Valley and the INEL was divided into five lines of ten stations. Thus, in Curlew Valley the mean proportion of scent stations visited was based on the proportion of the ten stations visited for each of 40 lines. At the INEL these proportions were based on 30 lines initially, then 50 lines. Differences in scent station visitations within and between study areas were determined with a non-parametric, two-sample randomization test (developed by R. A. Fisher) using a FORTRAN computer program, RANDTEST, written by Green (1977).

Scat Index. Relative abundance of coyotes also was estimated during the fall by collection of scats on dirt roads within each study area. In 1976, scat transects were located systematically within the areas on

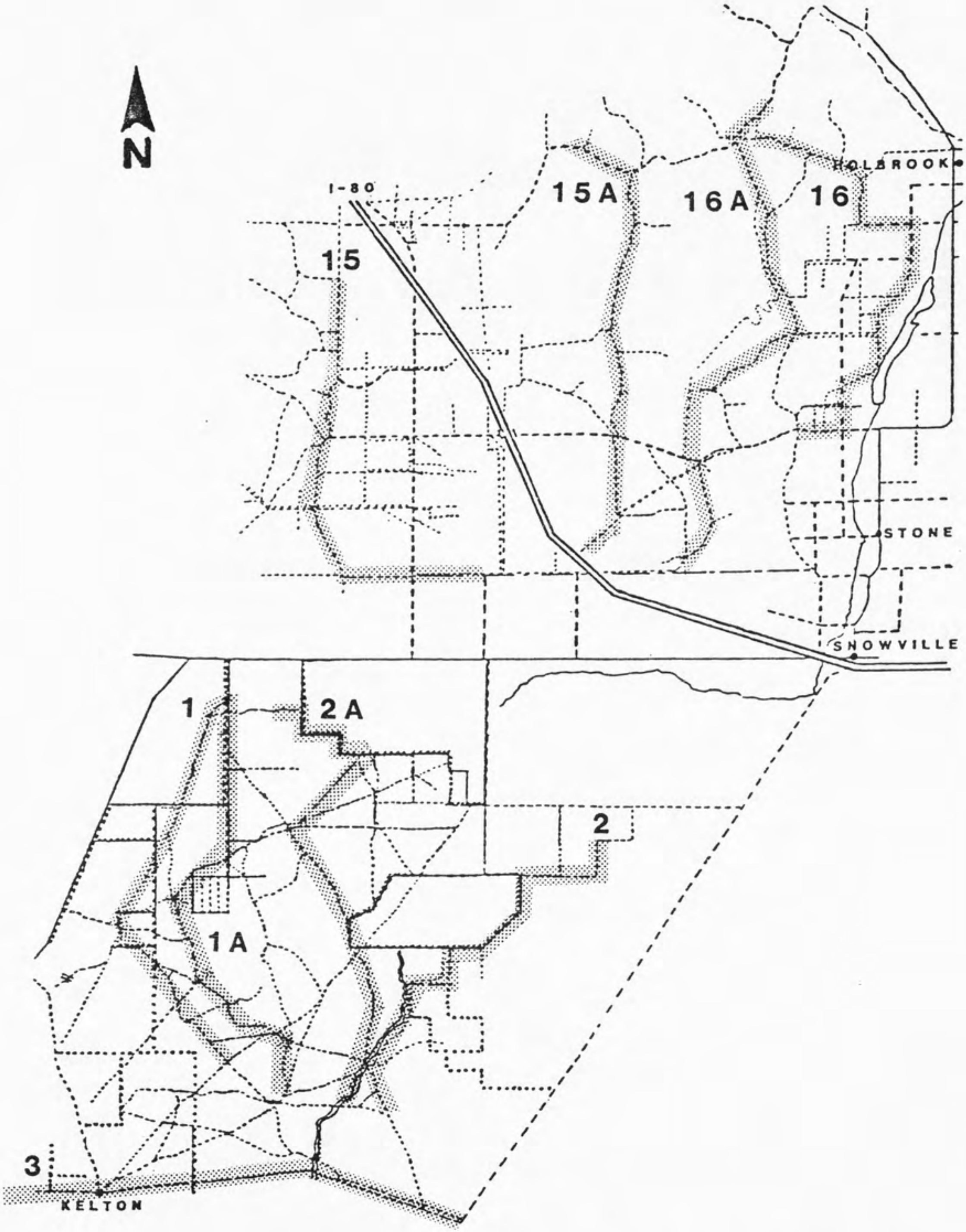

Figure 3. Location of scent station lines used to assess relative abundance of coyotes in Curlew Valley, 1975-1978. Line 1A was run only in 1975, and line 3 in all years except 1975. In fall 1976 scat transects were run on lines 15, 15A, 16, 1, 2, and 3.

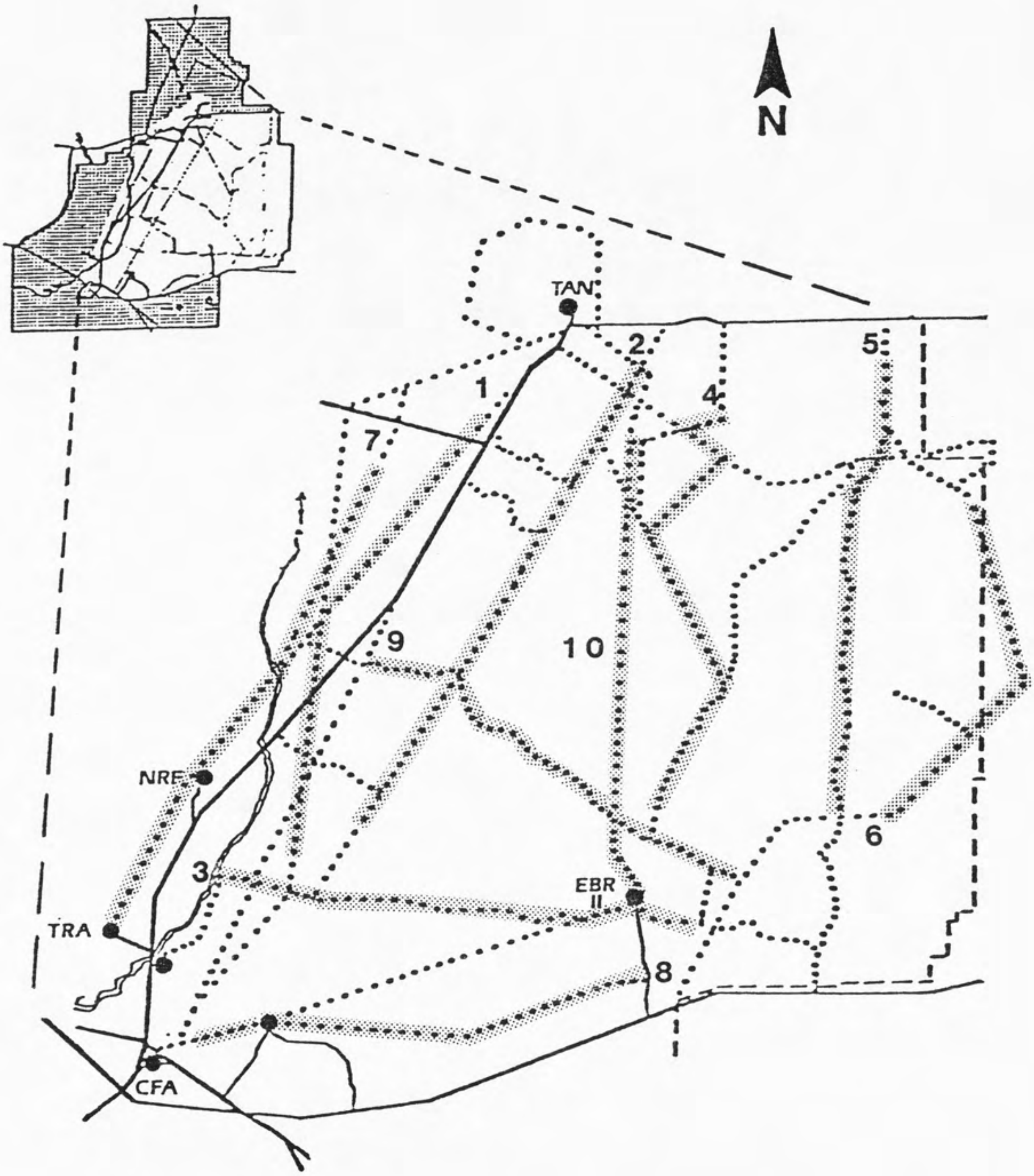

Figure 4. Location of scent station lines used to assess relative abundance of coyotes at the INEL, 1975-1978. Lines 7-10 were not run from spring 1975 through spring 1976. In fall 1976, scat transects were run on lines 1-6.

alternate 1.6 km (1.0 mi) lengths of scent station lines. Forty-eight transects were located on six of the eight scent station lines in Curlew Valley (Fig. 3) and at the INEL 46 transects were located on six of the ten scent station lines (Fig. 4). In 1977 and 1978, transects were located systematically within 1.6 km^2 (1.0 mi^2) sections that were selected randomly within each study area. Selection of sections in 1978 was independent of that in 1977. Transects were 1.6 km long, as in 1976, and were placed on the first nonpaved road that intersected the section boundary, when proceeding clockwise from the northwest corner of the section. Fifty transects were selected and run in Curlew Valley in 1977 and 100 in 1978 (Fig. 5). At the INEL, 35 transects were selected and run in 1977 (Fig. 6) and 101 in 1978 (Fig. 7).

Beginning and end points of transects were makred with flagging. Transect width varied with width of the road but was definable. A scat was defined as feces judged to have come from a single defecation. Transects were cleared of all scats in mid-October, with scat collections taking place 13-15 days later. In 1976 and 1977, a second collection was made approximately two weeks after the first. Clearing and collection of scats was accomplished by an observer who rode on the hood of a truck which was moving at about 10 km/hr. Each scat collected was placed in an individual paper bag labeled with the area, date, and transect number.

The scat index value computed for each study area was the mean number of scats collected per transect (1.6 km) per 14-day period. Differences between the scat index value for Curlew Valley and INEL, and

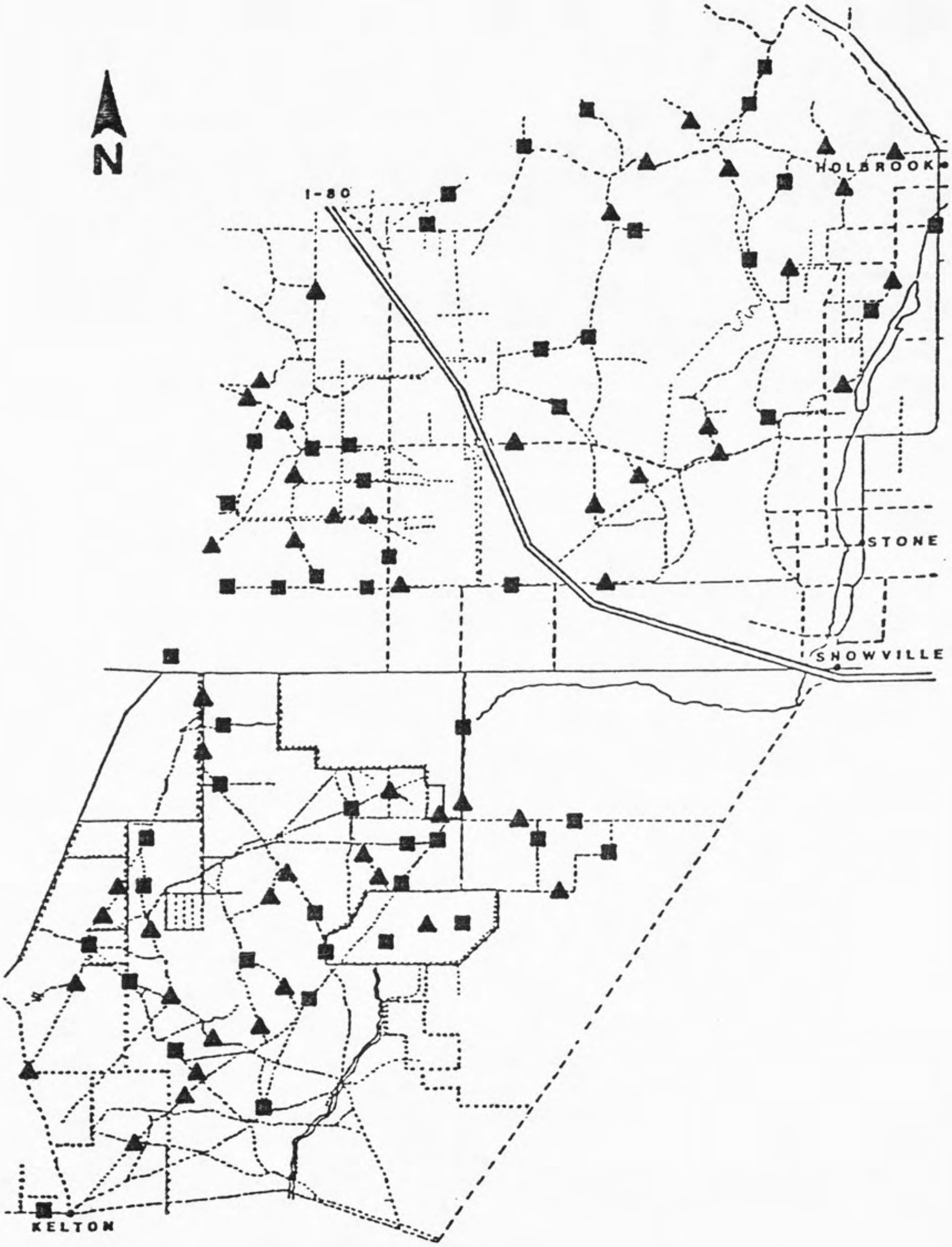

Figure 5. Location of 1.6 km scat transects used to assess relative abundance of coyotes in Curlew Valley. Fifty transects were run in fall 1977 (triangles), and 100 in fall 1978 (triangles and squares).

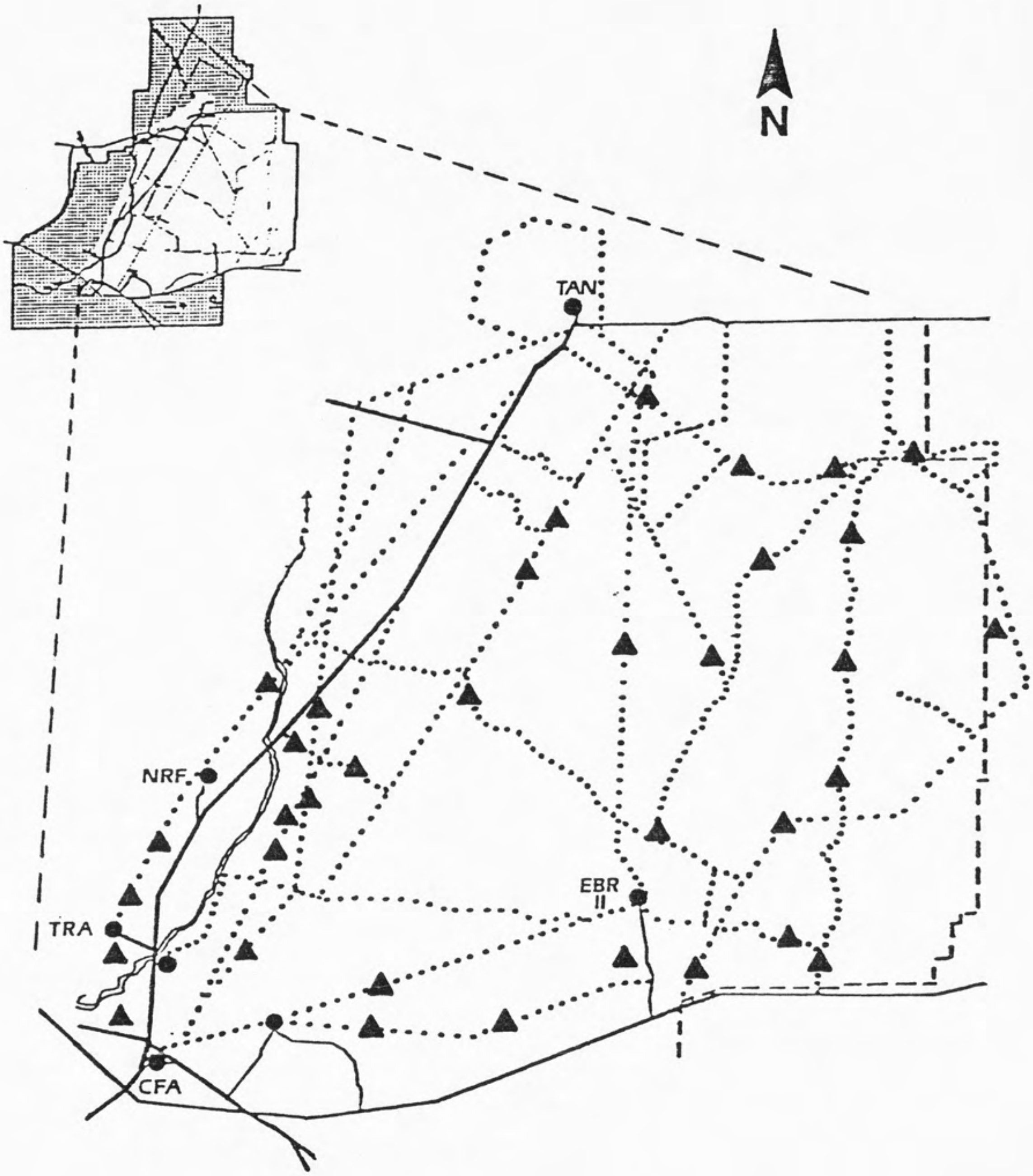

Figure 6. Location of 35, 1.6 km scat transects used to assess relative abundance of coyotes at the INEL in fall 1977.

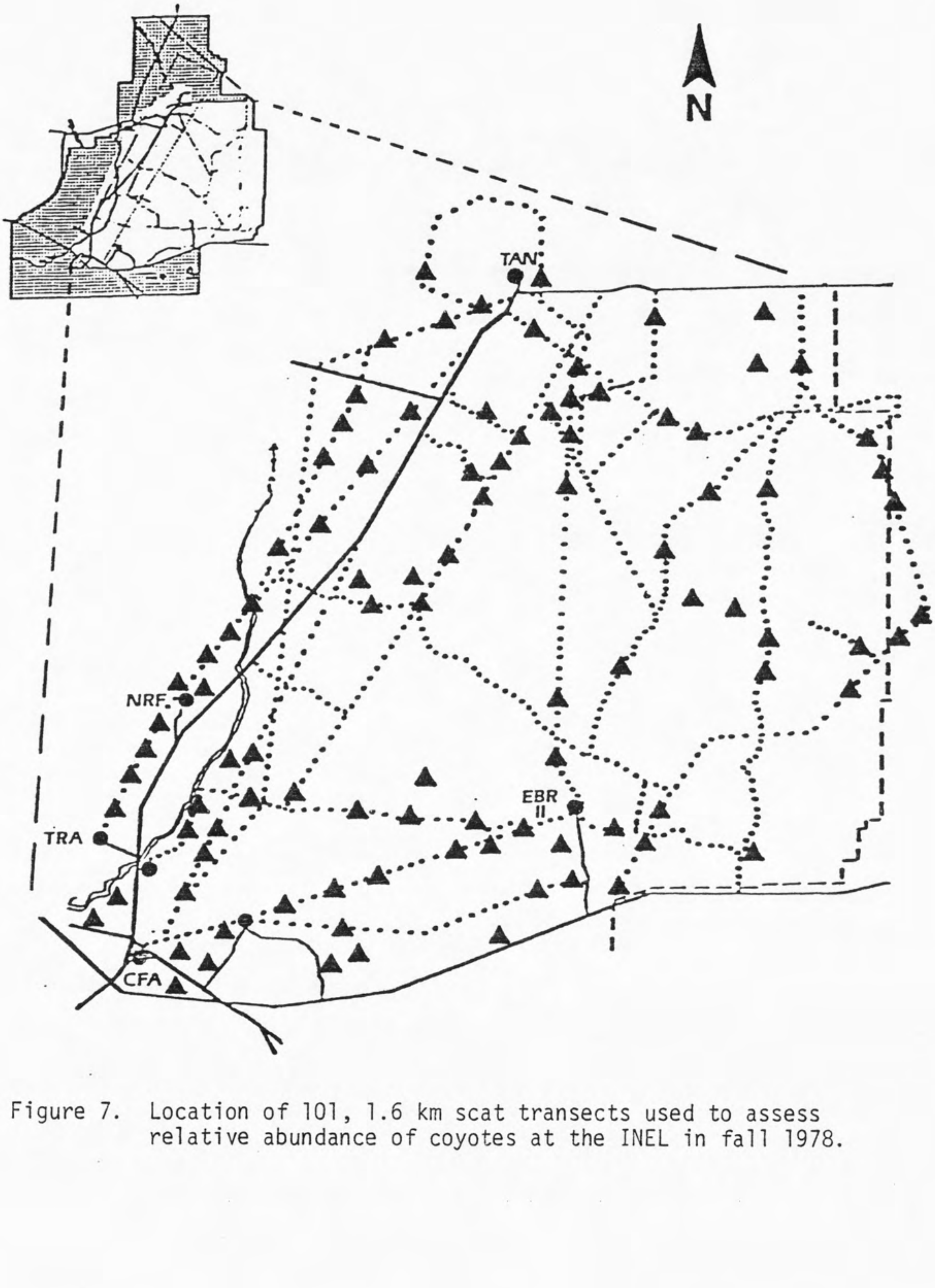

Figure 7. Location of 101, 1.6 km scat transects used to assess relative abundance of coyotes at the INEL in fall 1978.

between years within each study area, were tested statistically using Fisher's randomization test and RANDTEST program described previously.

Catch Effort Index. A third index of relative fall abundance of coyotes from 1975 to 1978 was based on the number of coyotes trapped for marking. In Curlew Valley, approximately 150 steel traps (3N Victor) with tranquilizer tabs (Balser 1965) were set in three lines by an experienced trapper each year (Fig. 8). At the INEL, about 200 traps (four lines) of the same type were set each year (Fig. 9). In each study area, traps were set at roughly 1.6 km intervals within 100 m of unpaved roads. Some discretion was given the trapper in placement of traps. Traps were run concurrently in each area for about 30 days, generally starting the first week in September (except in 1975 at INEL, when trapping began the first week in October). The condition of the traps was recorded daily. Sprung or inoperable traps were reset by a trapper every third day (Curlew Valley, and INEL 1975) or every fourth day (INEL except 1975). Traps found sprung or inoperable for the first time were considered to have been operable for one-half of the previous night. The number of coyotes caught per operable trap night included recaptures from previous years as well as from the same year.

The catch-effort index value for each area was the number of coyotes caught per 1000 operable trap nights.

Absolute Density

Estimates of the total number of coyotes present in the study areas during the fall were obtained with capture-recapture models using a technique involving isotopes. Isotopes have been used to study movements

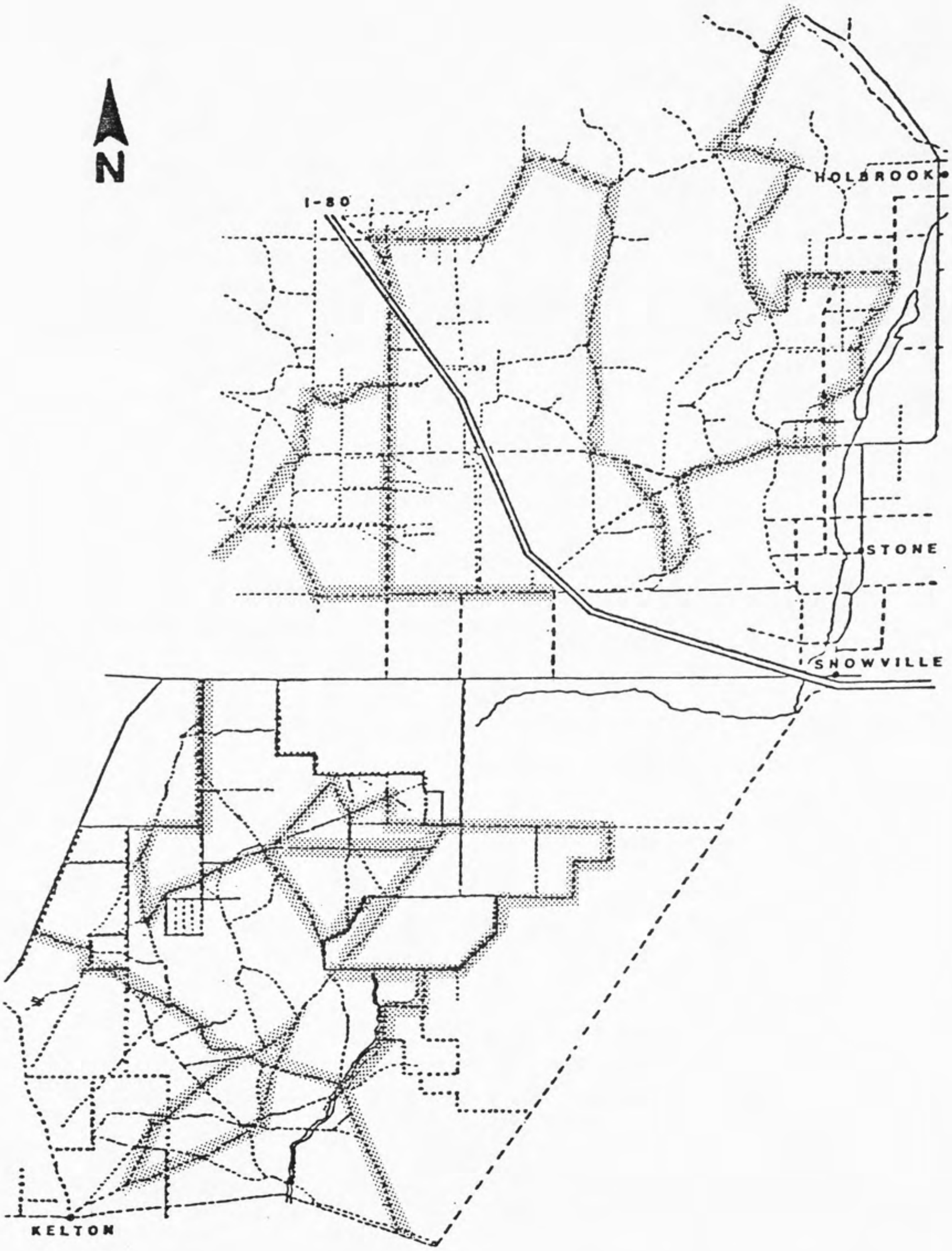

Figure 8. Location of coyote trap lines (150 traps at 1.6 km intervals) in Curlew Valley, 1975-1978.

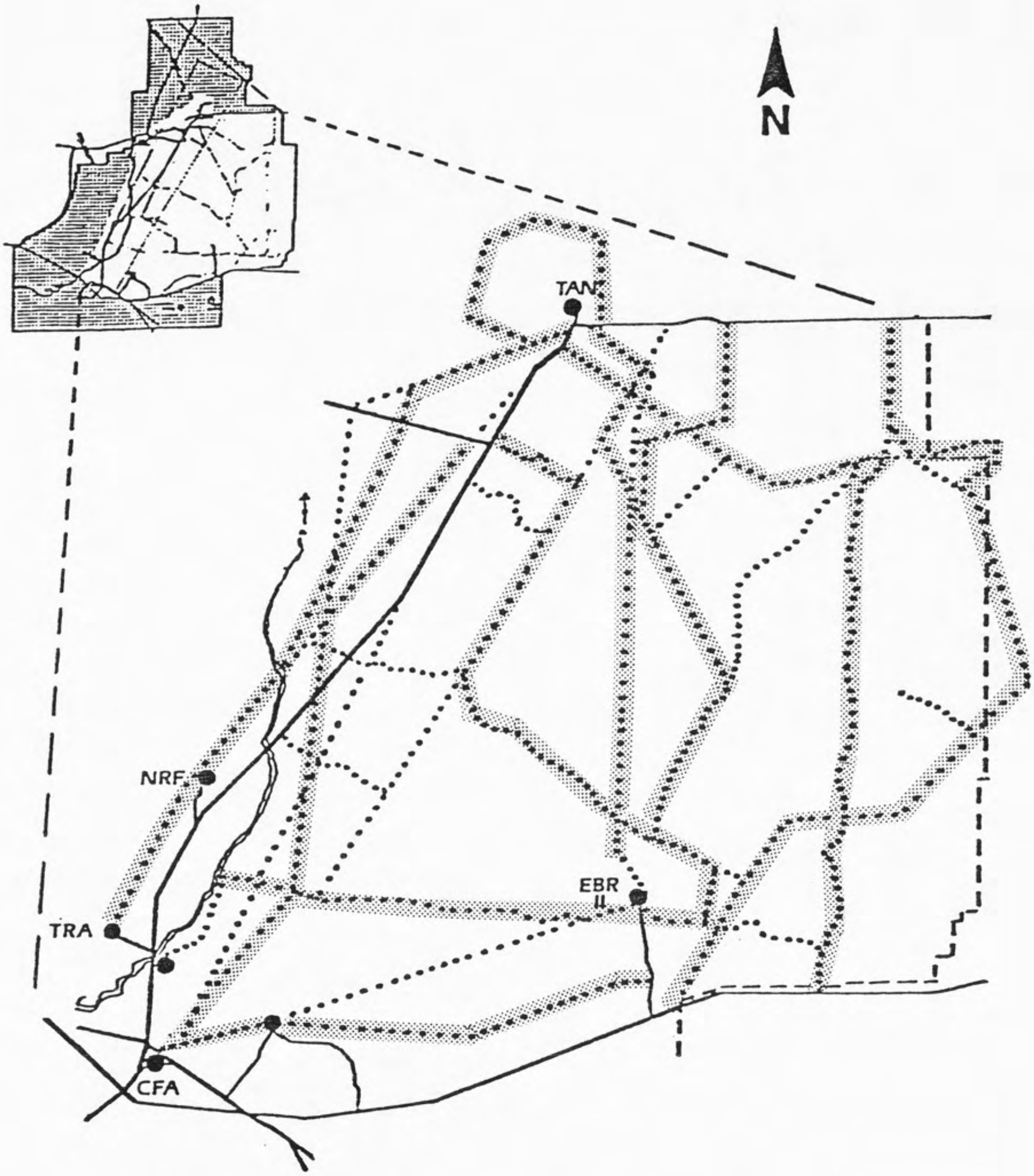

Figure 9. Location of coyote trap lines (200 traps at 1.6 km intervals) at the INEL, 1975-1978.

of small mammals, and their applicability to estimation of density was discussed by Pendleton (1956). Nellis et al. (1967) suggested the use of radioactive zinc (^{65}Zn) as a feces tag for estimating density of rabbits, foxes, and bobcats with capture-recapture models. Pelton and Marcum (1977) investigated six radioisotopes that were gamma emitters, with biological and physical half-lives of approximately one year. These isotopes were eliminated principally through the feces, and could be injected in solution at low dosage levels. Zinc (^{65}Zn) and manganese (^{54}Mn) were found to be the most suitable after tests with penned black bears (*Ursus americanus*). As a result, ^{65}Zn and ^{54}Mn were selected for evaluation with captive coyotes in June 1977. These isotopes were detected successfully in scats for over nine months after injection and were judged to be suitable for use in the field (Davison unpublished data).

Carrier-free ^{54}Mn and accelerator quality ^{65}Zn were ordered from New England Nuclear, Boston, Massachusetts. Isotopes were diluted with physiological saline to concentrations of 1.0 microcurie per cc (1977) and 5.0 microcuries per cc (1978). Diluted isotopes were transported via truck, in accordance with U. S. Department of Transportation regulations for "Shipments of Small Quantities of Radioactive Materials and Radiation Devices" (49-CFR, Transport of Radioactive materials, Chapter 1, Paragraph 179.391) and with the Idaho Operations Manual, Chapter ID-0579. Diluted isotopes were stored at the Experimental Farm of the Health Services Laboratory (INEL) and at the Utah State University Ecology Center Compound, Snowville, Utah (Curlew Valley).

Coyotes trapped in the two study areas, as described previously, were injected with solutions of diluted isotopes at the two locations given above. Injections were intramuscular in either hindquarter. In 1977, trapped coyotes judged to be adults were injected with 1.0 microcurie (1 cc) of ^{54}Mn per kg body weight. Coyotes judged to be pups that year were injected with the same dose of ^{65}Zn. In 1978, trapped coyotes judged to be adults received 15 microcuries (3 cc) of ^{65}Zn, while those considered to be pups received 10 microcuries (2 cc) of ^{54}Mn All coyotes that survived capture were injected with one of the two isotopes and released at the site of capture.

Collection of scats constituted the second or third (1977) capture occasion in the capture-recapture experiment and was conducted in 1977 and 1978 as described previously in the section titled "Scat Index." Scat transects, then, were cleared approximately 10 days following the end of the coyote trapping (first capture period). Scats were collected 14 (second capture period, 1977 and 1978) and 28 days (third capture period, 1977) later. Individual scats were saved for analysis as described previously.

Individual scats were analyzed for presence of ^{54}Mn and ^{65}Zn using a multi-channel peak-height analyzer (Nuclear Data Corporation) with a germanium-drifted lithium detector. Gamma ray emissions (835 MeV-^{54}Mn, 1115 MeV-^{65}Zn) from the scats were counted for four minutes by placing the paper bag in front of the detector. At the end of four minutes, the sum of the counts stored over that period was displayed on an oscilloscope. Based on this visual presentation, a decision was made as to whether there was any evidence of emissions at either 835 or 1115 MeV.

On a few rare occasions, emissions from scats were counted for longer periods when there was some question as to the presence of ^{54}Mn or ^{65}Zn. These questionable samples were invariably negative for presence of either isotope.

Estimates of the size of coyote populations in Curlew Valley and the INEL, assuming closure, were obtained with the Lincoln Index (number of trapping occasions (t)=2) or Schnabel estimator (t=3). Otis et al. (1978) refer to this class of estimators as Model M_t. Model M_t, for t=2, was used to estimate population size in 1978 and is given as $\hat{N}_t=n_1n_2/m_2$, where n_1 is the number of marked coyotes in the population after the first capture period, n_2 is the number of scats collected in the second capture period, and m_2 is the number of recaptures or marked scats in the second sample. Schnabel's model (t=3) was used to estimate population size in 1977 rather than the true maximum likelihood estimate M_t for t=3, which has no closed form solution. The use of Schnabel's model is justified because the number of marked animals in the population at time t=2 and t=3 was known a priori. Coyotes marked with isotopes also were fitted with radio-transmitters that allowed determination of whether they were members of the population on the second and third trapping occasions.

Estimates of variance were calculated for all models. Comparison of population size in Curlew Valley with that at INEL, as well as comparison between 1977 and 1978 within each area, was done as described by Chapman and Overton (1966) for Model M_t (t=2 or 3).

Estimation of Population Structure

Age Structure

Age structure of the coyote populations in the Curlew Valley and INEL study areas was inferred from the ages of coyotes captured on standardized trap lines in September and October (see "Catch-Effort Index"). Tzilkowski and Knowlton (pers. comm.) were successful in estimating the age of known-age coyotes from first premolars. Accordingly, age of captured coyotes in this study was determined from first premolars extracted from the mandible (usually) at the time of marking. Each extracted tooth was refrigerated in a 3-ml vial filled with water until processing. Processing involved using an X-ray technique to separate pups from the remainder of the sample, and analysis of tooth cementum layers to determine ages of that remainder judged not to be pups.

X-Ray Technique. Extracted first premolars were mounted laterally on a 25 x 30 cm posterboard and X-rayed. An exposure time of 0.5 seconds and tube to film distance of 85 cm at settings of 54 kv and 300 ma on Kodak X-Omatic fine film resulted in radiographs of high clarity. A light table was used to illuminate the radiograph and provide maximum contrast. The width of each pulp cavity and tooth were measured perpendicular to the axis of the tooth at the point where the pulp cavity width was greatest. Measurements were taken directly from the radiograph and were made to the nearest 0.1 mm with a vernier micrometer. Ratios of pulp cavity width to total tooth width were calculated, and from an histogram of these width ratios it was decided that the break in the distribution, which occurs at ratios from 0.28 to 0.32 with little overlap, represented the separation of pups (>0.32) from older animals (<0.28). In order to be conservative, however, all teeth with width ratios less than 0.40 were analyzed for cementum annuli.

Tooth Cementum Annuli. Ages of coyotes judged to be yearlings or older from the radiograph (width ratio <0.40) were determined by counts of cementum annuli of the extracted first premolars. Premolars with width ratios from 0.32 to 0.50 that had no annuli were judged to have come from pups. The technique is similar to that described for canines by Linhart and Knowlton (1967) and for premolars and molars by Monson et al. (1973), but most nearly follows that used by Tzilkowski (1980). Each first premolar was placed in a separate, labeled, tissue cassette (28 x 6 mm). Thirty such cassettes were added to 3.0 l of 5 percent nitric acid, allowing 100 ml of acid per tooth. The tissue cassettes were stirred continuously by aeration of the acid. Decalcification required 8-36 hours. Teeth were checked hourly after the first 4 hours and were removed to distilled water for periods when such checking was not possible. Following decalcification, teeth were rinsed in running tap water for at least 48 hours. Teeth were embedded in water and sectioned longitudinally on an International-Harris cryostat, Model CT. Six to 12 sections of each tooth were taken at 16μ. The sections were placed on a clean slide and allowed to dry at room temperature for approximately 24 hours. Once dry, the slides were dipped in stain for 15 to 30 seconds and rinsed with tap water. Stain was prepared by dissolving 0.365 g toluidin blue and 0.135 basic fuchsin in 50 ml of 70 percent ethanol. Slides were checked for quality of staining using a microscope, and the amount of staining was adjusted as necessary. Cementum annuli counts were made at 10X to 45X magnification using a green filter on the microscope illuminator to enhance the definition of annuli as suggested by Tzilkowski (1980) and Crowe (1972).

Sex Ratio

Sex structure of the coyote populations in the two study areas was inferred from the sex of animals trapped during September and October, as described in the section titled "Catch-Effort Index." Differences in sex ratios from equality were tested with the chi square statistic. Yearly comparisons of adult, juvenile, and combined sex ratios were made by means of 2 x 2 contingency tables. Test statistics used were either chi square or Fisher's exact test where one or more cell values were less than 5 (Siegel 1956).

Estimation of Recruitment Rates

Recruitment of pups in the fall (September-October) to the coyote populations of Curlew Valley and the INEL was estimated indirectly by two means.

Spring to Fall Increase in Relative Abundance

One measure of recruitment to fall populations was the percentage change in the mean indices of relative abundance from spring to fall as measured by scent station lines.

Age and Sex Structure

A second measure of recruitment was based on the age and sex structure of the coyote population in each area during the fall as determined from trapping. The number of pups per adult female, the proportion of pups in the fall population of pups and adult females (P_f), and the estimated proportion of pups in the spring population of pups and adult females (P_s) were calculated. The proportion of pups in the spring population (P_s) is a measure of the rate at which individuals are recruited into the breeding population, i.e., the rate at which pups reach one year of age. P_s was given by Ryel (1980:6) as:

$$P_s = f_s/(f_s + d_s)$$

$$P_s = (f_f \cdot S_f)/([f_f + d_f] \cdot S_t)$$

and, therefore, may be estimated as:

$$P_s = P_f \cdot S_f/S_t$$

where

f_s = the number of pups in the spring population

f_f = the number of pups in the fall population

d_s = the number of adult females in the spring population

d_f = the number of adult females in the fall population

S_f = the overwinter survival rate of pups, and

S_t = the weighted mean overwinter survival rate of all pups and adult females.

The survival rate, S_t, may be expressed as

$$S_t = S_f \cdot P_f + [S_d \cdot (1-P_f)]$$

where

S_d = the survival rate of adult females over winter.

Because virtually all mortality occurs during the winter months (see p. 73), estimates of annual survival rate for pups and adult females were used for S_f and S_d, respectively.

Differences in these proportions between the two study areas were estimated by an approximate confidence interval ($t \frac{\sqrt{P(1-P)}}{n}$) and z statistic:

$$z = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\bar{p}\ (1-\bar{p}\ (1/N_1 + 1/N_2)}}$$

where $\bar{x}_1$ and $\bar{x}_2$ are observed proportions in samples of size N_1 and N_2, and $\bar{p} = (N_1\bar{x}_1 + N_2\bar{x}_2)/(n_1 + N_2)$ is an estimate of the population proportion (Dixon and Massey 1969:249).

Estimation of Loss Rates

Mortality Rates

Mortality rates of the coyote populations in the Curlew Valley and INEL study areas were estimated from age structures and from recoveries of marked animals.

Estimation from Recoveries. Mortality rates were estimated from recovery of coyotes marked in the following manner. Each coyote trapped in the two study areas during the fall (except Curlew Valley 1975, 1978) was fitted with a transmitter collar. The transmitters were produced by the Denver Wildlife Research Center of the U. S. Fish and Wildlife

Service and were of the type described by Kolz et al. (1973). Transmitters operated on one of 12 frequencies within the 164 mH_Z band, with 30, 60, 75, 90, or 120 pulses per minute on each frequency. A transducer switched the pulse rate to 200-300 pulses per minute when a coyote remained motionless for approximately three hours. This feature was used to signal mortalities and aid in their location. Transmitters had either enclosed zig-zag (1975-76) or whip antennas (1977-78). Collars were fabricated from two- or three-ply rubber belting and had brass tags that offered a reward for return of the transmitter and provided an address to contact. Total transmitter collar weight was approximately 350 g. In addition to the transmitter collar, each trapped coyote was marked with self-piercing, Monel-metal, 30 mm ear tags, which also offered a reward for their return and an address to contact.

Factors that were thought to relate to the probability of survival were obtained and/or recorded at the time of marking. These included weight, general condition, condition of their foot, and blood samples.

Mortalities were detected and located from transmitted signals at the mortality pulse rate using a model LA12 AVM receiver (AVM Instrument Company, Champaign, IL) and a variety of antenna types. Initial detection and approximate location were made with an aircraft (Cessna 150, 172, 180, or 182) fitted with 3-element yagi antennas mounted on each wing strut. Antennas were directed laterally to the fuselage with the elements oriented vertically. A switching mechanism allowed the operator to determine relative signal strength from each antenna and infer the direction of the signal.

Marked coyotes were monitored from the air approximately every 2 weeks in order to detect mortality signals. Systematic flights were made over the study areas at an altitude of approximately 500 m above ground level (agl). Periodic searches were made at higher altitudes (500-2500 m agl) over surrounding areas and population centers for animals not found on flights over the study sites. Reception at maximum altitude (2500 m agl) was as great as 120 km.

Mortalities were recovered either by radio location techniques or by return of the transmitter and/or ear tags from cooperators. Mortalities detected on biweekly flights were located initially from the air at an altitude of approximately 150 m agl. Usually within 24 hours the mortality was relocated initially from a truck and then on foot with a single 3-element yagi or loop antenna. Information on mortalities was also obtained from cooperators who either notified the Predator Ecology and Behavior Project at Utah State University that they had a transmitter and/or ear tags or returned those items directly. Such cooperators were asked to provide information on date, location, and method of killing if known, and were paid a reward of $5.00 for each transmitter and $5.00 for each set of ear tags returned.

Time- and age-specific survival and recovery rates of marked coyotes were estimated using the inference procedures (estimation and hypothesis tests) described by Brownie et al. (1978). Briefly, data on recovered transmitters or tags from coyotes marked each of the four years of the study form an array representing the number of marked coyotes (R_{ij}) recovered in year j from those coyotes originally marked in year i (Table 1). Brownie et al. (1978) have described stochastic

Table 1. Symbolic representation of recovery data from coyotes marked for k years and recovered for a total of l years, where $l=k$

Year marked	Number marked	Year of recovery				
		1	2	3,	...	,k
1	N_1	R_{11}	R_{12}	R_{13}	...	,R_{1k}
2	N_2		R_{22}	R_{23}	...	,R_{2k}
3	N_3			R_{33}	...	,R_{3k}
.	.				.	.
.	.				.	.
.	.				.	.
k	N_k					R_{kk}

models that express the expected number of these recoveries in terms of numbers marked, and survival and recovery rate parameters. Each model represents a specific hypothesis about survival and recovery rates. Two types of procedures are described to statistically test various models and to select the simplest model (or set of assumptions on survival and recovery rates) that adequately fits a given data set. Based on goodness of fit tests and tests between models, the simplest model that adequately fits the recoveries of marked coyotes in this study was Model H02. The key assumptions of this model are that recovery rates vary from year to year, but that annual survival is constant from year to year. Model H02 allows estimation of both adult and first-year survival and recovery rates as well as testing the age-dependence of these rates (Table 2). Recovery rates in year i are denoted by f_i and f_i'. Constant annual survival rates are denoted by S and S'. The subscripts on f and S indicate year specificity, and the superscripts on f and S indicate age-dependence.

In addition to the specific assumptions given above, which form the structure of the model, there are numerous other assumptions involved in making inferences from banding data. Brownie et al. (1978:6) have summarized some important ones:

1. The sample is representative of the target population;
2. Age and sex of individuals are correctly determined;
3. There is no band loss;
4. Survival rates are not affected by the tagging itself;
5. The year of tag recoveries is correctly tabulated;

Table 2. Expected numbers of recoveries of marked coyotes under Model H02 (Brownie et al. 1978), expressed as a function of the number of adult (N_i) and young (M_i) marked, and the adult (f_i,S) and young (f_i',S') recovery and annual survival rates

Year marked	Number marked	Year of recovery 1	2	3	4
		Coyotes marked and released as adults			
1	N_1	N_1f_1	N_1Sf_2	N_1SSf_3	N_1SSSf_4
2	N_2		N_2f_2	N_2Sf_3	N_2SSf_4
3	N_3			N_3f_3	N_3Sf_4
4	N_4				N_4f_4
		Coyotes marked and released as young			
1	M_1	M_1f_1'	$M_1S'f_2$	$M_1S'Sf_3$	$M_1S'SSf_4$
2	M_2		M_2f_2'	$M_2S'f_3$	$M_2S'Sf_4$
3	M_3			M_3f_3'	$M_3S'f_4$
4	M_4				M_4f_4'

6. The fate of each marked animal is independent of (not correlated with) the fate of other marked individuals;
7. The fate of a given marked animal is a multinomial random variable; and
8. All marked individuals of an identifiable class (e.g., by sex) in the sample have the same annual survival and recovery rates.

Estimates of survival and recovery rate apply to the one-year period between successive releases of marked coyotes (September, year i, to September, year i+1). Survival rate (S) is a function of total survival, or of the mortality rate ($M = 1-S$) from all causes, not just from hunting. Recovery rates (f) in this study are a function of the kill rate (k), the nonhunting mortality rate (V), and the probability that a marked coyote is both retrieved and reported (λ), such that $f = \lambda(K+V) = \lambda M$ (Seber 1970). This interpretation of recovery rates differs from that given by Brownie et al. (1978) because recoveries of coyotes marked with transmitters were from nonhunting causes as well as hunting. Transmitters allowed recovery of all dead animals, including those either not retrieved or not reported by persons who killed animals. Thus, for the first year after marking, the probability of band retrieval and reporting was probably close to 1.0 ($f = (K+V) = M$). In subsequent years after marking, however, the probability of transmitter failure increased, with the result that not all marked coyotes dying in those years, particularly ones dying from nonhunting causes, were retrieved and/or reported ($\lambda<1.0$).

Estimation of recovery and survival rates, and testing and selection of models was accomplished by means of the computer program BROWNIE (age-dependent models) provided by Brownie et al. (1978).

Hypotheses regarding differences in survival and recovery rates over time and areas were tested with the following test statistic:

$$z = \frac{C_1 S_1 + C_2 \tilde{S}_2 + \ . \ . \ . + C_{k-1} \ \tilde{S}_{x-1}}{\sqrt{\sum_{i=1}^{k-1} (C_i)^2 \ \mathrm{Var} \ (\tilde{S}_i) + 2 \sum_{i=1}^{k-2} \sum_{j=i+1}^{k-1} \ C_i C_j \ \mathrm{Cov} \ (\tilde{S}_i \tilde{S}_j)}}$$

where:

1. $S_1, \ldots, S_{k-1}$ are estimated annual survival rates.
2. Var (S_i) and Cov $(S_i S_j)$, $i \neq j$, are the estimated sampling variances and covariances of these estimates, and
3. $C_1, \ldots, C_{k-1}$ are constants (Brownie et al. (1978:180).

Differences in recovery and/or survival rates by sex were tested with an option within program BROWNIE. The test statistic is the total chi square (Brownie et al. 1978:145).

Differences between areas in the distribution of mortalities by month were tested for using the Mann-Whitney U statistic (Siegel 1956: 116).

Estimation from Age Structure. Age structures of each population were also estimated from the ages determined for coyotes trapped in the fall. Methods of age determination and trapping have been described in previous sections. The Chapman-Robson model (Chapman and Robson 1960, Robson and Chapman 1961) was used to estimate annual mortality or survival rates from the age structures of the coyote populations sampled. Heincke's (1913, in Seber 1973) estimate of survival rate was used in conjunction with the survival rate from the Chapman-Robson model to test whether the youngest (0) age class was properly represented (Chapman and Robson 1960, Seber 1973). Age structures were recorded, and older age classes pooled or truncated as needed to fit the Chapman-Robson model.

Comparisons of survival rate estimates for a given population through time and for different populations were made using the following test statistic:

$$z = \frac{S - S_1}{\sqrt{\mathrm{Var}\ (S) + \mathrm{Var}\ (S_1)}}$$

Emigration Rates

Estimation of emigration rates initially required definition of types of movement by coyotes. Specifically, it was necessary to distinguish among emigration, dispersal, and a variety of other short (spatially or temporally) movements.

Lidicker (1975:104) has defined dispersal as "any movements of individual organisms or their propagules in which they leave their home area, sometimes establishing a new home area." Short-term exploratory movements (sallies) and shifts to new home ranges that overlap the previous home range are excluded by Lidicker in this definition. For this study, a further distinction was made regarding dispersal as defined above. Following Brown's (1975) suggestion, only movements of relatively long distances that otherwise met Lidicker's definition were considered to be dispersal. Smaller movements that fit Lidicker's and another's (Bowen 1978) conception of dispersal were considered to be spacing movements (Brown 1975).

Hibler (1976:40) found that those juvenile coyotes that dispersed moved an average of 18 km (n=10) "in a straight line from the boundaries of the home range areas from which they originated to the boundary of the succeeding home range areas," or, in some cases, to the furthest point located. Consequently, as an operational definition for this study, dispersal of juvenile coyotes was considered to be permanent or unidirectional movement greater than 20 km from where the coyote was trapped and released. Adult dispersal was defined as similar movement greater than 56 km based on the mean dispersal distance found by Hibler (1976) for three adult males.

With the methods of this study, it was not possible to distinguish whether shorter movements (<18 km for juveniles and <56 km for adults) represented spacing movements, sallies, or minor shifts in home range.

Emigration was considered to be dispersal, as operationally defined above, resulting in individuals leaving one of the populations under study. The populations under study are comprised of those coyotes whose home ranges are at least partially included within the boundaries of the two study areas. Hibler (1976) found that adult females had larger home ranges than adult males or juveniles, approximately 18 km^2. Bowen (1978) estimated home ranges of coyotes to be approximately 14 km^2 in Jasper National Park. Using 20 km^2 as an estimate of coyote home range, and assuming a circular shape, the average home range diameter of coyotes in this study would have been approximately 5 km. A workable definition for the limits of each of the two populations under study, then, was 5 km from the boundary of each study area.

Parameters related to emigration were measured with radiotelemetry techniques from 1976 to 1977 in Curlew Valley and from 1975 to 1977 at the INEL. Coyotes trapped during the fall were marked with transmitters and located every 10 to 14 days using the methods described previously for location and recovery of mortalities. Characteristics of the coyotes that were trapped thought to be relevant to emigration were recorded at the time of marking. These included sex, approximate age (juvenile or adult), weight, and general condition.

Exact locations were determined and recorded for coyotes found more than 20 km from where they were trapped and released. Once a coyote was located more than 20 km from where it was released it was located exactly on all subsequent flights. Periodic searches for coyotes not found on the study area were made at altitudes up to 2500 m agl and at distances up to 100 km from the study area boundaries. Additional information on emigration parameters was obtained from return of transmitters and/or ear tags from persons who had recovered them.

Emigration rate was estimated as the proportion of a given class of coyotes that moved unidirectionally more than 20 km to a point outside the population under study. The test statistic used to compare temporal and spatial differences in populations was the z statistic and approximate confidence interval for proportions (Dixon and Massey 1969:249) described previously under estimation of recruitment rates.

The timing of emigration, or the date emigration was initiated, was defined as the first time the animal was located outside the population and more than 20 km from where it was trapped and released, and the movement was permanent or unidirectional. Animals that could not be located during aerial searches often were found to have emigrated and been recovered. Based on information from cooperating individuals, coyotes that were recovered more than 20 km from their capture site and outside the limits of the population under study were considered to have initiated emigration the first time a location was not obtained.

Timing of emigration was estimated as the mean of the two-week intervals in which emigration was initiated. Differences in the distribution of dates of initiation were compared with the Mann-Whitney U test statistic (Siegel 1956:116).

Emigration distance was determined for those coyotes whose movement met the criteria established here, and was defined as the linear distance (km) from the point where the animal was captured and released to the latest location determined. Fisher's randomization test was used to compare differences in linear distance moved by those coyotes judged to have emigrated.

RESULTS

Density

Curlew Valley

Relative spring density of the coyote population in Curlew Valley, as estimated by scent station indices, did not differ from 1975 through 1978 (Table 3, Fig. 10). The proportion of scent stations visited for fall of 1975 was significantly lower than that for fall of 1976, 1977, or 1978. Although fall indices for 1977 were higher than for 1975, they were significantly lower than for either 1976 or 1978 (Table 3, Fig. 10).

Estimates of relative fall density from scat indices were not available for 1975 but otherwise were similar to those estimates from scent station indices. The number of scats collected/km/14 da in fall of 1978 was significantly higher than the number collected in 1977 but not different from the number collected in 1976 (Table 4). In contrast to the scent station estimates, however, the scat indices for 1976 and 1977 were not significantly different.

The number of coyotes caught per 1000 trap nights during September and October on standardized trap lines generally reflected the trends of the two other indices, with an increase from 7.6 coyotes caught 1000/ trap nights in 1975 to 12.6 coyotes captured/1000 trap nights in 1978. As with the scent station and scat indices, the catch effort index to density for fall of 1977 (7.4) was an exception to this trend, being lower than either 1976 (8.9) or 1978 (12.6).

Table 3.—Comparisons of the relative density of coyotes in Curlew Valley by season and year, as estimated by scent station indices. Tabular values for each comparison are the two-tailed probabilities that relative densities are not different using Fisher's randomization test

Year		1975		1976		1977		1978	
Season		Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	Indices	7.8	7.8	5.9	68.8	3.1	33.0	10.5	74.1
1975									
Spring	7.8		0.788	1.000		0.618		0.791	
Fall	7.8				0.001		0.078		0.000
1976									
Spring	5.9				0.001	0.499		0.637	
Fall	68.8						0.103		0.834
1977									
Spring	3.1						0.015	0.299	
Fall	33.0								0.055
1978									
Spring	10.5								0.000
Fall	74.1								

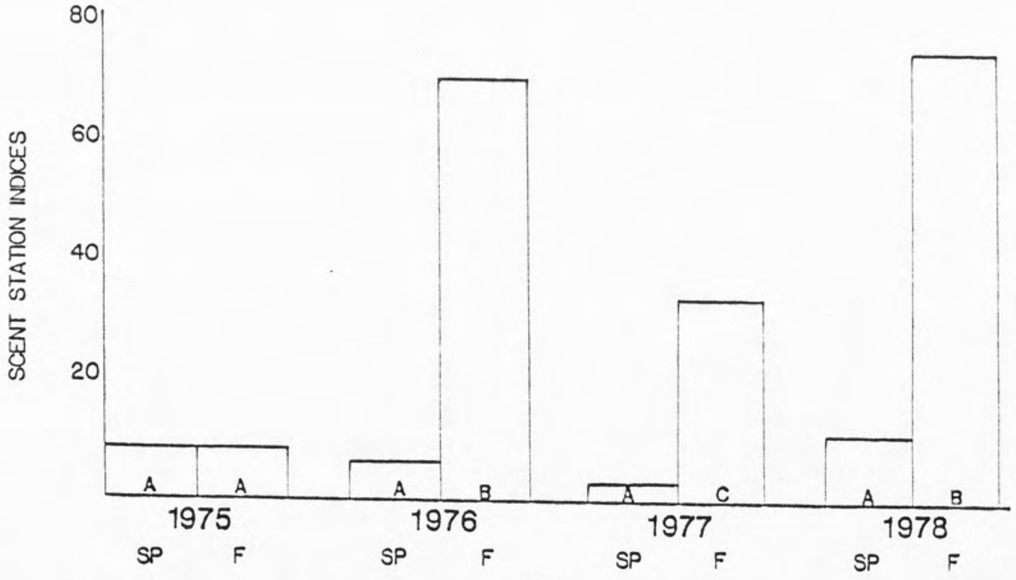

Figure 10. Comparisons of relative density of coyotes in Curlew Valley by season and year, as estimated by scent station indices. Columns with different letters are significantly different ($P<0.10$)

Table 4.—Yearly comparisons of the relative density of coyotes in Curlew Valley during the fall from 1976 to 1978 as estimated by scat indices

Number of transects	Mean number of scats/km/14 da	Year	Two-tailed probability that density indices are not different 1976	1977	1978
72	0.70	1976	-----	0.293	0.165
99	0.55	1977	0.293	-----	0.007
100	0.98	1978	0.165	0.007	-----

The estimates of absolute density from radioactive feces-tagging for fall of 1977 and 1978 were 0.17 and 0.24 coyotes/km^2, respectively (Table 5). The precision of these estimates was poor, and the estimates were not significantly different (Chapman and Overton 1966).

In summary, the estimates of relative and absolute fall density increased from 1975 through 1978. Densities were most likely not different in 1976 and 1978, but were greater in those two years than either 1977 or 1975. Fall density in 1977, although less than in 1976 and 1978, was probably greater than in 1975. In contrast, spring densities apparently remained unchanged over the four-year period.

INEL

Relative spring density of the coyote population at the INEL as estimated from scent station indices was not different from 1976 through 1978. Estimates of relative density for spring of 1975, however, were significantly less than for either 1976 or 1978 (Table 6, Fig. 11). Estimates of fall density from scent station indices for 1976 and 1977 were significantly higher than for 1975. Density estimates for fall of 1978, however, were not significantly different from those for the previous three years (Table 6, Fig. 11).

Relative fall density as estimated from scat indices was significantly less in 1978 in comparison with 1976 (Table 7). There were no differences in estimates of relative density between 1976 and 1977 or 1977 and 1978. The trends in fall density that may be inferred from these estimates are quite similar to those that may be inferred from the

Table 5.—Absolute fall densities of coyotes in Curlew Valley and at the INEL, 1977-1978, as estimated from capture-recapture models using isotope labeling techniques

Area	No. of marked coyotes known in population (n_t)	No. of scats (n_{t+1})	No. of marked scats (m_{t+1})	Estimated population size (N)	Estimated density (N/km^2)	95 percent confidence interval
Curlew Valley						
Fall 1977						
t=1	28	--	--	-	--	-
t=2	21	34	2	357	0.22	0.03-1.22
t=3	19	52	3	329	0.20	0.04-0.74
overall	--	86	5	284	0.17	0.07-0.53
Fall 1978						
t=1	45	--	--	-	--	-
t=2	33	157	13	399	0.24	0.13-0.42
INEL						
Fall 1977						
t=1	49	--	--	-	--	-
t=2	38	76	4	722	0.59	0.16-1.74
t=3	36	51	8	230	0.19	0.08-0.38
overall	--	127	12	363	0.30	0.16-0.57
Fall 1978						
t=1	44	--	--	-	--	-
t=2	25	147	10	368	0.30	0.14-0.56

Table 6.—Comparisons of the relative density of coyotes at the INEL by season and year, as estimated by scent station indices. Tabular values for each comparison are the two-tailed probabilities that relative densities are not different using Fisher's randomization test

Year		1975		1976		1977		1978	
Season		Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	Indices	3.3	26.7	17.0	66.6	9.4	58.8	20.0	46.2
1975									
Spring	3.3		0.012	0.025		0.142		0.024	
Fall	26.7				0.105		0.086		0.358
1976									
Spring	17.0				0.031	0.449		0.958	
Fall	66.6						0.717		0.344
1977									
Spring	9.4						0.000	0.282	
Fall	58.8								0.468
1978									
Spring	20.0								0.070
Fall	46.2								

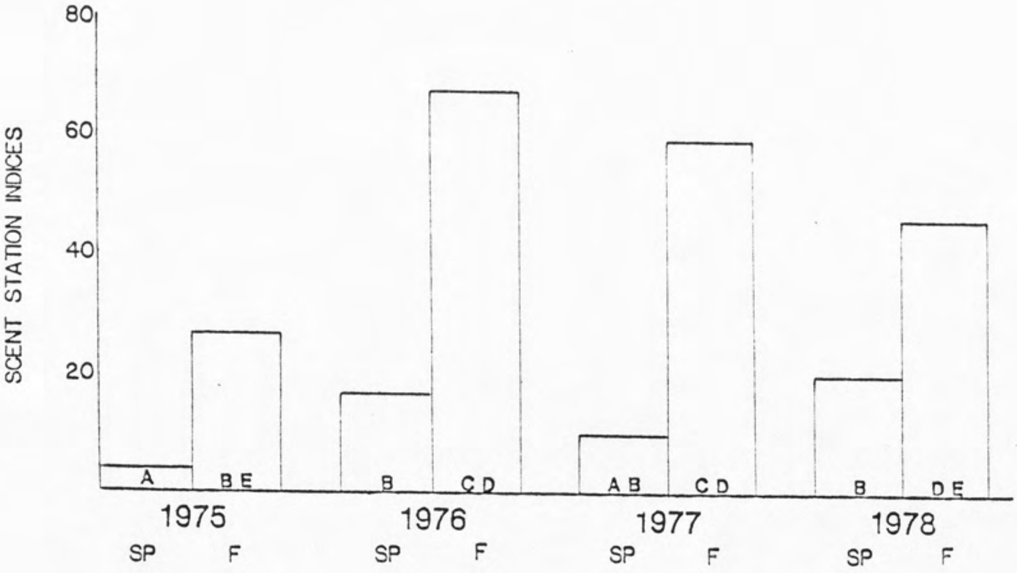

Figure 11. Comparisons of relative density of coyotes at the INEL by season and year, as estimated by scent station indices. Columns with different letters are significantly different (P<0.10)

Table 7.—Yearly comparisons of the relative density of coyotes at the INEL during the fall from 1976 to 1978 as estimated by scat indices

Number of transects	Mean number of scats/km/14 da	Year	Two-tailed probability that density indices are not different 1976	1977	1978
46	1.27	1976	-----	0.622	0.072
70	1.13	1977	0.622	-----	0.308
100	0.91	1978	0.072	0.308	-----

scent station estimates. No scat indices were available for fall of 1975, however.

Additional information on relative density at the INEL was provided by the number of coyotes caught in the fall/1000 trap nights. The catch per unit of effort was higher in 1977 and 1978 (9.9 and 9.3 coyotes/1000 trap nights, respectively) than in 1975 and 1976 (6.2 and 6.3).

Absolute fall density at the INEL, estimated by radioactive feces tagging, did not differ from 1977 to 1978 (Chapman and Overton 1966). In November 1977, there were an estimated 363 coyotes on the 1225 km^2 study area (0.30 coyotes/km^2) and 368 (0.30 coyotes/km^2) coyotes in November 1978 (Table 5). As in Curlew Valley, the precision of the estimates was poor, but the estimates were in agreement with the other measures of relative density.

In summary, it seems likely that fall density of coyotes in the INEL study area was less in 1975 than in subsequent years. Fall densities probably did not differ from 1976 through 1978. Spring density also appears to have been less in 1975 than subsequent years, although not significantly different than in 1977.

Comparison of Curlew Valley and the INEL

From 1975 through 1978, fall and spring scent station estimates of relative coyote density in Curlew Valley did not differ significantly from comparable estimates for the INEL (Table 8, Fig. 12).

Scat indices of relative coyote density in Curlew Valley for fall 1976 and 1977 were significantly lower than scat estimates of relative coyote density at the INEL (Table 9). There was no difference in these

Table 8.—Seasonal comparisons of the relative density of coyotes in Curlew Valley and at the INEL, 1975 to 1978, as estimated by scent station indices. Tabular values are the two-tailed probabilities that relative densities are not different between areas using Fisher's randomization test

Study Area		CURLEW VALLEY							
Year		1975		1976		1977		1978	
Season		Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	Indices	7.8	7.8	5.9	68.8	3.1	33.0	10.5	74.1
INEL									
1975									
Spring	3.3	0.197							
Fall	26.7		0.131						
1976									
Spring	17.0			0.228					
Fall	66.6				0.887				
1977									
Spring	9.4					0.299			
Fall	58.8						0.158		
1978									
Spring	20.0							0.362	
Fall	46.2								0.180

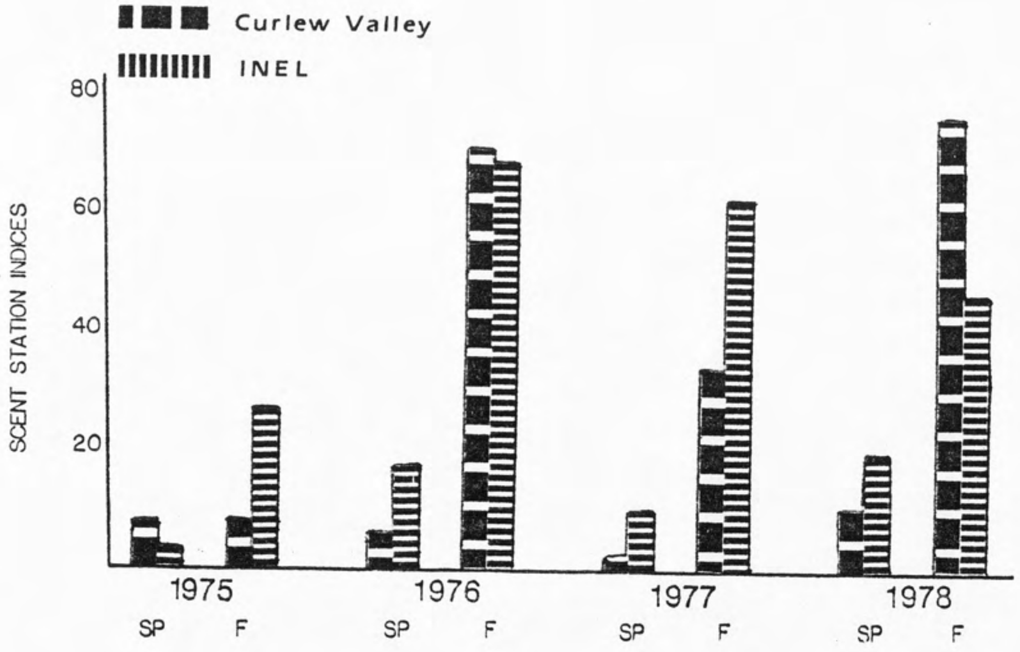

Figure 12. Relative density of coyotes in Curlew Valley and the INEL, 1975 to 1978, as estimated by scent station indices. For statistical comparisons between areas, see Table 8 above

Table 9.—Comparisons of the relative density of coyotes during the fall in Curlew Valley with that at the INEL from 1976 to 1978 as estimated by scat indices

	Mean number of scats/km/14 da		Two-tailed probability that indices of density are not different		
Year	Curlew Valley	INEL	1976	1977	1978
1976	0.70	1.27	0.015		
1977	0.55	1.13		0.002	
1978	0.98	0.91			0.694

estimates between areas for fall of 1978. However, transects in Curlew Valley probably were subject to higher vehicle use than at the INEL. This would reduce the number of scats collected and produce lower estimates for Curlew Valley.

There was no way to compare statistically the indices of catch-effort for the two areas; however, those fall indices were generally slightly higher for Curlew Valley.

Statistical analysis (cf Chapman and Overton 1966) of estimates of absolute density for the two study areas obtained from radioactive feces-tagging revealed no significant differences for either fall 1977 or fall 1978. In fall 1977, there were an estimated 0.17 coyotes/km^2 in Curlew Valley vs. 0.30 coyotes/km^2 at the INEL (Table 5). In fall 1978, the estimates were 0.24 and 0.30 coyotes/km^2 for Curlew Valley and INEL, respectively.

In summary, those measures of density judged to be freer from site-specific bias (scent stations and radioactive feces-tagging) did not differ between Curlew Valley and the INEL during the course of the study.

Sex Ratio

Curlew Valley

In Curlew Valley there were no significant differences between the sex ratios of adult and juvenile coyotes trapped any of the 4 years of the study or over all years combined (total $\chi^2_{(7df)} = 0.84$, $P = 1.00$). As a result, trapped samples of adults and juveniles were pooled for analysis within Curlew Valley. The overall sex ratio of coyotes trapped in the fall from 1975 to 1978 did not deviate significantly from equality ($\chi^2 = 0.46$, $P = 0.50$). On a yearly basis, only in 1977 was there a significant departure from an equal sex ratio ($\chi^2 = 3.57$, $P = 0.06$), with females outnumbering males two to one. The preponderance of females in that year was in the juvenile segment of the trapped sample. There were no significant differences between years in the sex ratio of trapped coyotes (Table 10).

INEL

As in Curlew Valley, at the INEL there were no significant differences between the sex ratios of adult and juvenile coyotes trapped any of the 4 years of the study or over all years combined (total $\chi^2_{(7df)} = 3.85$, $P = 0.80$). With trapped samples of adults and juveniles combined, then, the overall sex ratio from fall 1975 to fall 1978 did not deviate significantly from equality ($\chi^2 = 0.02$). Moreover, there were no significant deviations from an equal sex ratio in any given year. Finally, there were no significant differences in any of the yearly comparisons of sex ratios (Table 10).

Comparison of Curlew Valley and INEL

No differences were found between the two study areas in the sex ratios of coyotes trapped during the fall (Table 11). Sex ratio estimates for adults, juveniles, and the total sample did not differ between areas in any given year or over all years combined.

Table 10.—Yearly sex ratio comparisons of coyotes trapped in Curlew Valley and at the INEL, 1975 to 1978

Years	Curlew Valley ♂	Curlew Valley ♀	INEL ♂	INEL ♀
1975	16	15	12	12
1976	21	15	18	12
Chi Square	0.093		1.426	
1976	21	15	18	12
1977	9	19	24	28
Chi Square	3.350		0.958	
1977	9	19	24	28
1978	21	26	22	22
Chi Square	0.686		0.029	

Table 11.—Sex ratio comparisons, within age classes, of coyotes trapped in Curlew Valley and at the INEL, 1975-1978

Year Areas	Adults ♂	Adults ♀	Juveniles ♂	Juveniles ♀	Ages Combined ♂	Ages Combined ♀
1975						
Curlew Valley	4	5	12	10	16	15
INEL	8	5	4	7	12	12
1976						
Curlew Valley	3	4	18	11	21	15
INEL	10	5	8	7	18	12
1977						
Curlew Valley	3	4	6	15	9	19
INEL	4	12	20	16	24	28
1978						
Curlew Valley	4	2	17	24	21	26
INEL	8	5	14	17	22	22
All years combined						
Curlew Valley	14	15	53	60	67	75
INEL	30	27	46	47	76	74
Chi Square (1 df) =	0.02		0.05		0.23	

Age Structure

The number of pups and adults in fall samples of trapped coyotes, as determined from X-ray methods, is presented for both study areas under the following section titled "Recruitment." More detailed information with regard to ages of adults, as determined from cementum annuli, is presented in Table 12. In general, the age distributions from the INEL have more older animals in comparison to Curlew Valley. The pooled age distributions (1975 through 1978) from the two areas were significantly different ($P = 0.00$).

Recruitment

Curlew Valley

In 1975 there was no change from spring to fall in mean scent station indices. Percent change in indices from spring to fall for all subsequent years of the study was greater than for 1975, but declined from an 11-fold increase in 1976 (5.9 - 68.8) to a 10-fold increase in 1977 (3.1 - 31.0) to a 6-fold increase in 1978 (10.5 - 74.0).

Fall ratios of pups to adult females increased generally from a low of 4.40 in 1975 to a high of 20.50 in 1978, and averaged 7.53 over the 4 years (Table 13). The corresponding proportions of pups in the fall population of pups and adult females (P_f) increased from 0.81 in 1975 to 0.95 in 1978, and averaged 0.88 for the 4 years of the study. There were no significant differences found between years in the fall proportion of pups when the 90 percent confidence intervals were plotted

Table 12.—Age distributions of coyotes trapped in Curlew Valley and at the INEL from 1975 to 1978

Curlew Valley

Age class	1975	1976[a]	1977	1978	Pooled
n	31	35	28	47	141
0	.710	.829	.750	.872	.801
1	.161	.086	.179	.064	.113
2	.065	.057	.036	.043	.050
3	.065	.000	.036	.000	.021
4	.000	.000	.000	.021	.007
5	.000	.000	.000	.000	.000
6	.000	.029	.000	.000	.007

INEL

Age class	1975	1976	1977	1978	Pooled
n	24	30	52	44	150
0	.458	.500	.692	.705	.620
1	.125	.167	.154	.205	.167
2	.125	.067	.058	.045	.067
3	.042	.133	.038	.000	.047
4	.083	.067	.019	.000	.033
5	.125	.000	.000	.023	.027
6	.000	.033	.000	.023	.013
7	.042	.000	.038	.000	.020
8	.000	.033	.000	.000	.007

[a] Excludes one animal for which no age was determined.

Table 13.—Estimates of coyote recruitment rates for Curlew Valley and the INEL (1975-1978) based on fall ratios of pups to adult females, proportions of pups in the fall population of pups and adult females (P_f), and estimated proportions of pups in the spring population of pups and adult females (P_s)[1]

Area Year	No. of pups per adult female	P_f (s.d.)	P_s (s.d.)
Curlew Valley			
1975	4.40	0.81 (0.08)	0.67 (0.09)
1976	7.25	0.88 (0.06)	0.78 (0.07)
1977	5.25	0.84 (0.07)	0.72 (0.09)
1978	20.50	0.95 (0.03)	0.90 (0.05)
Average estimates	7.53	0.88 (0.03)	0.78 (0.04)
INEL			
1975	2.20	0.69 (0.12)	0.67 (0.12)
1976	3.00	0.75 (0.10)	0.73 (0.10)
1977	3.00	0.75 (0.06)	0.73 (0.06)
1978	6.20	0.86 (0.04)	0.85 (0.06)
Average estimates	3.44	0.78 (0.04)	0.76 (0.04)
Probability that average estimates are not different between areas	=	0.031	0.372

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[1] Estimates of P_s obtained by the method of Ryel (1980), see text.

(Fig. 13). A z test for differences in proportion, however, indicated that P_f was significantly higher in 1978 than 1975 ($P = 0.06$).

The proportion of pups in the spring population of pups and adult females (P_s) or the proportion of pups recruited into the next age class increased from 0.67 in 1975 to 0.90 in 1978, and averaged 0.78 for the 4-year period. P_s did not differ significantly among years.

Both estimates of recruitment rate were lower in 1975 in comparison to subsequent years. There also was agreement between the estimates that recruitment was reduced slightly in 1977 in comparison to 1976. However, the measures of recruitment were contradictory for 1978.

INEL

The percent increase in scent station indices from spring to fall was greatest at the INEL in 1975 (8-fold increase). In 1976 there was a 4-fold increase from spring to fall, and in 1978 there was a 2-fold increase. Spring to fall increase for 1977 was intermediate between increases for 1975 and 1976 (6-fold increase).

Fall ratios of pups to adult females increased from 2.20 in 1975 to 6.20 in 1978, and averaged 3.44 for the study period (Table 13). The proportion of pups in the fall population of pups and adult females (P_f) did not differ significantly between years, but increased from 0.69 in 1975 to 0.86 in 1978, and averaged 0.78 over the 4 years (Table 13, Fig. 13). The estimated proportion of pups in the spring population (P_s) increased from 0.67 in 1975 to 0.85 in 1978, and averaged 0.76, but did not differ significantly from year to year (Table 13).

Spring to fall increases in scent station visitation rates and recruitment rates estimated from fall age ratios were contradictory.

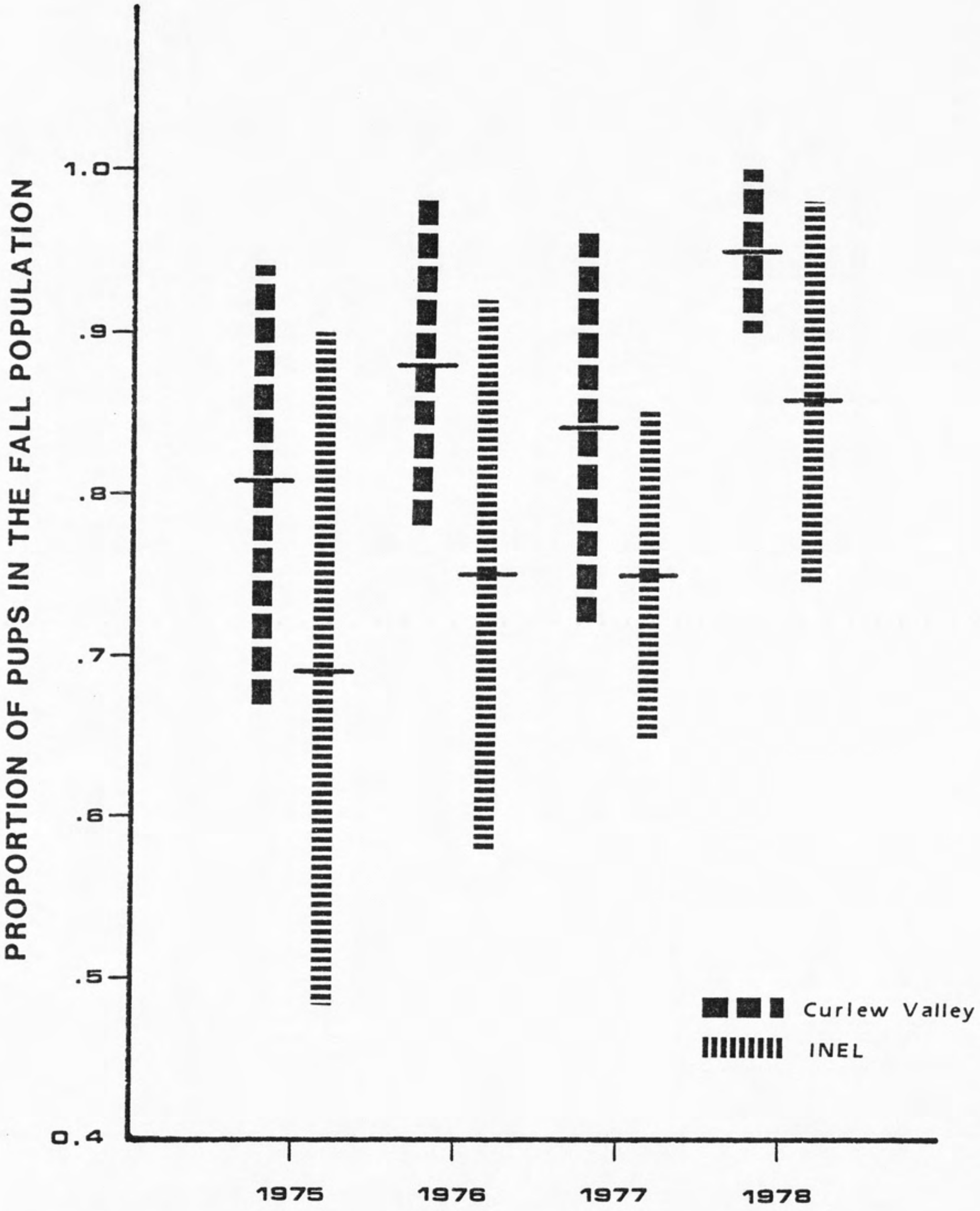

Figure 13. Proportion of coyote pups in the fall population of pups and adult females (P_f) and 90 percent confidence intervals for Curlew Valley and the INEL (1975-1978), as estimated from trapping.

In general, the former estimate of recruitment decreased from 1975 to 1978, while the latter estimate increased over the same period.

Comparison of Curlew Valley and INEL

For all years except 1975, spring to fall increases in scent station indices were greater in Curlew Valley than at the INEL. The proportion of pups in the fall (P_f) did not differ between areas for any given year ($P = 0.14$, Fig. 13). The average estimate of P_f for the 4 years, however, was significantly greater in Curlew Valley (Table 13). There were no differences between Curlew Valley and INEL in the yearly or average estimates of P_s (Table 13).

In general, the average rate of recruitment to the fall population appears to have been greater in Curlew Valley from 1975 to 1978. Average spring to fall increase in scent station visitation rate was greater in Curlew Valley than at the INEL. The average estimate of P_f was significantly greater for Curlew Valley. Recruitment to the spring population, however, was not significantly different.

Mortality

Curlew Valley

From 1975 to 1978, 142 coyotes were trapped during the fall in Curlew Valley. Ninety-six percent (136) of these were marked and released. Of the 136 coyotes marked, 56 percent (76) were recovered from 1975 to 1979 (Table 14). Sixty-one percent (17) of the 28 coyotes marked as adults and 55 percent (59) of the 108 coyotes marked as juveniles were recovered (Table 14).

Table 14.—Recoveries of adult and juvenile coyotes marked during the fall in Curlew Valley from 1975 to 1978

Year marked	Number marked	Year of recovery			
		1975-76	1976-77	1977-78	1978-79
Coyotes marked and released as adults					
1975	9	2	1	1	0
1976	6		3	1	2
1977	7			5	0
1978	6				2
Coyotes marked and released as juveniles					
1975	20	6	2	1	1
1976	28		14	4	2
1977	21			14	1
1978	39				14
All coyotes marked and released (adults and juveniles combined)					
1975	29	8	3	2	1
1976	34		17	5	4
1977	28			19	1
1978	45				16

Adult recovery rates in Curlew Valley, as estimated by Model H02 (Brownie et al. 1978) averaged about 0.43 for the 4 years of marking and recovery (Table 15). Model H02 assumes recovery rates are year-specific, and this assumption appears valid based on the model selection procedures and goodness of fit tests in program BROWNIE. Annual adult recovery rates varied from approximately 0.16 in 1975 to 0.60 in 1977. Recovery rates for 1976 and 1977, the years coyotes were marked with radio transmitters, averaged 0.584 (s.e. = 0.092).

Recovery rates for juveniles marked from 1975 to 1978 averaged approximately 0.45 (Table 15). Year-specific recovery rates varied from a low in 1975 to 0.295 to a high in 1977 of 0.639. In 1976 and 1977, recovery rates for radio-marked juveniles averaged 0.581 (s.e. = 0.066). Average adult and juvenile recovery rates were not significantly different (Table 15).

Average and annual adult and juvenile recovery rates were estimated for the period of study without regard to location or cause of recovery. From 1975-76 to 1978-79 there was sufficient information on recovery location for 46 of the 48 juveniles recovered in the first year following release (September-September). Seventy-four percent (34) of these juveniles were recovered within the population under study (see definition, p. 45). Adult recovery rates, locations, and causes are based on those individuals released as adults as well as adult survivors of juveniles marked in previous years. Recovery location information was available for 27 adults. Eighty-one percent (22) of these adults were recovered in the study area. Seventy-one percent of the juveniles and 78 percent of the adults marked with transmitters (1976-77) were

Table 15.—Recovery rates of adult and juvenile coyotes marked during the fall in Curlew Valley from 1975 to 1978 as estimated by Model H02 (Brownie et al. 1978)

Adult recovery rates (f_i)

Year	Estimate	Standard Error	95% Confidence Interval
1975	0.1597	0.1172	-0.0700-0.3894
1976	0.5692	0.1245	0.3251-0.8133
1977	0.5978	0.1350	0.3332-0.8624
1978	0.3822	0.1354	0.1169-0.6475
Average Estimate =	0.4272	0.0692	0.2916-0.5628

Juvenile recovery rates (f'_i)

Year	Estimate	Standard Error	95% Confidence Interval
1975	0.2949	0.0989	0.1012-0.4887
1976	0.5234	0.0886	0.3497-0.6971
1977	0.6390	0.0985	0.4458-0.8321
1978	0.3590	0.0768	0.2084-0.5095
Average Estimate =	0.4541	0.0474	0.3612-0.5469

Probability that adult and juvenile recovery rates are not different = 0.378

recovered within the study population. Overall, adults died an average of 9.3 km* (s.e. = 2.2) from where they were captured and released. Juvenile mortality occurred significantly further from capture sites, and averaged 22.8 km (s.e. = 4.2).

From 1975-76 to 1978-79 there was information on cause of recovery for 46 juveniles and 29 adults. Eighty-nine percent of the recoveries used to estimate juvenile recovery rates were due to exploitation. Of the recoveries used to estimate adult recovery rates, 93 percent were due to exploitation. Seven percent of the adult and juvenile recoveries were from unknown causes. In 1976 and 1977, the years coyotes were marked with transmitters, 92 percent of the juvenile recoveries were from hunting, 4 percent from road kills, and 4 percent from uncertain causes. Eighty-nine percent of adults were recovered as a result of hunting and 11 percent due to unknown causes. Of all mortalities due to hunting from 1975 through 1979, 26 percent were due to aerial hunting. In each of the years 1975-76, 1976-77, and 1977-78, aerial hunting accounted for 12 percent of all hunting losses. In 1978-79, however, aerial hunting was responsible for 60 percent of all hunting mortality.

From the information on location and cause of recovery from 1975-76 to 1978-79, it was estimated that 70 percent of all juvenile and 74 percent of all adult recoveries occurred both within the study population and as a result of exploitation.

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*Estimate excludes one 340 km movement.

Mortality of marked coyotes in Curlew Valley over the 4 years of the study occurred principally from November through January (Fig. 14). Sixty-four percent (48) of the marked coyotes were recovered during those three months. Eighty-seven percent (65) of the mortalities occurred from October through February.

Estimates of adult and juvenile annual survival rates are assumed to be constant from year to year under Model H02 (Brownie et al. 1978). Constant annual survival rates for adults and juveniles in Curlew Valley were estimated to be 0.471 and 0.228, respectively (Table 16). These estimates were significantly different ($P = 0.05$), but males and females did not differ significantly in either recovery or survival rates ($\chi^2_{(7df)} = 6.75$, $P = 0.54$). Additional information on survival was obtained from the pooled, sample age distribution (1975-1978 combined) in Table 12. However, the juvenile (zero) age class was over-represented relative to the older (1-6) age classes ($z^2 = 10.59$). Because average annual survival rate apparently was not constant throughout all age classes, no estimate could be calculated for the entire population using the Chapman-Robson model. Average annual survival rate was constant in the adult (1-6) age classes ($z^2 = 0.02$). The Chapman-Robson estimate and associated 95 percent confidence interval for this segment of the population was 0.438 and 0.296 to 0.579, respectively.

INEL

A total of 150 coyotes was trapped during the fall at the INEL from 1975 to 1978. Of those trapped, 97 percent (145) were marked and released. Sixty-four percent (93) of those marked and released were

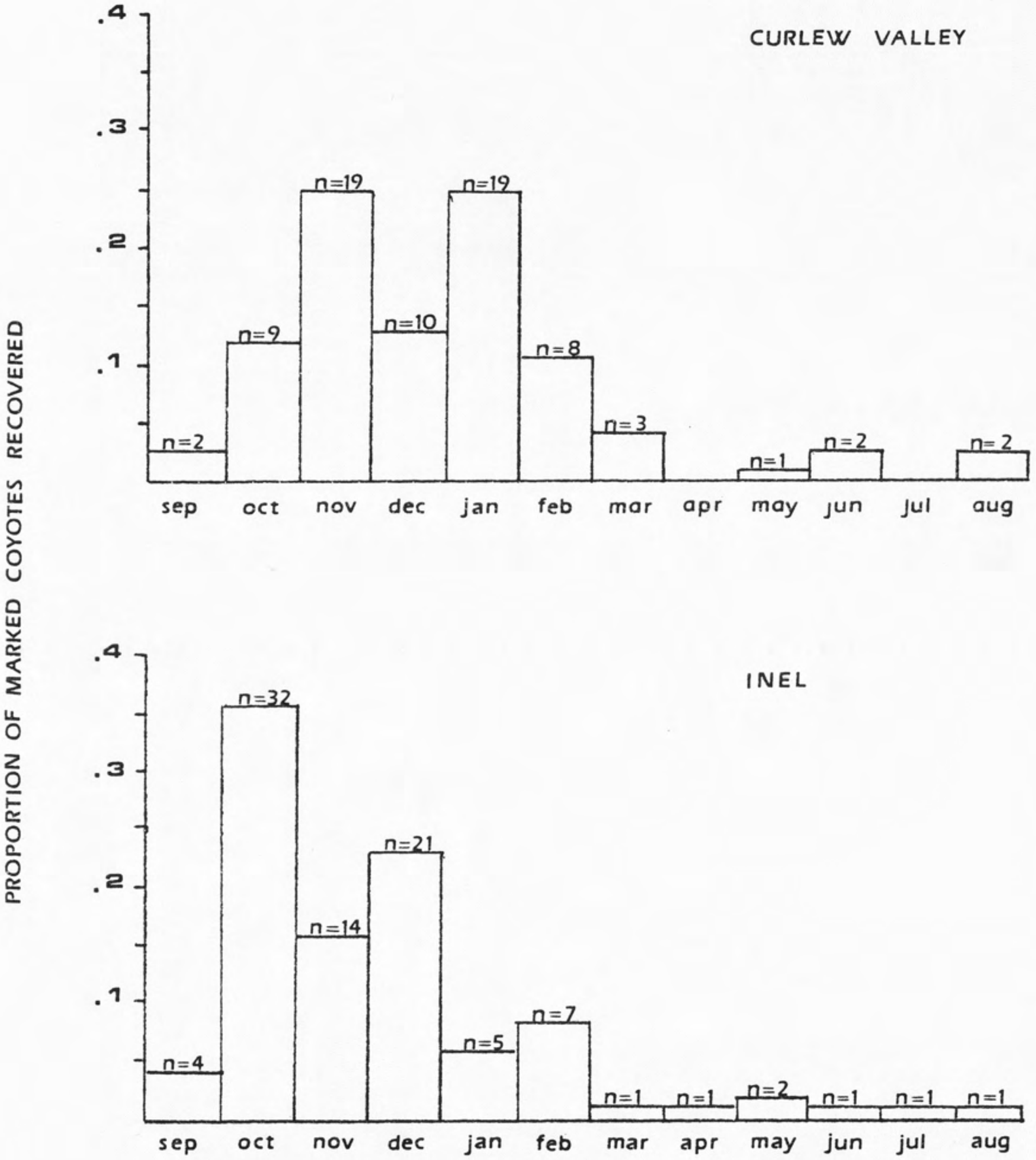

Figure 14. Proportion of all marked coyotes recovered in Curlew Valley and the INEL from 1975 to 1978 that were recovered in a given month.

Table 16.—Constant annual survival rates for adult and juvenile coyotes marked in Curlew Valley and at the INEL from 1975 to 1978. Estimates are from recovery data over the period 1975 to 1980 under Model H02 (Brownie et al. 1978)

Adults

Area	Estimate	Standard Error	95% Confidence Interval
Curlew Valley	0.4712	0.1131	0.2495-0.6930
INEL	0.5067	0.1203	0.2708-0.7425

Probability that survival rates are not different between areas = 0.390

Juveniles

Area	Estimate	Standard Error	95% Confidence Interval
Curlew Valley	0.2281	0.0679	0.0950-0.3612
INEL	0.4547	0.1590	0.1431-0.7662

Probability that survival rates are not different between areas = 0.169

subsequently recovered from 1975 to 1980 (Table 17). Approximately 44 percent (25) of the 57 coyotes marked as adults and 77 percent (68) of the 88 coyotes marked as juveniles were recovered (Table 17).

Estimates of average adult and juvenile recovery rates for 1975 to 1978 under Model H02 (Brownie et al. 1978) were 0.257 and 0.588, respectively (Table 18). This difference was highly significant ($P = 0.000$). Adult and juvenile recovery rates were year-specific. Adult rates varied from 0.17 in 1975 to 0.35 in 1978, while juvenile rates varied from 0.48 to 0.67 during the 4 years (Table 18).

Recovery location for juveniles released from 1975 to 1978 was estimated from 52 juveniles recovered in the first year following release. Of these 52, only 40 percent were recovered within the INEL population. Information on location of recovery was available for 37 of 41 adults (including adult survivors of juveniles marked in previous years) recovered from 1975-76 to 1979-80. Sixty-five percent (24) were recovered within the population under study. Overall, marked adults were recovered an average of 20.1 km (s.e. = 3.2) from capture locations. In contrast, marked juveniles were recovered significantly further from where they were trapped and released, an average of 30.1 km (s.e. 3.3).

Information on cause of recovery from 1975-76 to 1979-80 was available for 51 of the 52 recovered juveniles and 35 of the 41 recovered adults. Seventy-eight percent of the recoveries used to estimate juvenile recovery rates were due to exploitation, while 16 percent resulted from unknown causes. Of the recoveries used to estimate adult recovery rates, 83 percent were from exploitation and 11 percent from unknown causes. Six percent of the adult and juvenile recoveries were

Table 17.—Recoveries of adult and juvenile coyotes marked during the fall at the INEL from 1975 to 1978

		Year of recovery				
Year marked	Number marked	1975-76	1976-77	1977-78	1978-79	1979-80
Coyotes marked and released as adults						
1975	13	2	3	0	1	1
1976	15		3	2	1	0
1977	16			5	2	0
1978	13				5	0
Coyotes marked and released as juveniles						
1975	10	6	2	0	1	0
1976	14		7	1	1	0
1977	33			22	5	0
1978	31				17	6
All coyotes marked and released (adults and juveniles combined)						
1975	23	8	5	0	2	1
1976	29		10	3	2	0
1977	49			27	7	0
1978	44				22	6

Table 18.—Recovery rates of adult and juvenile coyotes marked during the fall at the INEL from 1975 to 1978 as estimated by Model H02 (Brownie et al. 1978)

Adult recovery rates (f_i)

Year	Estimate	Standard Error	95% Confidence Interval
1975	0.1670	0.1015	-0.0321 - 0.3660
1976	0.2874	0.0954	0.1005 - 0.4743
1977	0.2234	0.0789	0.0688 - 0.3781
1978	0.3508	0.1028	0.1492 - 0.5524
Average Estimate =	0.2571	0.0524	0.1544 - 0.3599

Juvenile recovery rates (f'_i)

Year	Estimate	Standard Error	95% Confidence Interval
1975	0.6659	0.1187	0.4332 - 0.8986
1976	0.4769	0.1240	0.2340 - 0.7199
1977	0.6604	0.0764	0.5107 - 0.8101
1978	0.5484	0.0894	0.3732 - 0.7236
Average Estimate =	0.5879	0.0567	0.4768 - 0.6991

Probability that adult and juvenile recovery rates are not different = 0.000

due to vehicle-related deaths. Aerial hunting accounted for approximately 25 percent of all deaths due to exploitation. Estimates of the percentage of all recoveries that occurred both within the study population and from exploitation were obtained from the information on location and causes of recovery from 1975-76 to 1979-80. These estimates were 22 percent for juveniles and 51 percent for adults.

Over the course of the study, marked coyotes were recovered mostly in fall and early winter. Seventy-four percent (67) of the 90 coyotes for which there was sufficient data were recovered October through December (Fig. 14). Recoveries in October accounted for nearly 30 percent of the total.

Constant annual survival rates were estimated to be 0.501 for adults and 0.455 for juveniles (Table 16). These estimates were not significantly different (P = 0.38), nor were there differences by sex in either recovery or survival rates ($\chi^2_{(8df)} = 2.92$, P = 0.94). Additional information on adult survival was obtained from the pooled age distribution (1975-1978 combined) sampled from the INEL population. This sample differed significantly from a geometric distribution ($z^2 = 16.49$) because the juvenile (zero) age class was over-represented relative to the older (1-8) age classes. While the assumption of constant average annual survival throughout all age classes was not met, it was met in the adult (1-8) segment of the sample age distribution ($z^2 = 1.19$). Using the Chapman-Robson model, the adult average annual survival rate was estimated to be 0.616. The 95 percent confidence interval was estimated to be 0.536-0.696.

Comparison of Curlew Valley and INEL

Average adult recovery rates were significantly different for coyotes marked in the two study areas (Tables 15 and 18, P = 0.058). The higher recovery rates for adults in Curlew Valley were more apparent when the rates based only on radio-marked coyotes (0.584) were compared with INEL (P = 0.003). Mean annual recovery rate for juveniles at the INEL was significantly higher than for juveniles in Curlew Valley (P = 0.08). However, when recovery rates from transmittered animals only were compared, there was no difference between the two areas (P = 0.397).

A significantly smaller proportion of juveniles was recovered within the study population at the INEL (0.40) in comparison to Curlew Valley (0.74, P = 0.001). There were no differences between areas in the proportion of adults recovered within the study populations (P = 0.15). The principal cause of recovery for juveniles and adults in both areas was exploitation, and the areas did not differ significantly in this respect with regard either to juveniles (P = 0.14) or adults (P = 0.19). The proportion of all juvenile recoveries that occurred within the study population as a result of exploitation differed greatly between areas (Curlew Valley = 0.70 vs. INEL = 0.22, P = 0.00). Significantly fewer adults were recovered within the INEL population as a result of exploitation (0.51) in comparison to Curlew Valley (0.74, P = 0.07).

Although adult coyotes marked at the INEL on the average were recovered at greater distances from their capture site (20 vs. 9 km), the difference was not significant (P<0.10). Similarly, there was no difference between juveniles with regard to recovery distance (P = 0.12), although individuals at the INEL moved an average of 30 km in comparison to 23 km in Curlew Valley.

There were no significant differences between the areas in proportions of coyotes dying from man-related causes, hunting, or aerial hunting ($P<0.10$).

The distribution of recoveries of marked coyotes in Curlew Valley and the INEL from 1975 to 1980 was significantly different (P = 0.02). In general, mortality at the INEL was greater in October and less January through March (Fig. 14).

Estimates of constant annual survival for adults in Curlew Valley (0.47) and INEL (0.51) were not different (P = 0.390, Table 16). Although the estimate of annual juvenile survival at the INEL (0.45) was nearly twice that in Curlew Valley (0.23), the difference was not significant (P = 0.17).

Chapman-Robson estimates of average annual adult survival rate were significantly different for the pooled, sample age distributions taken from the Curlew Valley and INEL populations (P = 0.04). Juveniles were over-represented in both sample age distributions. Such over-representation may have been due to lower juvenile survival rates relative to adults, but also may have been due to increasing population size, non-random sampling, or inaccurate age determination.

Emigration

Curlew Valley

From 1976 through 1977, 45 of the 49 juvenile coyotes that were marked with transmitters during September-October in Curlew Valley were subsequently accounted for over the following nine months (Table 19). Of those 45 with known status, 0.31 emigrated between date of release and June. Over the same interval, approximately 0.42 of the marked juveniles died within the study area, and 0.27 remained alive in Curlew Valley. There were no significant differences between 1976 and 1977 in any of these proportions. Of the 0.69 (31) that remained on the study area, 0.39 (12) survived to June (Fig. 15). Seventeen (0.90) of the 19 juveniles that died on the study area before June did so as a result of hunting and trapping. Six (0.43) of the 14 coyotes that emigrated survived to one year of age (June).

Sixty-four percent of the juvenile coyotes emigrating from Curlew Valley were female. However, chi-square tests for differences in sex ratio among juvenile coyotes that either emigrated, remained alive on the study area, or died on the study area were not significant; nor did any of the ratios differ from equality.

There were no significant differences in body weights at the time of capture among individuals who subsequently either emigrated, remained alive, or died on the study area (Table 20).

Fifty-seven percent of those juvenile coyotes that emigrated did so during December and January (Fig. 16). Another 28 percent emigrated

Table 19.—Comparison of emigration rates and related parameters for juvenile coyotes marked in Curlew Valley and at the INEL, 1975 to 1978. Estimates cover the period from marking (September-October) to June of the following year

Area Year	Number released	Number with known status	Proportion emigrating	 remaining alive in the area	 dying in the area
Curlew Valley					
1976	28	26	0.231	0.346	0.432
1977	21	19	0.421	0.157	0.421
Overall	49	45	0.311	0.267	0.422
INEL					
1975	10	10	0.500	0.200	0.300
1976	14	11	0.545	0.273	0.182
1977	33	31	0.484	0.226	0.290
Overall	57	52	0.500	0.231	0.269
Probability that overall proportions are not different			0.067	0.367	0.113

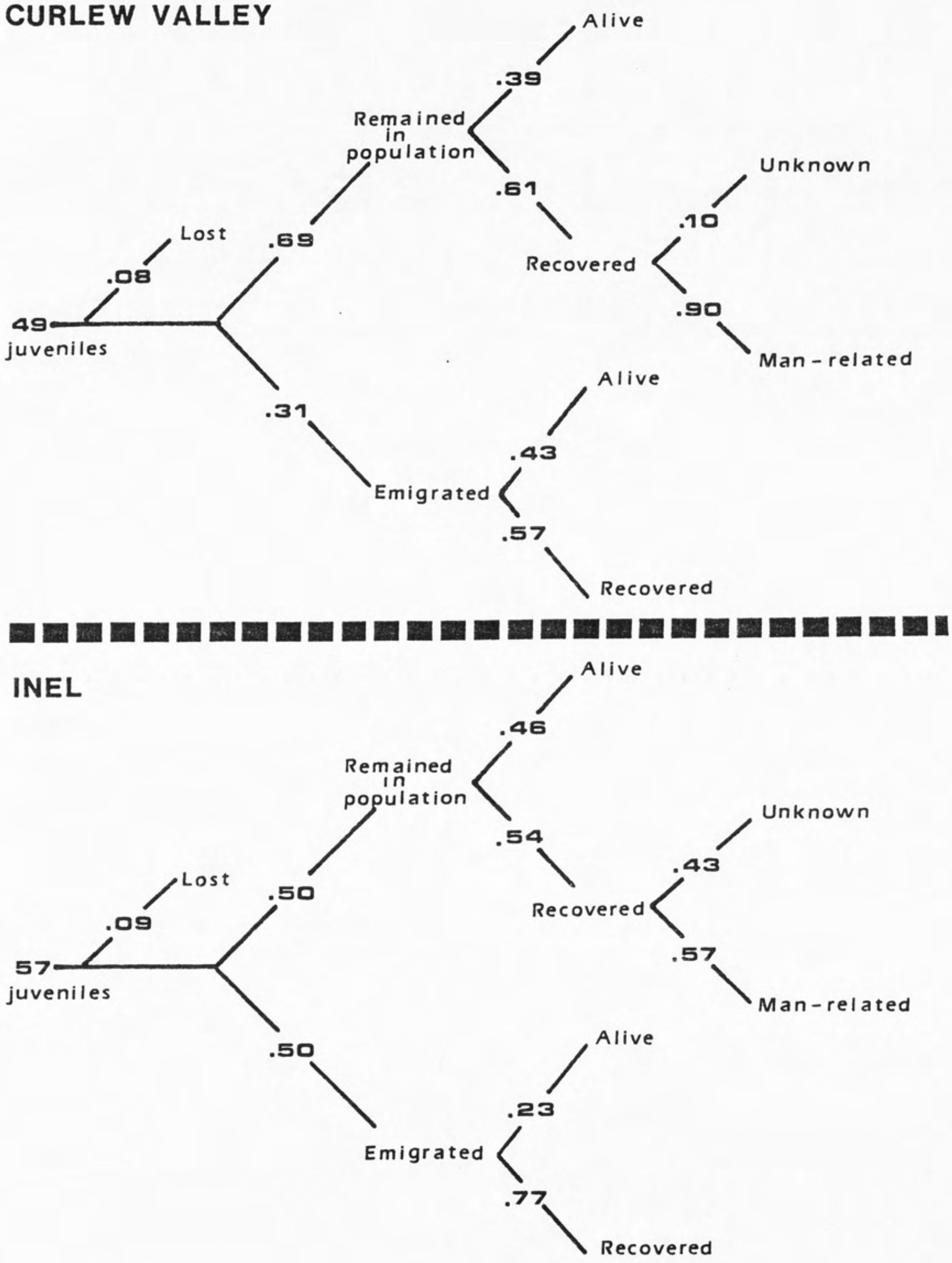

Figure 15. The fate of juvenile coyotes marked in Curlew Valley (1976-1977) and the INEL (1975-1977) from release in September-October to June.

Table 20.—Comparison of body weights at the time of capture based on an individual's subsequent status during the period from release (September-October) to June. Within Curlew Valley (1976-1977) and INEL (1975-1977), differences among mean body weights for the three classifications of status were tested for with one-way analysis of variance[1]

	Status				
	Emigrated	Alive on study area	Died on study area	F ratio	Prob.
<u>Curlew Valley</u>					
Mean weight at capture (kg)	7.24 A	7.92 A	7.96 A	1.56	0.222
Sample size	14	12	19		
<u>INEL</u>					
Mean weight at capture (kg)	7.21 A	8.66 B	7.56 AB	3.98	0.025
Sample size	26	12	14		

[1] Means in a given row followed by a different letter are significantly different ($P < 0.01$).

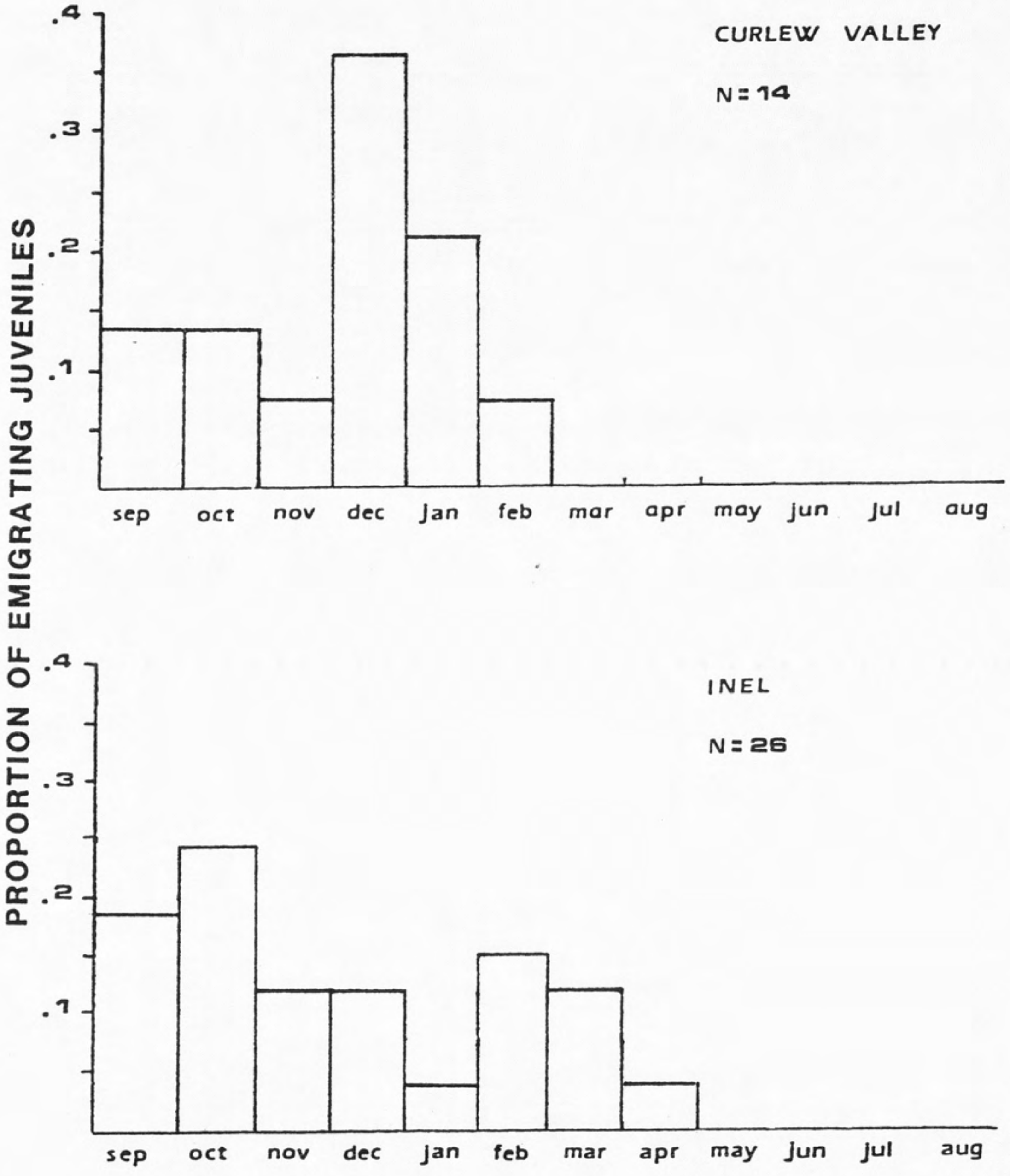

Figure 16. Proportion of all marked, juvenile coyotes emigrating from Curlew Valley (1976-1977) and the INEL (1975-1977) that emigrated in a given month.

in late September and October. No juveniles were observed to have emigrated after the first two weeks in February.

Emigrating juvenile coyotes in Curlew Valley moved a mean linear distance of 51.9 km (s.e. = 11.3) from their capture location during the period from release to June.

INEL

At the INEL, 0.91 (52) of the 57 juvenile coyotes marked from 1975 to 1977 had known status over the period September-October to June (Table 19). Of those followed successfully 0.50 emigrated prior to reaching one year of age. Of those remaining on the study area, approximately 0.27 died and 0.23 remained alive during the interval from release to June of the following year. There were no significant differences among years in the proportion emigrating, remaining alive, or dying. Of the 26 juveniles (0.50) with known status that did not emigrate, 0.46 (12) survived to one year of age (June). Only 0.43 (14) of the mortality of juveniles that died on the study area before June was man-related. Six (0.23) of the 26 emigrating juveniles survived from release to June.

Females comprised 48 percent of those juvenile coyotes known to have emigrated from the INEL. Chi-square tests for differences in sex ratio among juveniles that either emigrated, remained alive, or died on the study area were not significant. None of the observed sex ratios for the three classifications of status differed from equality.

Significant differences were found among mean body weights of juveniles at the time of capture based on the subsequent status of those juveniles during the period from release to June (Table 20). Juveniles remaining alive on the area averaged more than one kg heavier at the time of capture than individuals emigrating or dying on the study area. Emigrated weighed the least of all coyotes captured and significantly less than those coyotes remaining alive on the area ($P<0.01$, Duncan's new multiple range test, Steel and Torrie 1960:112).

Fifty-four percent of emigrating juveniles left the INEL from late September through November (Fig. 16). Forty-two percent emigrated during late September and October. Approximately 31 percent of those juvenile coyotes emigrating from the INEL did so from late February to early April. During the nine months following release, juveniles emigrated a mean linear distance of 36.2 km (s.e. = 4.1).

Comparison of Curlew Valley and INEL

Overall, a significantly greater proportion of juvenile coyotes emigrated from INEL (0.500) in comparison to Curlew Valley (0.311) for the years 1975-1977 and 1976-1977, respectively (Table 19). There were no significant differences between the study areas with regard to the proportions remaining alive or dying on the study area for the nine-month period following capture and release. Of those juveniles recovered within the study populations, a significantly greater proportion died from unknown causes at the INEL (0.43) in comparison to Curlew Valley (0.10, $P = 0.036$).

There were no differences between INEL and Curlew Valley in sex ratios of emigrators or those that remained within the study areas.

Coyotes trapped on the areas differed with regard to mean body weights at the time of capture for the three classifications of status as already discussed (Table 20).

Timing of emigration was distributed differently between the two areas ($P<0.10$). In general, emigration was greatest in September-October and February-March at the INEL in comparison to emigration in Curlew Valley, which was concentrated in December and January (Fig. 16).

Finally, there were no significant differences between areas in either the mean linear distance moved by emigrators ($P = 0.15$) or in the proportion surviving to one year of age ($P = 0.19$).

DISCUSSION

Population Synthesis

Summary of Estimates

Estimates of population parameters for coyotes in Curlew Valley and the INEL over the four years of the study are summarized in Table 21. A number of generalizations drawn from comparisons of the mean values also are presented.

The finite survival rate (S) is the proportion of marked coyotes that survive an annual period (September to September):

$$S = \frac{\text{Number of marked coyotes alive at the beginning of year } i+1 \text{ of those alive at the beginning of year } i}{\text{Number of marked coyotes alive at the beginning of year } i.}$$

The complement of S, of course, is total mortality rate (M), or the proportion of marked coyotes alive at the start of the year that die during the year:

$$M = \frac{\text{Number of marked coyotes dead in year } i \text{ from all causes}}{\text{Number of marked coyotes alive at the beginning of year } i.}$$

Estimates of these parameters in this study were provided principally by the procedures of Brownie et al. (1978).

Because recovery rates (f_i) were estimated from recoveries due to all causes, estimates of f_i (adult) and f_i' (juvenile) under Model H02 approximate the total probability of death from all factors. As a result, total mortality rates or survival rates could have been estimated by either $\hat{f}_i$ and $\hat{f}_i'$ or by estimates of adult and juvenile constant

Table 21. Summary of population parameter estimates (SE) for coyotes in Curlew Valley and at the INEL, 1975-1978

Parameter	Average Estimates			
	Adults		Juveniles	
	CV	INEL	CV	INEL
LOSS RATES				
Overall				
Total Mortality, $(1-\hat{S})$, $\hat{M}$	0.53 (.11)	0.49 (.12)	0.77 (.07)	0.55 (.16)
Hunting, $\alpha(1-\hat{S})$, $\hat{K}$	0.49 (.11)	0.41 (.10)	0.69 (.07)	0.43 (.13)
α	0.93 (.05)	0.83 (.06)	0.89 (.05)	0.78 (.06)
Nonhunting, $\hat{M}-\hat{K}$	0.04 (.03)	0.08 (.04)	0.08 (.04)	0.12 (.05)
In Situ				
Total Losses, $\hat{T}$	0.43 (.11)	0.32 (.10)	0.85 (.05)	0.70 (.12)
Mortality, $\gamma\hat{M}$	0.43 (.10)	0.32 (.10)	0.57 (.07)	0.22 (.05)
γ	0.81 (.08)	0.65 (.08)	0.74 (.07)	0.40 (.07)
Hunting, $\beta\hat{M}$	0.39 (.10)	0.25 (.07)	0.54 (.07)	0.12 (.05)
β	0.74 (.08)	0.51 (.08)	0.70 (.07)	0.22 (.06)
Nonhunting, $\gamma\hat{M}-\beta\hat{M}$	0.04 (.03)	0.07 (.03)	0.03 (.02)	0.10 (.04)
Surviving Emigrators, $\epsilon\hat{S}'$	-	-	0.08 (.03)	0.15 (.07)
ϵ			0.33 (.11)	0.33 (.11)
Emigration, $\hat{E}$	-	-	0.31 (.07)	0.50 (.07)
	Curlew Valley		INEL	
RECRUITMENT RATES				
P_f	0.88 (.03)		0.78 (.04)	
P_s	0.78 (.04)		0.76 (.04)	
DENSITY				
Scent Station Indices				
Spring	6.8		12.4	
Fall	45.9		49.6	
Isotope Tagging (Fall 1977, 1978)	0.21 km^{-2}		0.30 km^{-2}	

annual survival rates ($\hat{S}$ and $\hat{S}'$). However, estimated mean recovery and constant annual survival rates were not complements, perhaps as a consequence of the large variability associated with each estimate. Estimates of constant annual survival rate are less biased statistically and probably biologically than estimates of mean recovery rate. Recovery rate estimates are dependent on transmitter longevity. Therefore, only estimates of S and S' will be used in the calculation of loss rates that follows.

Estimated survival rates ($\hat{S}$ and $\hat{S}'$) were slightly lower for adults and substantially lower for juveniles in Curlew Valley, although neither rate was significantly different from those estimated for adults and juveniles at the INEL (Table 21). It is important to remember that these estimates apply to all marked coyotes regardless of whether they remained members of the study population.

The kill rate or hunting mortality rate (K) is the proportion of those marked coyotes alive at the start of the year that die from hunting during the year:

$$K = \frac{\text{Number of marked coyotes dead in year i from hunting}}{\text{Number of marked coyotes alive at the beginning of year i.}}$$

K reflects all deaths due to hunting, including those coyotes not retrieved and/or not reported. Estimates of K were calculated from the proportion of all recoveries due to hunting (α):

$$\hat{K} = \alpha\, \hat{M} = \alpha\, (1-\hat{S}).$$

Hunting mortality rates were higher for adults and significantly higher for juveniles marked in Curlew Valley than at the INEL (Table 21).

Nonhunting mortality rate (V) is the proportion of marked coyotes alive at the start of the year that die to all causes other than hunting during the year:

$$V = \frac{\text{Number of marked coyotes dead in year i due to all causes other than hunting}}{\text{Number of marked coyotes alive at the beginning of year i.}}$$

V was estimated as follows:

$$\hat{V} = (1-\alpha)\cdot(1-\hat{S}) = \hat{M} - \hat{K}.$$

Estimated nonhunting mortality rates were higher for adults and significantly higher for juveniles marked in the control area (Table 21).

While the above discussion has focused on mortality rates for all coyotes marked, of greater interest here is the level of exploitation for animals continuing to reside within the treatment and control areas. The experimental design of the study was based on the premise that hunting mortality rates were substantially higher in the treatment area, Curlew Valley. To determine the validity of this premise, total loss rate (T) was estimated for resident populations within the treatment and control areas. The complement of total loss rate is in situ survival rate ($S_{\{in\ situ\}}$). Total loss rates for resident juvenile populations (T') include mortality from all causes as well as losses from juveniles that emigrate but survive from year i to year i+1:

$$\hat{T}' = 1 - \hat{S}'_{\{in\ situ\}} = \hat{K}' + \hat{V}' + \varepsilon\hat{S}'$$

where ε is the proportion of marked juveniles that both emigrated and survived. Hence, the rate $\varepsilon\hat{S}'$ represents losses to resident juvenile populations from surviving emigrators that are in addition to those accounted for by $\hat{K}'$ and $\hat{V}'$. For example, T' was calculated as follows for

Curlew Valley:

$T' = 0.69 + 0.08 + (0.33)(0.23) = 0.85$, and for

INEL:

$T' = 0.43 + 0.12 + (0.33)(0.45) = 0.70$.

Estimates of losses from surviving emigrators ($\varepsilon S'$) were lower for the treatment population, but the difference was not significant. In situ total loss rates for juveniles also did not differ significantly between Curlew Valley and the INEL. Estimates of T' assume that estimated overall survival rates ($\hat{S}'$) or total mortality rates ($\hat{M}'$) did not differ for resident and nonresident juveniles marked in a given study area.

Total loss rates for resident adult populations (T) were estimated from the proportion of all recoveries that occurred within the study populations (γ) and were equivalent to the in situ mortality rates:

$$\hat{T} = \gamma\hat{M} = \hat{M}_{\{\text{in situ}\}}$$

In situ total loss rates for adults residing within the two study areas did not differ significantly. If adults that died more than 5 km from the study area boundaries were still members of the populations, then overall estimates of total mortality rate would reflect losses to resident adult populations more accurately than in situ rates.

In situ hunting mortality rates were estimated from the proportion of all recoveries that occurred both within the study areas and as a result of exploitation (β):

for adults

$$\hat{K}_{\{in\ situ\}} = \beta\hat{M}, \text{ and}$$

for juveniles

$$\hat{K}'_{\{in\ situ\}} = \beta\hat{M}' = \beta(\hat{T}' - \varepsilon\hat{S}').$$

As required by the experimental design of the study, hunting mortality or exploitation rates were indeed substantially higher for juveniles and adults residing in the treatment area (Table 21). Juvenile kill rates for the treatment population were approximately 4 times as great as those for the control population, while adult in situ kill rates were 50 percent higher in Curlew Valley. However, only the difference between areas in juvenile kill rates was significant.

In situ nonhunting mortality rates were estimated as follows:

$$\hat{V}_{\{in\ situ\}} = \hat{M}_{\{in\ situ\}} - \hat{K}_{\{in\ situ\}}$$

where $M_{\{in\ situ\}}$ was estimated from the proportion of all recoveries that occurred within the study areas (γ). Estimates of $V_{\{in\ situ\}}$ were higher for adults and significantly higher for juveniles residing in the control population (Table 21). A procedure approximately equivalent, then, to the one given above for estimating total juvenile loss rate would be as follows:

$$\hat{T}' = \hat{K}'_{\{in\ situ\}} + \hat{V}'_{\{in\ situ\}} + \hat{E}$$

where E is the rate of emigration given in Table 19. Emigration rates were significantly greater at the INEL.

The above relationships between finite rates given variously as

$M = K + V$, or

$T = K_{\{in\ situ\}} + V_{\{in\ situ\}}$, or

$T' = K' + V' + \varepsilon S' \doteq K'_{\{in\ situ\}} + V'_{\{in\ situ\}} + E$

are true regardless of whether the loss processes are additive or compensatory, or when during the year the forces of mortality or emigration occur. These relationships do not indicate how the <u>observed</u> rates $\hat{M}$, $\hat{K}$, $\hat{V}$, $\hat{S}$, or $\hat{T}$ change in relation to one another. One would like to know, for instance, what the nonhunting mortality rates are when $K=0$, or, alternatively, what the hunting mortality rates are when $V=0$. Anderson and Burnham (1976) have termed the former a "conditional nonhunting mortality rate, V_0," and the latter a "conditional kill rate, K_0." The parameter K_0, however, is an abstract rate that is not estimable unless hunting is assumed to be a totally additive form of mortality. The nonhunting mortality rate in the absence of deaths from hunting (V_0) commonly has been estimated by solving Ricker's (1958) equation $M = K_0 + V_0 - K_0V_0$ for V_0, so that $V_0 = (M-K_0)/(1-K_0)$. However, this estimation procedure makes the assumption, as above, that loss rates are additive and independent. Even if this assumption were made, the investigation of how mortality rates change in relation to one another is complicated further with consideration of losses due to emigration. Thus, the observed rate $\hat{K}'_{\{in\ situ\}}$ is the juvenile hunting mortality rate in the presence of not only the observed nonhunting mortality rate, $\hat{V}'_{\{in\ situ\}}$, but also the observed rate of emigration, $\hat{E}$.

It seems most likely that loss rates do not function independently or as an additive process, but rather function as competing risks (cf David and Moeschberger 1978 or Birnbaum 1979). Moreover, the risks of loss from hunting, nonhunting causes, and emigration are dependent upon the magnitude of one another. That is, the number of coyotes emigrating is dependent upon the extent to which the risks of death due to hunting and nonhunting causes materialize first. Such loss processes are a classical example of a problem in competing risks. Unfortunately, in the case where risks are dependent, as seems virtually certain in this study, the theory of competing risks remains poorly developed (Birnbaum 1979).

Consequently, comments about how various mortality and emigration parameters change in relation to one another will be limited to a comparison of observed rates in the treatment and control populations. Such comparisons will be discussed more fully in a subsequent section, but a few generalizations are appropriate here. First, adult survival rates were similar in the treatment and control populations. In the control population, lower kill rates were offset by higher nonhunting mortality rates, while in the treatment population higher kill rates were offset by lower nonhunting mortality rates. Total loss rate of juveniles was slightly, but not significantly higher in the treatment area. Significantly lower kill rates for juveniles in the control area were accompanied by significantly higher nonhunting mortality and emigration rates, suggesting some compensation among loss rates.

Estimates of recruitment to the fall treatment and control populations based on age and sex ratios generally increased over the study period, while those estimates based on scent station indices generally decreased. Both estimates are subject to problems. Because the relationship between density and scent station indices is not understood, spring to fall changes in such indices only provide qualitative information on overall trends and may be relatively insensitive measures of recruitment. For example, in 1975 recruitment in Curlew Valley was estimated to be zero using spring to fall changes in the proportion of scent stations visited. Moreover, there was no valid statistical means of comparing percentage change in indices from spring to fall between years within an area or between areas. More specific and perhaps sensitive estimates of recruitment that could be compared statistically were those based on sex and age structure of coyotes trapped in the fall (P_f and P_s). However, these estimates may be subject to age and sex specific sampling biases. Nevertheless, much of the discussion that follows will require estimates of actual recruitment rates that can be compared statistically, rather than information on trends. Hence, age and sex ratio estimates will be used as the principal estimates of recruitment (reproduction, post-natal survival, immigration). Given the contradictory nature of recruitment estimates within each area, it is important to emphasize that estimates of recruitment from scent station indices and age and sex ratios were in good agreement with regard to differences between Curlew Valley and the INEL.

Although estimates of P_f were not significantly greater in Curlew Valley for any of the years on an individual basis, they were consistently greater for each of the 4 years. The average proportion of pups in the fall population of pups and adult females (P_f) reflected this consistent difference and was significantly greater in Curlew Valley for the 4 years of the study (Table 21). If biases in samples from trapping are similar in the control and treatment populations, these differences between areas in P_f may reflect differences in recruitment to the respective fall populations. Such differences may have been due to greater reproduction, summer survival, or immigration in Curlew Valley. Because estimates of overwinter survival were substantially lower for juveniles in Curlew Valley, the proportion of pups in the spring population of pups and adult females (P_s) did not differ between areas in any given year or overall. Thus, greater reproduction, survival, or immigration in Curlew Valley prior to fall sampling appears to have been offset by lower overwinter survival of pups. Similarities in recruitment to spring populations in both areas suggest average rates of growth in the two populations also were similar from 1975 to 1978.

The high estimates of P_f for both the treatment and control populations, particularly in 1978, suggest that pups were over-represented in the samples relative to the true value of the parameter P_f. A less likely alternative is that the high estimates of P_f, particularly in Curlew Valley, are not biased but reflect immigration during August and September. Most commonly, however, it has been assumed that juveniles are more susceptible to trapping than are older coyotes.

Without rejecting this assumption, it must be noted that differential vulnerability to trapping by age has never been well documented in canids.

In relation to the above problem, pups were found to average approximately 50 percent of samples from aerial hunting in and surrounding Curlew Valley during January and February, 1977 and 1978 (Davison unpublished data). If the total loss rates for juveniles and adults (T and T') in Curlew Valley are applied to the sample age structures from trapping in fall 1976 and 1977, roughly 65 percent, not 50 percent, of the subsequent aerial hunting samples in January and February would have been expected to be juveniles. Knudsen (1976) used a similar line of reasoning to conclude samples from fall trapping were not representative of the population in Curlew Valley. However, there are at least two problems with such an approach. First, the aerial hunting and trapping samples were not drawn from the same geographic area or, most likely, the same population. Second, adults during the breeding months of January and February may be more vulnerable to aerial hunting than juvenile coyotes. Therefore, at best, evidence of age-specific biases in fall trapping based on winter aerial hunting samples is inconclusive. Thus, while recognizing potential biases may exist in age and sex structure data derived from trapping, such data do provide the best estimates available in this study for comparison of recruitment rates.

Greater rates of recruitment to the fall population in the treatment area also were associated with similar or slightly higher total adult and juvenile loss rates, similar recruitment to the spring population, and similar spring and fall densities in the two study areas.

The latter conclusion is based on the estimates of density judged to be the most comparable between the two areas, i.e., those provided by the scent station indices and isotope tagging. As noted earlier, comparisons of relative density between areas based on scat indices may be unsound due to suspected differences in vehicle traffic on the scat transects in the two areas. The lack of an acceptable means of determining the variability in catch-effort indices also precludes meaningful comparisons of relative density based on trapping.

Estimates of fall density for 1977 and 1978 from isotope tagging averaged 0.21 coyotes km^{-2} in Curlew Valley and 0.30 coyotes km^{-2} at the INEL. Because fall scent station indices at the INEL did not differ significantly from 1976 to 1978, 0.30 coyotes km^{-2} is most likely a reasonable estimate of fall density for all years but 1975. Fall scent station indices for Curlew Valley were similar in 1976 and 1978 (68.8 and 74.1). If densities also were similar in those two years, the estimate for fall 1978 of 0.24 coyotes km^{-2} probably would be reasonable for fall 1976. An average estimate of fall density from 1976 through 1978, then, would be 0.22 coyotes km^{-2}. These estimates for Curlew Valley and INEL are not significantly different and lie within the range of density estimates (0.1-0.6 coyotes km^{-2}) reported for coyotes (U. S. Fish and Wildlife Service 1978:70). Although estimates of relative spring density and 1975 fall density did not differ between areas, both probably were significantly lower than the 0.22 and 0.30 coyotes km^{-2} given above as average fall densities from 1976 to 1978 for Curlew Valley and the INEL.

Validity of Estimates

Validity of the estimates of total loss rates, recruitment, and changes in density was assessed using modified Leslie (1945, 1949) matrix population projection techniques. Projections were made from September (year i) to September (year i+1). Because overall sex ratios for the control and treatment populations did not differ from equality and survival did not differ by sex, projections were made only for the female segment of the respective populations. Initial population vectors were constructed from the pooled, sample age distributions given in Table 12. Measures of recruitment were used as the fecundity elements of the projection matrices. The recruitment measure used was the average number of female pups per adult female based on the September trapping samples. Fecundity of pups was assumed to be zero, while adult fecundity was assumed to be constant with age. Estimated survival rates for adults ($\hat{S}$) and juveniles ($\hat{S}'_{\{in\ situ\}}$) were used as the survival elements of the projection matrices. Projection of the 7 x 7 (Curlew Valley) and 9 x 9 (INEL) matrices was done in one-year time steps using a computer program developed by G. S. Innis (1975). Projections were made for 15 years, and the rate of population increase (λ) was calculated after a stable age distribution was reached; all runs were deterministic.

The initial population vectors, projection matrices, and stable age distributions for Curlew Valley and the INEL are shown in Figure 17. For both study populations, the projected age distributions remained virtually unchanged from the pooled, sample age distributions

$$\begin{array}{cccc} & \text{Population projection matrix} & \text{Initial age vector} & \text{Stable age distribution} \\ \text{CURLEW VALLEY} & \begin{bmatrix} 0.000 & 4.000 & 4.000 & \cdots & 4.000 \\ 0.151 & & & & \cdot \\ & 0.471 & & & \cdot \\ & & 0.471 & & \cdot \\ & & & \ddots & \cdot \\ & & & \ddots & \cdot \\ & & & & 0.471 \end{bmatrix} \times & \begin{bmatrix} .80 \\ .11 \\ .05 \\ .02 \\ .01 \\ .00 \\ .01 \end{bmatrix} = & \begin{bmatrix} .79 \\ .11 \\ .05 \\ .02 \\ .01 \\ .01 \\ .00 \end{bmatrix} \end{array}$$

$$\begin{array}{cccc} \text{INEL} & \begin{bmatrix} 0.000 & 1.741 & 1.741 & \cdots & 1.741 \\ 0.303 & & & & \cdot \\ & 0.507 & & & \cdot \\ & & 0.507 & & \cdot \\ & & & \ddots & \cdot \\ & & & \ddots & \cdot \\ & & & \ddots & \cdot \\ & & & \ddots & \cdot \\ & & & & 0.507 \end{bmatrix} \times & \begin{bmatrix} .62 \\ .17 \\ .07 \\ .05 \\ .03 \\ .03 \\ .01 \\ .02 \\ .01 \end{bmatrix} = & \begin{bmatrix} .63 \\ .19 \\ .09 \\ .05 \\ .02 \\ .01 \\ .01 \\ .00 \\ .00 \end{bmatrix} \end{array}$$

Figure 17. Projection matrices, initial age vectors, and stable age distributions for coyote populations in Curlew Valley and the INEL, 1975-1978

used as the initial population vectors. Age distributions are the outcome of fecundity and survival rates. Similarities between the projected age distributions and the observed pooled, sample age distribution indicate that estimated survival and recruitment rates are consistent with the observed age structures. In other words, the observed age structures for the Curlew Valley and INEL populations were the stable age distributions that would have resulted from the constant rates of recruitment and survival estimated for each population. Rates of increase for Curlew Valley and the INEL were 5 percent (λ = 1.05) and 2 percent (λ = 1.02), respectively. Higher adult and juvenile losses in the treatment population were offset by higher recruitment to the fall population, resulting in a rate of increase similar to the rate of increase in the control population.

Given the large sampling error in estimates of recruitment and survival rates, estimates of λ must be viewed with caution. Nevertheless, the finding from these deterministic projections that both populations were approximately stationary generally is corroborated by the estimates of density for 1976 through 1978. As noted earlier, densities in those years were probably similar for each population, although densities in 1975 were probably lower. Thus, there was approximate agreement between the projected and observed rates of increase, as well as between the projected and observed age distributions. The consistency among estimates of recruitment, in situ survival, age structure, and density for the treatment and control populations apparent from the projections support the validity of the estimates.

The Role of Prey Availability and Utilization

The extent to which comparisons of the parameters and dynamics of the Curlew Valley and INEL populations are affected by differential prey availability and utilization is important because food has been shown to be an important factor influencing coyote populations. Changes in coyote density reportedly reflect changes in the availability of carrion (Todd and Keith 1976, Weaver 1977), microtines and snowshoe hare (Nellis and Keith 1976), and small rodents (Gier 1968, Knowlton et al. 1971). Response of reproductive parameters of coyotes to increasing abundance of prey has been shown by Gier (1968) and Clark (1972). Significant differences between the Curlew Valley and INEL populations with regard to prey availability and utilization would weaken subsequent discussion and conclusions about the effects of exploitation.

Information on prey utilization by coyotes in Curlew Valley and the INEL came from Hoffman (1979) and Johnson (1978), respectively. Hoffman examined 2,359 scats collected from Utah and Idaho portions of Curlew Valley from September 1973 to May 1975. Johnson collected 979 scats on the INEL study area from October 1975 to July 1977. To facilitate comparison of Hoffman's and Johnson's findings, the food habits data from each have been summarized in terms of percent occurrence (Table 22). Some taxonomic classifications have been organized differently. Percent occurrence was lower for nearly all prey species reported at the INEL and may reflect the substantial differences in methods of analysis by Johnson (1978:14-16) and Hoffman (1979:22-23).

Table 22.—Year-round coyote feeding patterns in Curlew Valley (September 1973-May 1975) and the INEL (October 1975-July 1977)

	Percent Occurrence	
Prey	Curlew Valley[1]	INEL[2]
Lagomorph		
Lepus californicus	44.0	2.8
Sylvilagus spp.	15.5	35.5
Rodent		
Cricetidae		
Microtinae	22.5	17.4
Cricetinae		7.8
Peromyscus maniculatus	13.3	-
Reithrodontomys megalotis	11.3	-
Heteromyidae		
Perognathus parvus	18.8	7.5
Dipodomys ordii	11.1	6.8
Sciuridae		
Eutamias minimus	4.9	4.0
Spermophilus townsendii	4.1	7.8
Odocoileus hemionus	4.0	-
Antilocapra americana	-	4.4

[1] From Hoffman (1979:51-52). Percent occurrence for Utah and Idaho portions of Curlew Valley were combined.

[2] From Johnson (1978:55).

Lagomorphs were the most frequent prey item found in coyote scats collected from each study area. Coyotes in Curlew Valley apparently consumed blacktailed jackrabbits more commonly than other lagomorphs, while the principal lagomorph prey items of coyotes at the INEL were species of *Sylvilagus*. The very low occurrence of jackrabbits in scats of coyotes at the INEL may have been due, in part, to Johnson's (1978:17) difficulty in distinguishing between juvenile jackrabbits and cottontails.

Microtine rodents probably were the second most frequent prey item in scats from both Curlew Valley and INEL. Cricetines, pocket mice, and Ord's kangaroo rats occurred with similar frequency, although lower than microtine species. Townsend's ground squirrel was a more common prey item in scats from the INEL, and the least chipmunk occurred with similar frequency in scats from the two areas. Utilization of deer by coyotes in Curlew Valley appears to have been similar to utilization of pronghorn by coyotes at the INEL. Thus, coyote feeding patterns in the two study areas appear to have been quite similar, with the major difference being the type of lagomorph consumed.

The principal information available on lagomorph abundance was from Stoddart (unpublished data) on relative density of blacktailed jackrabbits in the Curlew Valley and INEL study areas from 1975 to 1979 (Table 23). Interpretations of those data suggest densities of blacktailed jackrabbits increased in both areas during the coyote study period. Density indices for both areas in spring of 1979 were more than 50 times the indices in spring of 1975. In general, jackrabbit density indices were somewhat higher in Curlew Valley for all years, although

Table 23.—Mean black-tailed jackrabbit density indices[1] for semiannual censuses in Curlew Valley and at the INEL, 1975-1979[2]

	Curlew Valley	INEL	Probability that indices do not differ between areas[3]
Spring 1975	0.16	0.09	0.62
Fall 1975	0.82	0.83	0.81
Spring 1976	0.20	0.00	0.20
Fall 1976	1.52	0.69	0.11
Spring 1977*	0.53	----	----
Fall 1977	3.30	2.27	0.30
Spring 1978	2.23	0.99	0.02
Fall 1978	10.37	2.56	0.00
Spring 1979	7.70	3.85	0.00

[1] Obtained by the method of Gross et al. (1974).

[2] From Stoddart (unpublished data) Wildlife Science Department, Utah State University.

[3] Probabilities were determined using RANDTEST, Grenn (1977).

*The census was not run at the INEL in Spring 1977.

the difference between areas was not significant until spring of 1978. Thus, jackrabbit densities may not have differed greatly until the last year of the coyote study. While no data were available on densities of cottontail and pygmy rabbits for either area, *Sylvilagus* spp. densities were almost certainly higher at the INEL during the study period.

Availability of rodent species in the Curlew Valley and INEL study areas could be estimated only for *Peromyscus maniculatus, Perognathus parvus, Dipodomys ordii,* and *Eutamias minimus* (Stoddart unpublished data). These were the only species caught in sufficient numbers with both snap and live traps to permit density estimation. In general, densities of rodents, particularly of *Eutamias minimus* and *Dipodomys ordii,* were higher at the INEL (Table 24). In no case, however, were either spring or fall densities significantly different between areas. Within each study site, relative numbers of rodents appeared to have been generally constant from 1975 through 1978, but indices of *Peromyscus maniculatus* fluctuated noticeably (Stoddart 1978). Very few microtines were caught in either area, although such species were the most frequently occurring rodents in coyote scats from both Curlew Valley and the INEL.

Thus, estimates of prey availability for the two study areas were not significantly different, except for jackrabbits, which were significantly more abundant in Curlew Valley from 1978 to 1979. Somewhat higher densities of jackrabbits in Curlew Valley for all years may have been offset by generally higher rodent and probably *Sylvilagus* densities at the INEL, particularly in view of the pattern of lagomorph utilization by coyotes at the INEL.

Table 24. Spring and fall mean snap trap indices and estimates mean densities for four rodent species in Curlew Valley and at the INEL, 1975 to 1978[1]

		Mean index	Density (no/ha)	95% C.I.	Index-density[2] regression
Peromyscus maniculatus					
Spring					
	Curlew Valley	18.9	4.6		$y = 0.13x + 2.23$
	INEL	10.4	3.8	2.5-5.2	$y = 0.12x + 2.54$
Fall					
	Curlew Valley	7.1	3.1		
	INEL	9.6	3.7	2.4-5.1	
Perognathus parvus					
Spring					
	Curlew Valley	1.6	1.3		$y = 0.40x + 0.67$
	INEL	0.6	1.7	-0.2-3.7	$y = 2.05x + 0.51$
Fall					
	Curlew Valley	0.9	1.0		
	INEL	0.3	1.1	-1.3-3.5	
Dipodomys ordii					
Spring					
	Curlew Valley	1.1	0.6		$y = 0.24x + 0.37$
	INEL	1.5	1.5	0.0-3.1	$y = 0.86x + 0.14$
Fall					
	Curlew Valley	2.0	0.9		
	INEL	1.7	1.6	0.0-3.3	
Eutamias minimus					
Spring					
	Curlew Valley	0.8	0.5		$y = 0.07x + 0.44$
	INEL	2.4	2.6	0.7-4.1	$y = 0.64x + 1.05$
Fall					
	Curlew Valley	0.7	0.5		
	INEL	3.3	3.2	1.7-4.9	

[1] From Stoddart (unpublished data).

[2] Regression equations for Curlew Valley from Hoffman (1979).

Coyote densities in both study locations increased from 1975 to 1976 but otherwise were fairly constant through fall of 1978, and thus were only roughly correlated with jackrabbit density indices. Recruitment rates of both coyote populations (P_f), however, closely paralleled increases in jackrabbit abundance (Fig. 13 and Table 23).

The Effects of Exploitation

In the previous section it was shown from the best available evidence that coyote feeding patterns and abundance of prey probably did not differ significantly between Curlew Valley and INEL. In addition to similarities in the role of food resources in the two populations, extrinsic climatic factors also were comparable (see study area descriptions). Other extrinsic influences such as interspecific competition also may have been similar, as scent station visitation rates for other mammalian carnivores did not differ greatly between the two study areas (Stoddart unpublished data). Hunting and other forms of exploitation by man were extrinsic factors that did differ in their influence on the two populations, as evidenced by significantly higher adult and juvenile kill rates in Curlew Valley (Table 21).

The effects of exploitation depend on the level of kill rates and also on the timing of hunting losses during the year. For instance, Knowlton (1972) has pointed out that removal of coyotes would be most effective in suppressing density if it occurred immediately prior to the whelping season. Losses due to hunting at that time, he argues, are more likely to be additive to losses from nonhunting causes and emigration and are more likely to reduce gains from reproduction.

Exploitation of the treatment population in this study, however, occurred principally from November through January (Fig. 14). Following Knowlton's (1972) reasoning, reductions during late fall and early winter are more likely to supplant normal attrition and are less likely to effect a reduction in reproduction. Heavy losses from hunting during this period could, in fact, have an opposite effect of stimulating reproduction. Thus, in the discussion of the effects of exploitation that follows, it is important to remember the conclusions apply to coyote removal during fall and early winter. Control efforts, including killing of pups at dens, from March through June may produce effects on coyote population parameters that are substantially different from the ones presented below.

Discussion of the impact of exploitation begins in most general terms with a look at its effects on density. During a given annual period, the effects of exploitation on density may differ depending on the timing of hunting and on adjustments within and between rates of recruitment and loss. For example, Connolly and Longhurst (1975) simulated the effect of fall-winter control on coyote populations and concluded that adult and juvenile kill rates of 50 percent reduced breeding (spring) densities by about 30 percent, but increased maximum (fall) densities slightly. These results were a consequence of the assumptions of compensation between natural and hunting losses, and of strong density-dependent effects on reproduction.

In this study, indices of spring abundance generally were somewhat lower in the treatment population, while differences in fall density between the two populations were more variable (Fig. 12, Table 21).

Overall, however, measures of fall abundance also were slightly less for the Curlew Valley population. Nevertheless, neither spring nor fall differences between populations were significant despite differences in in situ hunting mortality rates. In situ kill rates for adults and juveniles in the treatment population (0.39 and 0.54, respectively) may not have differed sufficiently from the control population (0.25 and 0.12, respectively) to produce detectable differences in either spring or fall densities. The model of Connolly and Longhurst (1975) suggests such differences in kill rates between populations might reduce spring density in the treatment area roughly 20 percent below that in the control area.

Differences in spring densities between areas may have been less than 20 percent due to the apparent compensatory nature of losses from emigration. Connolly and Longhurst (1975) did not consider emigration. In this study, significantly lower juvenile in situ kill rates for the control population were associated with significantly higher emigration from the control population (Table 21).

Based on the greater annual recruitment rates of the treatment population (Table 13), it would be expected that fall densities in Curlew Valley would have been higher than those at the INEL, if spring densities were similar in the two areas. If spring densities were indeed 20 percent or more lower in Curlew Valley, perhaps due to incomplete compensation among loss rates, then similar fall densities might be expected. That such alternative processes could not be differentiated probably reflects that spring to fall changes in scent station visitation rates were a relatively insensitive measure of changes in density and, therefore, recruitment to fall populations.

From the foregoing discussion, it is apparent that the hypothesis (H1), spring and fall densities do not change significantly as a result of substantial differences in observed levels of exploitation, cannot be rejected. Subsequent discussion will attempt to elucidate the functioning of recruitment and loss rates that produced similar spring and fall densities in the treatment and control populations.

In contrast to the findings of this study, there is some limited evidence that exploitation may reduce coyote densities over appreciable areas. For example, Robinson (1961) reported that coyote numbers in Colorado, Wyoming, and New Mexico declined in 1960 to 8 percent of the 1940-41 level as a result of the use of new control methods. Similarly, from population indices based on the mean annual number of coyotes taken per man-year of effort, Wagner (1972) concluded that coyote densities in some western states during years of poisoning with Compound 1080 were approximately half pre-1080 densities. However, these non-experimental approaches cannot isolate the effect of new control methods or Compound 1080 from numerous other extrinsic factors influencing coyote numbers during the 20-30 year periods examined. Those experimental approaches that have demonstrated reductions in coyote density due to exploitation have done so for quite small areas subject to intensive control. Beasom (1974) reported short-term (3-6 months) reductions in indices of coyote abundance on a 25 km^2 area subject to intensive control, and Guthery (1977) inferred a 60 percent reduction in density for a 15.5 km^2 area based on success rates from helicopter gunning.

Recruitment to the fall populations in the treatment and control areas, as estimated by the proportion P_f, generally increased from 1975 to 1978 (Table 13). These annual increases in P_f for both populations were related positively to increases in indices of jackrabbit abundance in the two areas. Increases in recruitment to fall populations may be a function of increases in reproductive parameters such as litter size and percentage of females pregnant, or in survival and immigration. Gier (1968) stated that food availability and weather influenced the percentage of pups and adults that became pregnant, as well as litter sizes. In years of high food availability, reproductive performance might be expected to be three times greater than in years of low food availability, based on Gier's (1968) estimates. Clark (1972) reported positive relationships between jackrabbit densities and two reproductive parameters--litter size and percentage of females breeding. In this study, no estimates were available for the components of recruitment (post-natal survival, immigration, reproduction), but based on Gier's (1968) and Clark's (1972) findings, it seems likely that increases in recruitment within each study population were a result of response by reproductive parameters to increasing lagomorph abundance.

The annual estimates of P_f did not differ between the treatment and control populations. However, estimates of recruitment were consistently higher in Curlew Valley (Fig. 13), resulting in recruitment for all years combined being significantly greater (Table 13). Overall differences in P_f may have been due to differences in densities that were not detected with the census methods used. If spring densities in the treatment area were consistently lower, as might be inferred from the scent station estimates, then slightly but consistently greater annual post-natal survival and/or immigration, and hence significantly greater recruitment rates for all years combined may have resulted. Immigration and spring to fall survival of juveniles were not estimated separately from recruitment, but fall trapping in Curlew Valley in 1978 and in years previous to this study revealed little movement by pups tagged at dens three or four months earlier, and may indicate immigration was minimal. If estimates of density in May, census the same population present in March, as seems likely given the small proportion of mortalities during this period (Fig. 14), then slightly but consistently lower spring densities also may have resulted in slightly greater reproduction. In this context, Knowlton (1972) suggested litter size was positively related to the level of exploitation, and presumably inversely related to density.

Higher overall rates of recruitment in the treatment population also may have been due to consistently higher densities of jackrabbits in Curlew Valley. These differences in jackrabbit abundance between areas were quite great in the last year of the study (spring 1978 to spring 1979). *Sylvilagus*, not jackrabbits, were the most important component of the coyote diet at the INEL. *Sylvilagus* densities were unknown but on a subjective basis appeared to have increased with jackrabbit densities. In addition, generally higher rodent densities at the INEL suggest food resources may not have played an important role in observed differences between areas in recruitment rates. Thus, the second hypothesis proposed, that exploitation does not affect recruitment rates significantly, is rejected.

While the preceding discussion was concerned with the relationship between exploitation and recruitment rates, there apparently have been no attempts to determine the relationship among rates of annual survival, hunting mortality, nonhunting mortality, and emigration for canid populations. The following discussion makes such an attempt to relate exploitation and exploitation rates to other components in coyote population loss processes.

Losses due to mortality of adults and juveniles are considered separately. The model selection procedure of Brownie et al. (1978) used to estimate survival rates from recovery data indicated that annual survival and/or recovery rates for adults and juveniles differed significantly for coyotes marked in Curlew Valley and the INEL. Lower juvenile survival also might be inferred from analysis of the pooled, sample age distributions using the Chapman-Robson model, providing population size was constant and age distributions were stable during the study. Leslie matrix projections indicated that these two conditions may have been met. Evidence of age-specific differences in annual survival rates of coyotes is remarkably uncommon in the literature and generally has been inferred from age structure data (Rogers 1965, Knowlton 1972, Nellis and Keith 1976, Mitchell 1979), although Knudsen (1976:88) and Tzilkowski (1980:61) did suggest such differences on the basis of differential recovery data.

Adult annual survival rates were constant during the study period and probably were similar for the treatment and control populations. There remains the possibility, however, that adult survival rates were lower in Curlew Valley than at the INEL, as estimates from the models of Brownie et al. (1978) and Chapman-Robson were slightly lower and significantly lower, respectively. Neither hunting nor nonhunting adult mortality rates differed significantly between areas. There was an inverse relationship between estimated hunting and nonhunting mortality rates, but this relationship was based on only two data points and does not clarify whether mortality rates were additive or compensatory. If a linear relationship is assumed between V and K, Anderson and Burnham (1976:11) have shown that the theoretical slope (b) is -1.0 when hunting is a completely compensatory form of mortality, and that b is still negative but closer to zero when hunting is completely additive. An approximation to b in the latter case is

$$b = - \alpha \frac{1 - S - K}{1 - \alpha K},$$

where α was believed by Anderson and Burnham (1976:54) to range from 0.90 to 1.0 based on numerical cases for mallards, and bears no relation to α defined earlier as the proportion of recoveries due to exploitation. Theoretical estimates of b, then, for Curlew Valley and the INEL range from -1.0 (hunting completely compensatory) to -0.10 (hunting completely additive) for adults, when α is assumed to be 0.95. The slope of the observed relationship between hunting and nonhunting mortality rates undoubtedly lies within the range given, but could not be estimated by the method of Anderson and Burnham (1976:62). Estimates of b obtained from regressing $\hat{V}$ on $\hat{K}$ are inappropriate because the estimators are subject to sampling variation and covariation. Interpretation of the slight inverse relationship between adult annual survival and hunting mortality rates is subject to the same difficulties, but may suggest losses from nonhunting causes were not completely compensatory.

Juvenile annual survival rates also were constant during the study period and did not differ significantly between Curlew Valley and the INEL, although overall and in situ survival estimates for juveniles marked in Curlew Valley were approximately one-half the INEL estimates. Overall and in situ juvenile hunting mortality rates were significantly higher in Curlew Valley, and in situ nonhunting mortality rates for that population were significantly lower than for the INEL. As in the case for adults, the observed slope of the inverse relationship between finite juvenile hunting and nonhunting mortality rates was not estimable and may have ranged from -1.0 if compensation between rates was complete to approximately -0.21 if mortality rates were completely additive. Similarly, although there was an apparent inverse relationship between annual juvenile survival and hunting mortality rates suggesting additivity, annual survival between areas did not differ despite significant differences in hunting mortality rates. Therefore, hypothesis H3, that annual survival rates are not related to intensity of harvest rates, cannot be rejected for either juveniles or adults. However, in the case of juveniles conclusions regarding this compensatory hypothesis clearly are questionable given the relatively low statistical power of the z test used to compare survival estimates.

While increased juvenile losses to hunting may not have been compensated for completely by reduced mortality from nonhunting causes, non-significant differences between areas in total in situ loss rates may have resulted, in part, from differential rates of emigration from the treatment and control populations. If exploitation in the fall and winter has the effect of increasing hunting mortality rates but reducing losses from nonhunting causes and emigration in a largely compensatory manner, such exploitation should not decrease the size of the population the following spring. Similarities in spring and fall densities of the treatment and control populations lend support to this corollary of the hypothesis of compensatory loss rates (Anderson and Burnham 1976).

Rates of emigration loss from canid populations have not been considered previously in relation to mortality rates in particular or to the dynamics of populations in general. Most authors have reported findings on the timing and distance of dispersal by sex (Garlough 1940, Robinson and Grand 1958, Knowlton 1972, Nellis and Keith 1976, Andrews and Boggess 1978). Information of the proportion of canids dispersing does exist for red foxes (*Vulpes vulpes*, Storm et al. 1976) and coyotes (Hibler 1976, Berg and Chesness 1978, Bowen 1978). However, estimates of dispersal rates by these authors are not considered in relation to the dynamics of a particular population. In contrast, in this study, dispersal was considered relevant to population processes only if it resulted in losses (emigration) from one of the study populations. Moreover, there have been no studies in which emigration, or even dispersal rates, of canids have been measured in relation to the effect of an extrinsic factor such as exploitation, although Knowlton (1972) discussed aspects of dispersal with regard to lightly and heavily exploited areas, and Hibler (1976) suggested dispersal rates in Curlew Valley may have been lower than other reported estimates as a consequence of exploitation.

The hypothesis (H4) that emigration rates are not affected by substantial levels of exploitation was rejected based on the significant differences in emigration from Curlew Valley and the INEL noted above. The inverse relationship between emigration rates and in situ juvenile hunting mortality rates in this study, however, supports the inferences of Knowlton (1972) and Hibler (1976). Further comparisons between estimates of emigration rates in this study with estimates of dispersal rates by other authors are inappropriate, because emigration was defined conservatively as a subset of dispersal. Comparisons of other aspects of juvenile movements, such as sex and weight of individuals and timing, probably are not significantly affected by such differences in definitions. Thus, although there was no significant difference between Curlew Valley and the INEL in the sex ratios of emigrators, ratios at the INEL were approximately equality while there was a somewhat greater preponderance of female emigrators in Curlew Valley (64:36). The findings for Curlew Valley are consistent with other reports of sex ratios of dispersing coyotes (Knowlton 1972, Hibler 1976).

The timing of emigration from Curlew Valley and the INEL differed significantly, although the estimates for both areas followed the general pattern described in the literature (cf Berg and Chessness 1978). Peak emigration from Curlew Valley began in December and January (Fig. 16) and was similar to catch rates in an area of intensive control in south Texas described by Knowlton (1972). Knowlton suggested that high catch rates during these months represented an influx of emigrators from surrounding, and presumably less exploited, areas. However, this interpretation is not consistent with observed differences in timing of emigration between heavily and lightly exploited areas in this study. Higher catch rates reported by Knowlton (1972) may, in fact, reflect increased emigration from heavily exploited areas during December and January.

Emigration from coyote populations in this study probably was of the type described by Lidicker (1975:105) as saturation dispersal or emigration, i.e., "the outward movement of surplus individuals from a population living at or near its carrying capacity." Lidicker hypothesized that such individuals most likely would be juveniles and those in poor condition or otherwise unable to cope with local conditions. From a graphical model relating habitat quality, social rank, and dispersal, Gauthreaux (1978:28) inferred that during a period when resources were limited

> the dominance rank of an individual can be expressed in terms of the distance it has moved from its place of birth or in terms of the quality of the habitat it occupies, or both. Dominants are close to their place of birth in prime habitat, while subordinates, forced to emigrate, occupy areas in poorer quality habitats.

Body weight is an indicator of general health and physical condition, and may be an approximate indicator of social rank in coyotes (Knight 1978). Considering the hypotheses of Lidicker (1975) and Gauthreaux (1978), then, coyotes emigrating from the two populations in this study would be expected to weigh less than individuals remaining in the areas. Based on body weight at the time of capture, juveniles remaining alive within the INEL population did weigh significantly more than emigrators, and, therefore, residents may have been dominants or at least individuals in better physical condition (Table 20). In Curlew Valley, emigrating juveniles also weighed less at the time of capture than individuals that did not emigrate, but the difference was not significant (Table 20).

Knight (1978) also reported that in late summer, male juveniles generally were dominant to females. Thus, a greater proportion of emigrators might be females if emigrators usually are of lower social rank than residents. Sixty-four percent of juveniles emigrating from Curlew Valley were females, but sex ratios of emigrators did not differ significantly from equality for either population.

Interpretations of the significant differences in rate and timing of emigration between areas suggest that while emigration processes in Curlew Valley and the INEL may have been the same, the manifestations of the processes were different. Higher in situ hunting mortality rates for Curlew Valley may create refuge areas within that population where potential emigrators are willing to go. Lidicker (1975:117) has termed these areas "dispersal sinks." The creation of dispersal sinks in the treatment population as a result of exploitation would be expected to reduce emigration. In contrast, there were probably few dispersal sinks available to juveniles within the control population, given the high adult survival rate and low in situ kill rates. Emigration under these circumstances would be expected to be higher than in the situation hypothesized for Curlew Valley. The models proposed above are consistent with the observed differences in rates of emigration.

If egress from coyote populations in this study was saturation emigration (Lidicker 1975:105) as hypothesized earlier, then differences between Curlew Valley and the INEL in timing of emigration also may have been due to differences in the number of dispersal sinks available. The greater number of sinks created in Curlew Valley by hunting may have taken longer to be filled; and, consequently, may have postponed as well as reduced emigration. Thus, while emigration was greatest from the INEL in September and October, peak emigration from Curlew Valley did not occur until December and January (Fig. 16).

The relative number of sinks available in the two study areas may explain why in Curlew Valley, unlike INEL, emigrators did not weight significantly less than residents. It seems likely that more individuals in poorer condition and/or lower social rank would have been able to find refuge areas in Curlew Valley in comparison to the INEL. In the latter area there apparently were very few dispersal sinks, and those sinks were available only to individuals in very much better physical condition and/or higher social rank.

To summarize this section on the effects of exploitation, observed differences in fall-wainter adult and juvenile kill rates did not produce significant differences in densities or annual survival rates, but did significantly affect recruitment and emigration rates. Changes in the timing of exploitation, or increases in kill rates, might be expected to result in different interpretations. For example, the somewhat lower estimates of density and survival rates for the treatment population may suggest that observed hunting mortality rates for that population were within a "threshold region" where further increases in hunting would reduce annual survival and density significantly.

(Anderson and Burnham 1976:5). Implications of the findings in this study that are relevant to the control of depredations by coyotes are discussed in the next section.

Before proceeding to a discussion of management implications, it should be noted that although empirical evidence of the effect of exploitation on density, recruitment, survival, and emigration generally has not been presented for coyotes prior to this study, such evidence is available for a number of other species. Interpretations of the effects of exploitation vary with the biology of the species considered and the magnitude, timing, and age and sex specificity of harvest rates. For instance, exploitation has been reported to not reduce significantly density and/or survival rates of woodchucks (Davis et al. 1964), gray squirrels (Mosby 1969), scaled quail (Campbell et al. 1973), woodpigeons (*Columba palumbus*, Murton et al. 1974), black bears (Beecham pers. comm.), and mallards (Anderson and Burnham 1976). Conversely, reductions in densities and survival rates have been reported for fox squirrels (*Sciurus niger*, Nixon et al. 1974) and elk (Kimball and Wolfe 1974, 1979).

Variations in density due to exploitation have been reported to produce density-dependent responses in birth rates and age at first reproduction for white-tailed deer (*Odocoileus virginianus*, Hesselton et al. 1965), elk (Knight 1970, Fowler and Barmore 1978), wolves (Mech 1970), hippopotamus (*Hippopotamus amphibius*, Marshall and Sayer 1976), and a number of marine mammals (Laws 1962, Gambell 1973, Lett and Benjaminsen 1977). Finally, there is some evidence that emigration rates are positively related to population density for *Microtus* (Myers and Krebs 1971, Krebs et al. 1976), but there is no well-documented information on the relationship between emigration rates and exploitation for mammalian species.

Management Implications

The management implications of the findings presented in this study vary with the objectives of depredation control programs. Knowlton (1972:380) discussed four basic coyote control situations that will be re-examined here. First, Knowlton recognized situations where there was "occasional need for general population suppression" to preclude epizootics or significant economic hazards. Local depredations of short duration were a second situation he identified. In other cases coyotes may have to be extirpated from areas of high perennial risk, such as lambing ranges. The fourth situation Knowlton described was the need to restrict infiltration from areas adjacent to those where intensive control is required.

Exploitation in Curlew Valley varied with regard to the type and purpose of activity, but most closely resembled the situation where general population suppression is desired. Aerial hunting for furs and to control depredations on livestock accounted for approximately one quarter of all exploitation and, along with sport hunting and trapping, resulted in adult and juvenile in situ kill rates 56 and 350 percent higher, respectively, than corresponding rates at the INEL. Such differences in kill rates may not have been clearly effective in reducing spring and fall densities in Curlew Valley because of the timing of exploitation. Hunting losses during fall and early winter were largely offset by reduced emigration and nonhunting losses, and by increased recruitment from immigration of juveniles dispersing from lightly exploited areas similar to the INEL and/or by greater reproduction the following spring. Thus, this study supports Knowlton's (1972:380) hypothesis that control efforts during the fall "merely supplant normal processes" and "may invite immigration from adjacent areas, when annual dispersal occurs."

The current Federal control program is directed more toward temporary depredation problems in local areas and chronic problems associated with areas of high risk. Beasom (1974) and Guthery (1977) have reported on the effectiveness of intensive control techniques in the former situation. Implications from this study suggest that efforts at spot control in fall and winter might create emigration sinks that would be quickly filled by potential emigrators when control ends. Such short-stopping of emigration also makes it unlikely that more general or less efficient approaches to problems in local areas would be effective. Adjustments among recruitment and loss rates observed in the Curlew Valley and INEL populations also are consistent with Knowlton's (1972:380) suggestion that it is unrealistic to expect the effects of a spot control program to persist through the following year.

In the situation where chronic depredation problems are experienced, Knowlton (1972:381) indicated that year-around reductions might be required, with removal efforts concentrated just prior to whelping season. Losses from nonhunting causes and emigration were quite low in this study just prior to whelping season. Moreover, emigration from the lightly exploited area (INEL) had diminished greatly by early spring, and therefore, little immigration would be expected into areas subject to intensive control immediately preceding the whelping season. From these observed demographic events in Curlew Valley and the INEL, it may be inferred that losses from removal efforts in late winter or early spring would be more likely to be additive and thus effect a reduction in density. Removal of animals just before whelping season, however, would be expected to require greater effort per animal taken (Connolly 1978). In any case, there is a need to test experimentally the effectiveness of control efforts during this time of the year in reducing coyote densities.

Control efforts tend to be concentrated in areas where depredations are the most severe. The result of this pattern of removal is to create areas of intensive control that are surrounded by areas of relatively little control. If these latter areas are similar to the INEL, then populations within these lightly exploited areas produce surplus individuals, mainly juveniles, that emigrate and may repopulate areas of more intensive control. Knowlton (1972:381) has suggested the "establishment of buffer zones around high risk areas" to reduce infiltration. Juveniles in these zones would be removed either through the use of reproductive inhibitors, denning, or conventional methods prior to emigration in the fall.

While the coyote population in Curlew Valley was not subject to a coherent control program with specific objectives, such as the four situations discussed, interpretations from this study indicate that substantial fall-winter removal rates are ineffective in reducing coyote densities; that this resilience to fall-winter removal is due to adjustments among loss rates, and to adjustments between rates of recruitment and loss; and that emigration is an important demographic factor influencing the effectiveness of control efforts in each of the basic coyote control approaches examined.

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