

## LONG-TERM PATTERNS IN MAMMALIAN ABUNDANCE IN NORTHERN PORTIONS OF THE GREAT BASIN

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We collected long-term indices of mammalian abundance at 2 sites in the Great Basin: Curlew Valley in northern Utah, and the Idaho National Laboratory in southeastern Idaho. Abundance patterns were examined for 1 predator, the coyote (*Canis latrans*), and its prey community including 9 species of rodents and 3 species of lagomorphs. Our results suggest cycles with a period of 10–11 years among the main prey species, *Lepus californicus*. Responses of *C. latrans* to prey fluctuations were variable among study areas, with abundance levels of coyotes remaining high during declines in prey populations in Curlew Valley. Abundance indices were generally low for all species of rodents except *Peromyscus maniculatus*. Although many of the rodents demonstrated consistent biannual fluctuations, we could not statistically confirm multiseasonal cyclic patterns. Population levels of coyotes seem to reflect a combination of factors including abundance of both monitored species of prey and alternate prey groups, and human harvest.

Key words: abundance, black-tailed jackrabbit, *Canis latrans*, coyote, lagomorph, *Lepus californicus*, long-term data, mammal community, rodents

Understanding changes in wild populations, including species distributions, population trends, trophic interactions, habitat use, and competition, depends on the quality of available information. In the absence of specific knowledge, interpretations are frequently based upon generalized information organized in the form of models and hypotheses. The propriety and value of these are directly related to the quality of the initial data, including knowledge of normal patterns and relationships. Long-term data sets are valuable in providing perspectives for understanding fluctuations in abundance as well as developing and testing population models and hypotheses (Brady and Slade 2004; Elton and Nicholson 1942; Errington 1946; Hanski et al. 1991, 2001; Keith 1963; Korpimäki and Krebs 1996; Krebs et al. 2001). On the contrary, data sets from short time series can lead to inappropriate questions, failure to detect effects, or result in spurious and erroneous interpretations (Tversky and Kahneman 1971, in Loehle 1987).

Although studies of fluctuations and patterns in animal abundance are not new to population ecology (Elton 1924; Elton and Nicholson 1942; Lotka 1925; Volterra 1926), few studies assess changing abundances in mammals over extended periods. Many are limited to 3–5 years of data because of changing personnel, inadequate logistical support in terms of funding and site access, or design and measurement difficulties. Consequently, there are relatively few long-term monitoring projects related to mammalian abundance, especially over extensive areas. Some notable examples include the Hudson's Bay Company records on Canadian lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*—Elton and Nicholson 1942), which employs indirect data sources; Errington's study of muskrats (*Ondatra zibethicus*—Errington 1943, 1946); studies of voles (*Microtus*) and lemmings (*Lemmus lemmus*) in Fennoscandia (e.g., Elton 1924; Hanski and Korpimäki 1995); and some studies of desert (e.g., Brown and Heske 1990; Friggens et al. 2003) and grassland (e.g., Brady and Slade 2004) rodent communities. Studies that combine overall community structure, including both predators and prey, also are sparse. Some exceptions include the Kluane project (Krebs et al. 1995, 2001); Yellowstone Ecosystem studies (Keiter and Boyce 1991); studies of rodent communities in Fennoscandia

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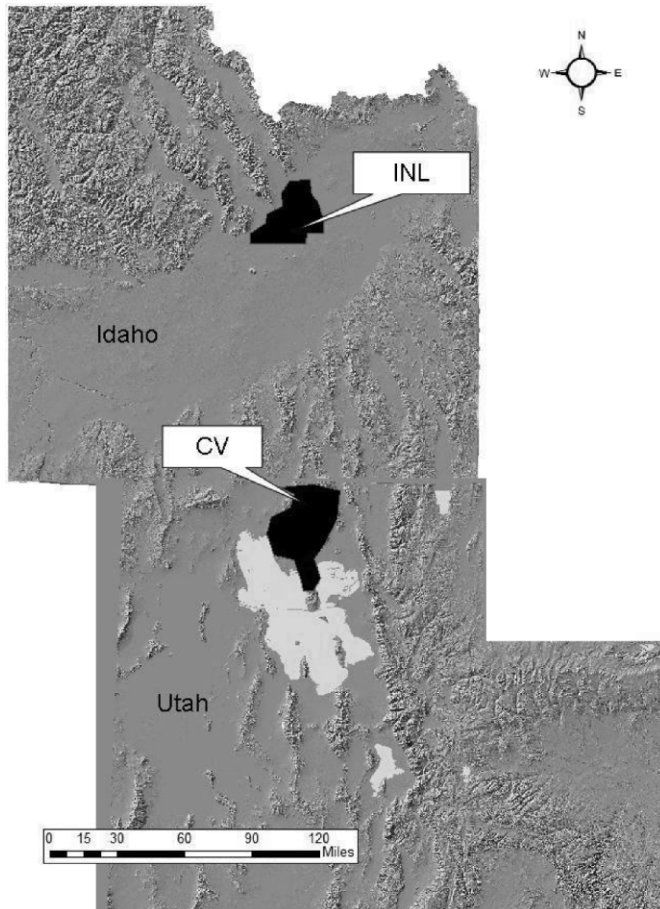


FIG. 1.—Geographic location of study sites at Curlew Valley (CV), Utah, and Idaho National Laboratory (INL), Idaho.

(Hanski et al. 1991, 2001; Hansson and Henttonen 1988); studies of large mammal communities in the Serengeti, Tanzania (Mduma et al. 1999); studies of community structure of Isle Royale (Peterson and Vucetich 2003); and more recently, studies sponsored by the United States Long Term Ecological Research network (<http://www.lternet.edu>), including those on the Seville National Wildlife Refuge in the intermountain region (Friggens et al. 2003; Parmenter et al. 1995).

Our interest in patterns of mammalian abundance originated with studies related to an apparent cycle in the abundance of black-tailed jackrabbits (*Lepus californicus*) in Curlew Valley (CV) initiated by Fred Wagner (Gross et al. 1974; Wagner and Stoddart 1972) and a series of his graduate students in 1962. Their inquiry expanded to coyotes (*Canis latrans*) as the major mammalian predator upon jackrabbits (Clark 1972; Knowlton and Stoddart 1992). Although the primary investigation initially focused on jackrabbits and their principle predator, for 13 years (1973–1986), we also attempted to monitor trends of rodent abundance on a scale meaningful within the context of jackrabbit–coyote interactions. For 11 years (1975–1986), we added a 2nd study area, the Idaho National Laboratory (INL), as a partial replicate of the CV study. Our principle interests are in describing changes in the abundances of the more common mammals of the area and promoting an understanding of normal patterns of fluctuations in abundance within

the mammal community of the Great Basin. We take advantage of a long-term data set based on standardized monitoring in 2 sites (11 and 32 years, respectively) to examine patterns of abundance of a carnivore predator, *C. latrans*, and its prey community consisting of 9 species of rodents and 3 lagomorphs. We predicted that trends in prey availability would influence abundance patterns in coyotes over time, with the strongest relationships between the predator and its main prey species, *L. californicus*. Additionally, we believed there would be evidence of interactions between rodent population trends and abundance patterns of coyotes. Last, we expected that the mammal communities would display similar trends in abundance between both study areas given their geographic proximity.

## MATERIALS AND METHODS

**Study area.**—We used data from 2 sites: a major portion of the CV in northern Utah and the INL site (formerly known as the National Reactor Test Site, the Idaho National Engineering Laboratory, or the Idaho National Engineering and Environmental Laboratory) in southeastern Idaho (Fig. 1). The CV data series was collected from a 700-km<sup>2</sup> portion located in Box Elder County, Utah. This valley is a semiarid intermountain basin formed by Pleistocene Lake Bonneville (Gross et al. 1974; Hoffman 1979). Elevations on the valley floor near the edge of Great Salt Lake at the southern edge of the area are approximately 1,280 m, with an average rise of 5.7 m/km from south to north (Gross et al. 1974). Although most (60%) of the study area is public land managed by the Bureau of Land Management, the remainder is state land or privately owned.

Vegetation of the CV is characteristic of the Intermountain Semidesert and Desert Province (Bailey 1998) and the Northern Desert Shrub Biome (Fautin 1946). Generally, 1 or 2 types of shrubs or trees dominate each vegetation zone, being limited by soil moisture and salinity (Gross et al. 1974; Hoffman 1979). Sage-annuals were the principal vegetation type, composing 49% of the study area. Big sagebrush (*Artemisia tridentata*) was the dominant shrub, usually associated with green or gray rabbitbrush (*Chrysothamnus nauseosus* or *C. viscidiflorus*) and greasewood (*Sarcobatus vermiculatus*). Agricultural crops located primarily in the northern and western portions include crested wheatgrass (*Agropyron cristatum*) and alfalfa (*Medicago sativa*) where irrigation is practical. Some areas of sagebrush were plowed and seeded with crested wheatgrass as a range improvement practice (Hoffman 1979). Additional areas were reseeded with a variety of grasses and forbs following an extensive range fire in 1983 (Bartel 2003).

Established as the National Reactor Testing Station in 1949, the INL complex is a 2,305-km<sup>2</sup> government-owned site with limited public access. Its mission broadened in the 1970s, and in 1975 became the nation's 2nd largest National Environmental Research Park, providing a site for studying a relatively undisturbed ecosystem (Idaho National Laboratory 2008). We obtained mammalian abundance data from a 1,036-km<sup>2</sup> portion of the INL site. The study area is flat to gently rolling, high-desert terrain about 1,500 m above sea level and known locally as the Upper Snake River Plains. Remnants of volcanic flows are

evident in the form of low rocky ridges and abrupt escarpments. Most (94%) of the land is undeveloped, with some 269 species of vertebrates, including 47 mammals, 210 birds, 11 reptiles, and 1 amphibian, and >400 species of plants recorded for the site (Anderson et al. 1996; Idaho National Library Environmental Surveillance, Education, and Research Program 2007).

In general, vegetation on INL consists of a shrub overstory with an understory of perennial grasses and forbs. The most common shrub is big sagebrush (*A. tridentata*). Other common shrubs include green rabbitbrush (*Ericameria teretifolia*), winterfat (*Krascheninnikovia lanata*), spiny hopsage (*Grayia spinosa*), prickly phlox (*Leptodactylon pungens*), broom snake-weed (*Gutierrezia sarothrae*), and horse-brush (*Tetradymia canescens*). Native grasses such as thick-spiked wheatgrass (*Elymus lanceolatus*), bottlebrush squirreltail (*Elymus elymoides*), Indian ricegrass (*Oryzopsis hymenoides*), needle-and-thread grass (*Stipa comata*), and Nevada bluegrass (*Poa secunda*) compose the understory (Anderson et al. 1996). Although sheep and cattle graze approximately 60% of the area, INL supports a high diversity of forbs including tapertip hawksbeard (*Crepis acuminata*), Hood's phlox (*Phlox hoodii*), hoary false yarrow (*Chaenactis douglasii*), paintbrushes (e.g., *Castilleja angustifolia*), globe-mallow (*Sphaeralcea munroana*), buckwheats (e.g., *Eriogonum mancum*), evening primrose (*Oenothera caespitosa*), lupines (e.g., *Lupinus argenteus*), bastard toadflax (*Comandra umbellata*), milk-vetches (*Astragalus*), and mustards.

**Fauna.**—Numerous species of mammal inhabit both study sites. Species of rodents occurring on both sites include deer mice (*Peromyscus maniculatus*), western harvest mice (*Reithrodontomys megalotis*), Great Basin pocket mice (*Perognathus parvus*), Ord's kangaroo rats (*Dipodomys ordii*), chisel-toothed kangaroo rats (*Dipodomys microps*), least chipmunks (*Tamias minimus*), northern grasshopper mice (*Onychomys leucogaster*), and sagebrush voles (*Lemmys curtatus*). White-tailed antelope ground squirrels (*Ammospermophilus leucurus*) are present on the CV site, whereas Townsend's ground squirrels (*Spermophilus townsendii*) inhabit the INL site (see Bartel [2003] for a species list for CV and Idaho National Laboratory Environmental Surveillance, Education, and Research Program [2007] for a list for INL). Lagomorphs present include black-tailed jackrabbits, mountain cottontails (*Sylvilagus nuttallii*), and small numbers of pygmy rabbits (*Brachylagus idahoensis*). Among the 3 species of lagomorphs seen on the CV site, *L. californicus* was most common, with *S. nuttallii* and *B. idahoensis* occasionally observed in select habitats. The latter 2 were not detected with sufficient frequency to warrant including among the indices for the CV site. All 3 lagomorphs also were present on the INL site, along with a 4th species, white-tailed jackrabbits (*Lepus townsendii*). The latter was seen infrequently in northern portions of the INL site but numbers were insufficient to provide reliable indices of abundance. Ungulates such as mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) are present, with elk (*Cervus elaphus*) occurring on the INL site. Domestic sheep graze both sites on a seasonal basis and cattle are present in CV during spring.

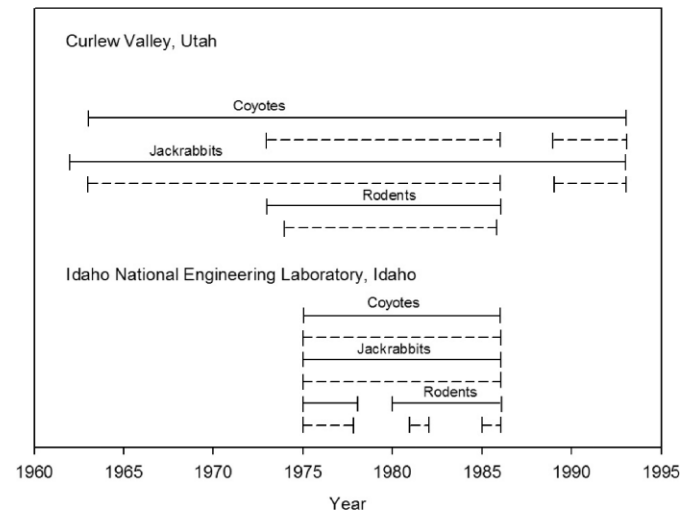


FIG. 2.—Chronology and duration of monitoring of relative abundances of various mammal groups on Curlew Valley, Utah, and Idaho National Laboratory, Idaho, study sites, 1963–1993. Solid lines represent fall and dashed lines represent spring index periods.

Carnivores that inhabit both study areas include coyotes, badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*), and long-tailed weasels (*Mustela frenata*). Kit foxes (*Vulpes macrotis*), red foxes (*V. vulpes*), and mountain lions (*Puma concolor*) also have been documented occasionally on both sites (Hoffman 1979; Idaho National Laboratory Environmental Surveillance, Education, and Research Program 2007). Although evidence of *V. vulpes* and *V. macrotis* was occasionally noted on the CV site, indices of abundance were only obtained for *C. latrans*.

We monitored abundances of various mammals via standardized procedures in CV from 1963 through 1993 and on INL from 1975 to 1986. A detailed description of the methods for data collection and handling, and the data are accessible at Ecological Archives publication E086-172 (Bartel et al. 2005). Abundance indices concentrated on coyotes, black-tailed jackrabbits, and 9 species of rodents (Fig. 2). All measurements involved indices of abundance. Comparisons are constrained within individual taxa because responses to our inventory procedures vary among taxa. Procedures used in this study were within the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and in accord with the Animal Care and Use Committee of the National Wildlife Research Center under Study Plans DF-931.07 and DF-931.09.

**Indices of lagomorph abundance.**—We collected data on abundance of *L. californicus* in CV by using the same series of 1.6-km<sup>2</sup> flushing transects (0.4-km per side) located in randomly selected land-survey sections described by Gross et al. (1974), who reported the first 10 years of demographic data on *L. californicus*. We extended this data set for an additional 20 years in CV and conducted similar surveys on INL for 11 years (Fig. 2). Density estimates were calculated from observations of right-angle distances between the transect and flushing points of each individual and frequency

distributions of perpendicular flushing distances using the Fourier series estimator in program TRANSECT (Burnham et al. 1980). We walked 59–65 transects each spring and fall in CV and 79 in INL. Density estimates obtained from these transects were later considered indices after experimental transects conducted on horseback provided a 141% higher estimate of abundance (Wywiałowski and Stoddart 1988). Two additional species of lagomorphs, *S. nuttallii* and *B. idahoensis*, were monitored on the INL site. Because positive identification between the 2 species was not always accomplished, we used a combined index for these species.

*Indices of coyote abundance.*—Because of increasing detection of caveats associated with various sampling techniques, the methods used to assess relative abundance of *C. latrans* evolved throughout the study (Knowlton 1984). Although numerically different, trends from 3 indexing techniques were generally similar, and ultimately contributed to our assessments of abundance of *C. latrans*, including capture-rates from capture efforts of approximately 3,000 trap nights in CV (Clark 1972); visitation rates to 240 artificial scent stations (Linhart and Knowlton 1975; Roughton and Sweeney 1982) in CV and 300–500 scent stations on INL; and scat deposition rates, based upon the number of *C. latrans* scats retrieved over a 4-week period from 23–53 miles of transects in CV and 100 miles in INL and expressed as scats  $\text{mile}^{-1} \text{day}^{-1}$ . We synthesized a single index of relative abundance of *C. latrans* for each spring and fall period by standardizing the values obtained from each of the 3 techniques to a common mean and then averaging the independent values, with equal weighting, whenever multiple techniques were acquired for a single sampling period (Stoddart 1987a, 1987b).

*Indices of rodent abundance.*—Rodent abundance was assessed each spring and fall via a series of 24.5-km rodent survey routes, each consisting of 25 trapping transects. Transects were spaced 0.96 km apart, oriented perpendicular to and on alternate sides of the survey routes, and consisted of 10 trap stations, spaced 10 m apart. At each station we placed 1 Victor M-4 snap-trap (Woodstream Corporation, Lititz, Pennsylvania) with an expanded treadle (Carley and Knowlton 1971). Traps were baited with a mixture of peanut butter and rolled oats and checked daily for 3 consecutive trap-nights during each sampling period. Indices of rodent abundance were normalized by trapping effort (Hoffman 1979; Mills 1987; Mills and Knowlton 1991; Stoddart 1987a, 1987b). In CV, we had 4 survey routes with a goal of 3,000 trap-nights per survey period and on INL there were 6 survey routes with an intended goal of 4,500 trap-nights per sampling period. Indices are presented as captures per 100 trap-nights, adjusted for sprung traps (Bartel et al. 2005; Hoffman 1979; Stoddart 1987a, 1987b).

We also examined rodent density indices for evidence of synchronicity among the 9 species monitored in Curlew Valley and indications of whether rodent populations on our 2 study sites fluctuated similarly with respect to time. To avoid problems associated with different seasonal patterns in abundance among species, we computed Pearson correlation coefficients separately for spring and fall indices among species pairs.

We assessed evidence of cyclic trends for all monitored species using an autocorrelation analysis, which resulted in correlograms (Case 2000). Correlograms allowed us to evaluate population cycle lengths and time lags by comparing a given population's size at a specific time and its size lags over a defined interval. We plotted correlation coefficients as a function of time lags. We compared correlations between abundance values of populations for consecutive years using PROC ARIMA in SAS version 9.1 (SAS Institute Inc. 2004).

## RESULTS

*Lagomorphs.*—Indices of abundance for *L. californicus* in CV were available from fall 1962 through fall 1993, with spring values missing for 1987 and 1988 (Fig. 2). During the 32 years for which indices are available for this site, 3 peaks in abundance are evident, 1971, 1981–1982, and 1991–1993 (Fig. 3a). During intervening years, index values dropped to very low levels, with <5 individuals sometimes seen on more than 80 km of flushing transect. A cycle in abundance of *L. californicus* was evident, with a period of 10–11 years and amplitude approaching 325-fold. Abundance values in spring were typically half the abundance values of the preceding fall throughout most of the series.

Data on abundance of *L. californicus* for the INL site were available from spring 1975 through fall 1986 with 1 dramatic peak in abundance in spring 1981 (Fig. 3b). Fall indices ranged from 0.0 to 119.5 (slightly lower than CV), whereas abundance indices in spring had a much larger range (0.0–422.0). The timing of peak index values on the INL site coincided with a similar cyclic peak on the CV site (Fig. 3). A unique aspect of the INL data during the population irruption is that spring values greatly exceeded values of the preceding fall. Although peak fall index values from INL and CV appear similar, the spring values for INL are more than 3 times larger than those for the CV site.

The combined index for *S. nuttallii* and *B. idahoensis* on the INL site suggests an increase and subsequent decline in abundance that coincided with the rise and fall in abundance of *L. californicus*, but at appreciably lower levels (Fig. 3c). Unlike *L. californicus*, the combined spring index values for *S. nuttallii* and *B. idahoensis* on the INL site were typically lower than values obtained the preceding fall (Fig. 3c).

*Coyotes.*—Measurements of coyote abundance were originally collected in CV as fall indices in 1963 that continued through fall 1993. Indices of abundance in spring were incorporated in 1974, continuing through spring 1993 with the exception of 1987 and 1988 (Fig. 2). The abundance of *C. latrans* in fall appeared to decline systematically from 1963 through 1969, whereupon it rose dramatically through 1973, followed by a 4-year period of reduced abundance, although somewhat higher than in the late 1960s (Fig. 3d). A dramatic surge in fall abundance of *C. latrans* occurred from 1978 through 1982, followed by a moderate and gradual decline through 1992, with an apparent abrupt drop in fall abundance between 1992 and 1993. Abundance values in spring were

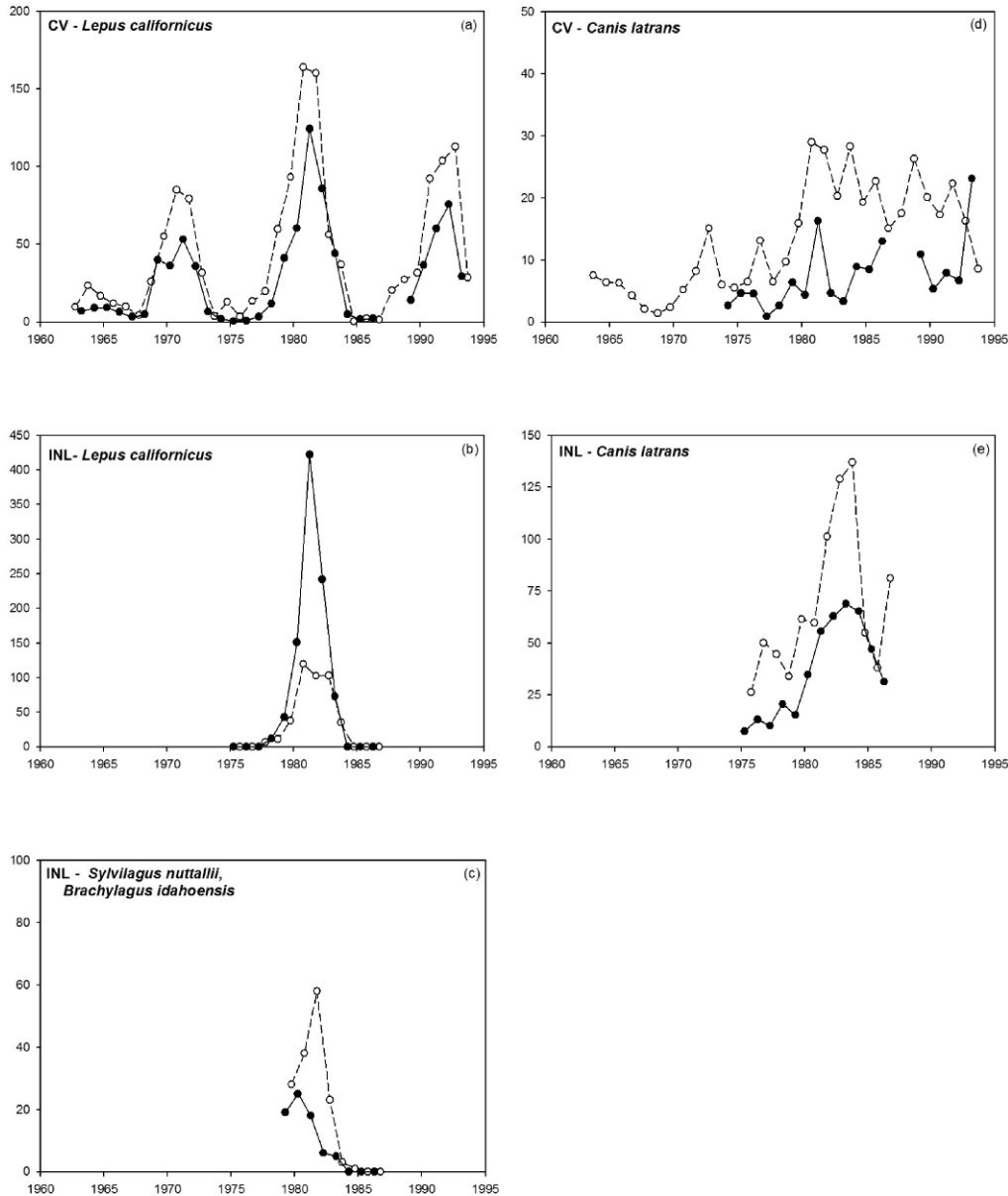


FIG. 3.—Spring (closed circles) and fall (open circles) indices of abundance of 3 species of lagomorphs and 1 canid on Curlew Valley (CV), Utah, and Idaho National Laboratory (INL), Idaho, study sites, 1973–1986. See text for explanation of various index values represented along the y-axes.

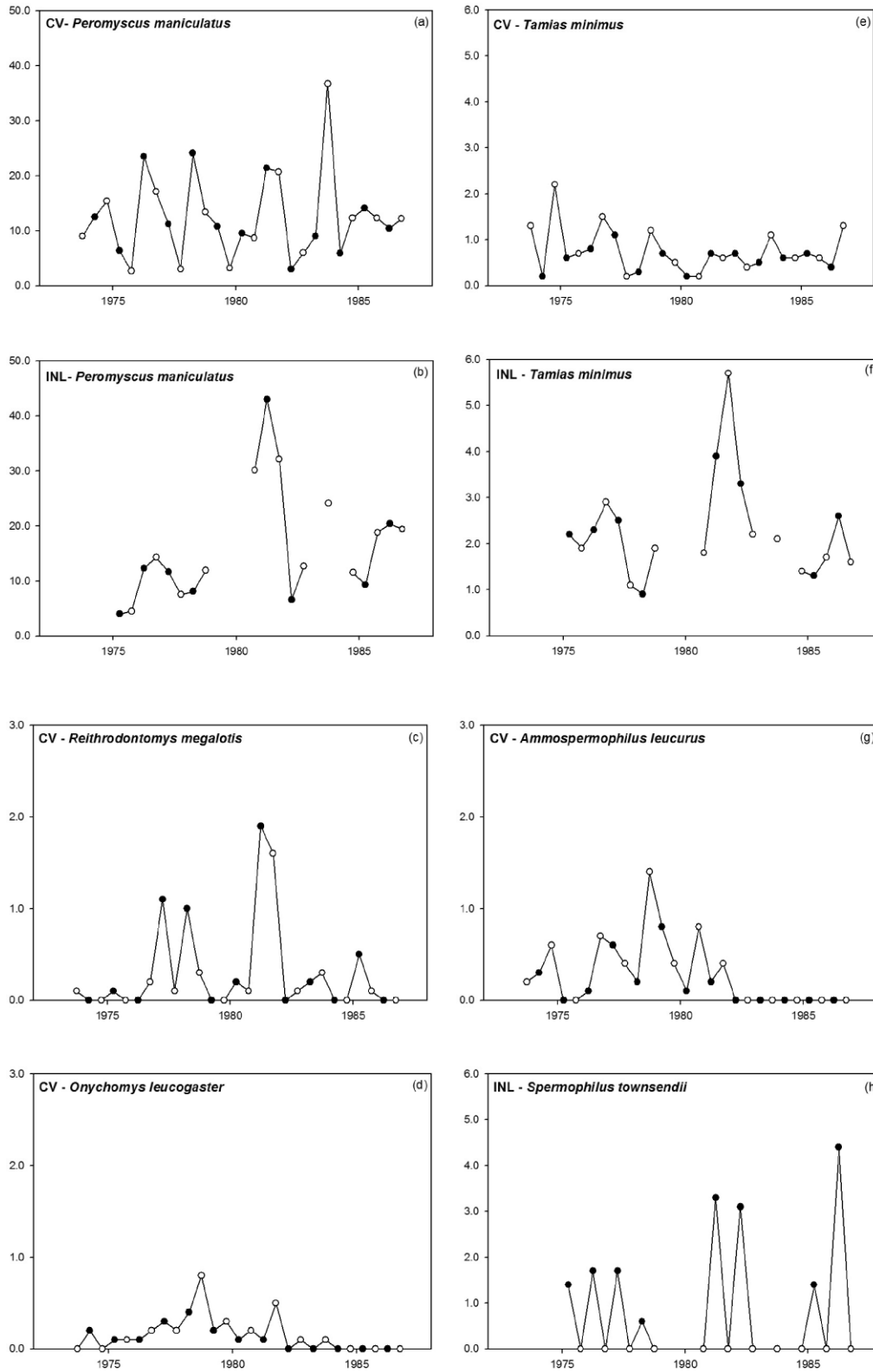
invariably lower than the preceding fall values with the sole exception of 1993.

Abundance data for *C. latrans* were obtained from INL from spring 1975 through fall 1986. Both spring and fall index values increased 5- to 10-fold between 1979 and 1983, followed by an equally dramatic decline through 1986 (Fig. 3e). Although spring values for INL in 1975 were similar to those obtained in CV, the index on INL increased 4 times more on INL than CV (Figs. 3d and 3e). As on the CV site, index values in fall typically were double the values of the preceding spring except during the radical population decline.

**Rodents.**—We obtained indices of rodent abundance twice annually in CV between 1973 and 1986 ( $n = 14$  fall samples, 13 spring samples) and in INL between 1975 and 1986 ( $n = 11$  fall samples, 8 spring samples; Fig. 2). In CV, sufficient data

were obtained to assess trends in abundance for 8 species of rodents including 3 cricetids, 3 heteromyids, and 2 sciurids. The data set for INL included useful information for only 1 cricetid, 2 heteromyids, and 2 sciurids. We had concurrent abundance indices from both sites for 4 species: *P. maniculatus*, *P. parvus*, *D. ordii*, and *T. minimus*. Difficulties in maintaining logistical support resulted in incomplete data sets on rodent abundance from INL, especially for spring assessments (Fig. 2).

*Peromyscus maniculatus* was the most commonly trapped rodent on both study sites (index ranges = 3.0–43.0) with similar mean abundance values (Figs. 4a and 4b) for periods when concurrent data were available for the 2 areas (CV and INL = 16.2 and 15.9, respectively). In CV, abundance of *P. maniculatus* appeared to oscillate at about 2-year intervals with



**FIG. 4.**—Spring (closed circles) and fall (open circles) indices of abundance of 3 species of Cricetidae and 3 species of Sciuridae on Curlew Valley (CV), Utah, and Idaho National Laboratory (INL), Idaho, study sites, 1973–1986. See text for explanation of various index values represented along the y axes.

8-fold amplitude in both spring and fall seasons (Fig. 4a). Although peak index values typically occurred in spring, this was not always the case, with the single highest value occurring in fall 1984. The range in capture rates and trends at INL were comparable to those observed in CV (Fig. 4b). Although similarities in patterns and trends between the 2 study areas were expected because of their proximity, apparent lapses in synchrony make the relationship ambiguous. The highest abundance index for *P. maniculatus* in CV, 36.7, occurred in fall 1983 (Fig. 4a), whereas the highest abundance index in INL, 43.0, occurred in spring 1981 (Fig. 4b).

Two other species of cricetids were captured on the CV site but not on the INL. Capture rates of *R. megalotis* were erratic, with none captured in 11 of our 27 sampling periods and in only 4 sampling periods was the index  $> 1.0$  (Fig. 4c). Peak captures typically occurred in fall. Small numbers of *O. leucogaster* were consistently captured between 1974 and 1983, but captures were rare, or nonexistent thereafter (Fig. 4d). Overall, mean fall values were 0.35, whereas mean spring values were 0.18. In only 2 instances, both in fall, was the index for *O. leucogaster*  $> 0.5$ .

Three species of sciurids were included among the rodents captured but only *T. minimus* was captured on both sites. Mean index values for *T. minimus* were more than 3.2 times higher at INL than at CV (2.28 versus 0.72) for the periods when concurrent measures were available. Although peak indices were typically observed in fall, fall indices were not necessarily larger than those in the preceding spring (Figs. 4e and 4f). Examination of data from CV suggests moderate peaks at 2- to 3-year intervals with 2- to 5-fold changes in abundance of *T. minimus* (Fig. 4e). A basic pattern of decline in fall values noted from 1974 through 1981 in CV followed by a slight resurgence was not reflected in the trends of the spring indices (Fig. 4e). The data set from INL is insufficient for further useful analysis (Fig. 4f).

*Ammospermophilus leucurus* was only captured on the CV site. Peak capture rates occurred at 2-year intervals and fall indices were typically twice as high as spring indices (Fig. 4g). None were captured after the fall of 1981 (Fig. 4g). Although an index  $> 1.0$  was noted once, indices generally ranged between 0.25 and 0.5, indicating that  $< 10$  were caught during most sampling periods.

On INL, *S. townsendii* appeared to be a replacement species for *A. leucurus* in CV, with an average spring index of 2.2 captures per 100 trap-nights (Fig. 4h). None were caught during fall assessments and none were caught on the CV site.

Two species of heteromyids were captured on both study sites, *P. parvus* and *D. ordii*. On the CV site, *P. parvus* was frequently captured between spring 1973 and spring 1977 (index  $> 1.0$  for 7 of 8 sampling periods;  $\bar{X} = 3.2$ ), but thereafter the index fluctuated around 0.5 until a slight resurgence in spring samples of 1985 and 1986 (Fig. 5a). Spring index values ( $\bar{X} = 1.7$ ) were typically twice as high as those obtained the preceding fall ( $\bar{X} = 0.9$ ). On the INL site, *P. parvus* was routinely captured in small numbers ( $\bar{X} = 0.3$ ), with spring values also typically larger than the respective preceding fall values (Fig. 5b). *D. microps* was caught in small

numbers on the CV site. Their capture rates decreased as the monitoring period progressed, with indices between 0.75 and 1.0 common between 1974 and 1978, followed by a steady decline until none were caught after 1983 (Fig. 5c). *D. ordii* was caught in moderate numbers on both sites, especially early in the time series. A decreasing trend in abundance of *D. ordii* on the CV site occurred between 1974 through 1982 (Fig. 5d) and they were caught infrequently thereafter. No such trend was noted on the INL site (Fig. 5e). Seasonal differences in capture rates are not apparent, although the highest values on each site occurred in fall.

Four of 6 pairwise correlations among the 3 species of heteromyids (2 pairwise correlations from each season) were positive ( $P \leq 0.10$ ; Table 1). Although correlation coefficients of only 2 of 10 pairwise comparisons among heteromyids and sciurids were significant ( $P \leq 0.05$ ) among spring indices, 5 of 10 comparisons among fall indices were significant (1 at  $P \leq 0.10$ , 4 at  $P \leq 0.05$ ; Table 1). Fluctuations in cricetid populations did not appear to be correlated. Exceptions were between *R. megalotis* and *P. maniculatus* in spring ( $P \leq 0.10$ ), and *R. megalotis* and *O. leucogaster* in fall ( $P \leq 0.10$ ). We detected no significant relationships among sciurids, but we did observe a correlation between a sciurid and cricetid (*A. leucurus* and *O. leucogaster* in fall,  $P \leq 0.05$ ). The levels of significance presented with these correlation coefficients are likely liberal because they do not take into account any measure of autocorrelation, especially among species that declined to, and remained at, low density.

Correlograms were difficult to assess for many of the species given the constraints of the available data. We only found evidence of cyclic behavior in *L. californicus* in CV populations in both fall and spring indices ( $P < 0.0001$  for all lags in both series; Fig. 6). Annual cycles of approximately 10–11 years were indicated by negative autocorrelations at time lags of 6 and 18 years for both seasons and additionally at 30 years for fall indices, and significant positive autocorrelations at year 12 years for both seasons and 24 years in the spring (Fig. 6). We also observed “cyclic” behavior of 2- to 3-year intervals in 3 rodent species, *P. maniculatus*, *T. minimus*, and *A. leucurus*, using the more complete data series from CV; however, none of these relationships were statistically significant using autocorrelation analyses.

## DISCUSSION

Our studies were initiated to provide a description of the apparent cyclic pattern in populations of *L. californicus* and expanded to include aspects related to its principle mammalian predator, *C. latrans*. Some aspects of those analyses are presented by other authors (see Gross et al. 1974; Knowlton and Stoddart 1992; Stoddart et al. 2001; Wagner and Stoddart 1972). While observing coyote–jackrabbit dynamics, we additionally monitored abundances of rodents for a number of years. Although we detected evidence of population cycles in *L. californicus* in CV, we did not observe the same trend in INL. Patterns of abundance of *L. californicus* were similar at both study sites, although the seasonal magnitudes of change

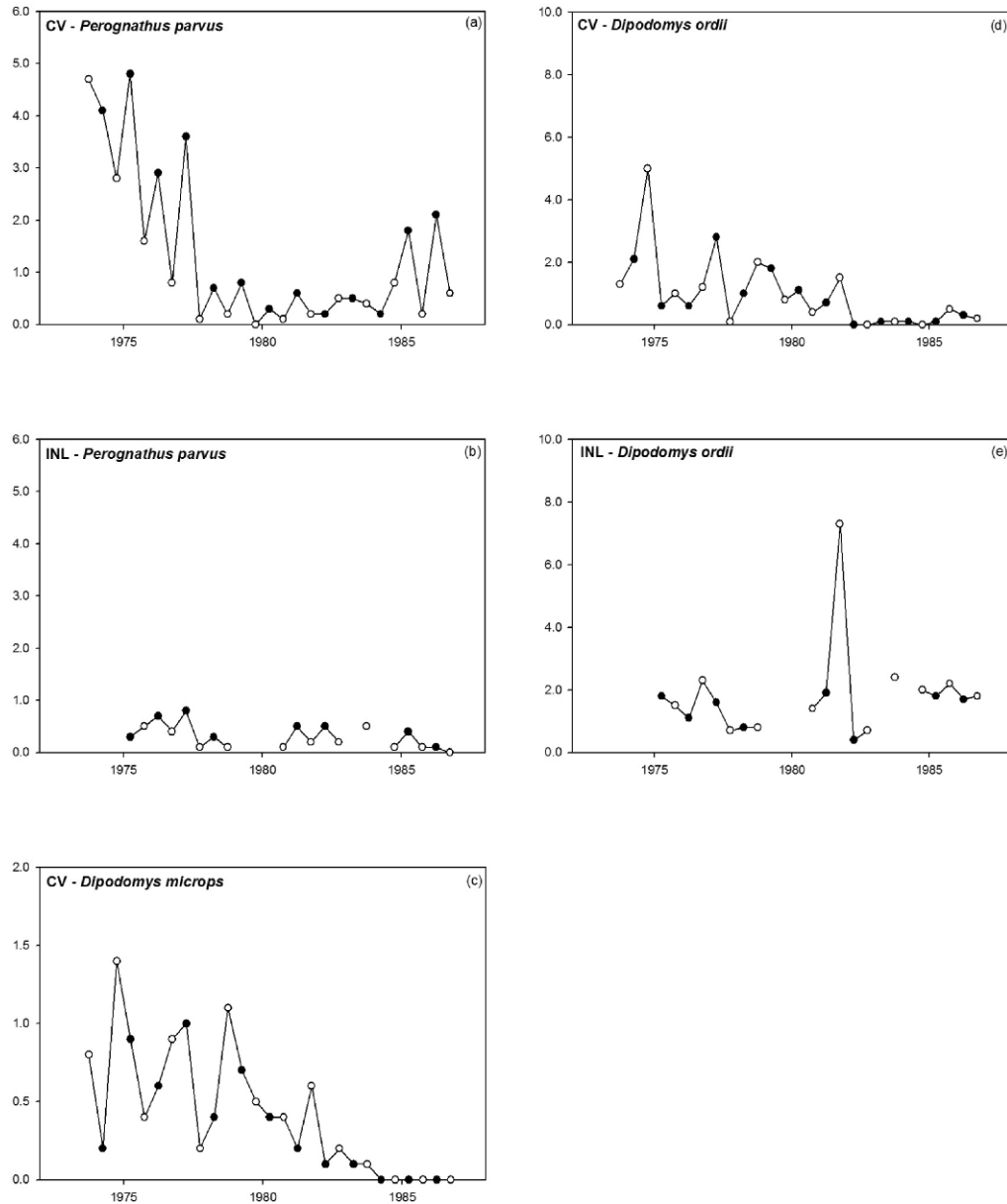


FIG. 5.—Spring (closed circles) and fall (open circles) indices of abundance of 3 species of Heteromyidae on Curlew Valley (CV), Utah, and Idaho National Laboratory (INL), Idaho, study sites, 1973–1986. See text for explanation of various index values represented along the y-axes.

were quite different. Fluctuations in abundance of *C. latrans* were dissimilar between study areas, with the population of coyotes at INL matching trends in abundance of *L. californicus*. In the longer data series from CV, the abundance of *C. latrans* remained elevated during the later cycles of jackrabbit abundance in the mid-1980s and early 1990s instead of declining with decreasing jackrabbit abundances. Comparisons of patterns in rodent abundance between sites were more difficult to assess given the variable presence of some species and data overlap in time. However, population trends in several of the heteromyids were similar between the sites.

*Lagomorphs*.—Abundance of *L. californicus* on both study sites appeared cyclic during our study period, with a period of approximately 10 years and >150-fold change in amplitude. Autocorrelation analyses and correlograms of spring and fall

population indices support this for the CV population. Given the smaller range of available data for INL, we can only assess trends qualitatively. Although methods among studies varied, the apparent cyclicality was a synchronized, regional event, with Eberhardt and Van Voris (1986) reporting peak abundances on Dugway Proving Ground in central Utah in 1971 and 1978–1982 and Knick (1991) reporting peak jackrabbit populations in 1979 and 1989 for the Birds of Prey Natural Area near Boise, Idaho. These peaks coincide with peak abundances reported for both of our study areas, with comparable changes in amplitude. During our study, populations of *S. nuttallii* and *B. idahoensis* on INL surged in synchrony with that of *L. californicus* (Fig. 3), suggesting that all 3 species were responding to similar environmental events.



**TABLE 1.**—Correlation coefficients comparing spring and fall trends in abundances among pairs for 8 species of rodents monitored in Curlew Valley, Utah, 1977–1986.

Species	Correlation coefficients for spring indices ( $n = 13$ ; $P_{(0.10)} = 0.473$ ; $P_{(0.05)} = 0.566$ )							
	<i>Peromyscus maniculatus</i>	<i>Reithrodontomys megalotis</i>	<i>Onychomys leucogaster</i>	<i>Tamias minimus</i>	<i>Ammospermophilus leucurus</i>	<i>Perognathus parvus</i>	<i>Dipodomys ordii</i>	<i>Dipodomys microps</i>
<i>Peromyscus maniculatus</i>		0.549*	0.020	−0.002	0.140	0.030	0.141	0.100
<i>Reithrodontomys megalotis</i>	0.410		0.261	0.277	0.206	−0.117	0.226	0.121
<i>Onychomys leucogaster</i>	0.069	0.520*		0.139	0.293	−0.198	0.264	0.188
<i>Tamias minimus</i>	0.410	−0.114	−0.121		0.323	0.161	0.146	0.428
<i>Ammospermophilus leucurus</i>	0.002	0.145	0.761**	0.211		0.123	0.842**	0.587**
<i>Perognathus parvus</i>	−0.067	−0.207	−0.410	0.564**	−0.125		0.437	0.537*
<i>Dipodomys ordii</i>	0.113	0.082	0.134	0.741**	0.458*	0.472*		0.649**
<i>Dipodomys microps</i>	0.045	0.123	0.397	0.658**	0.712**	0.456	0.874**	

Correlation coefficients for fall indices ( $n = 14$ ;  $P_{(0.10)} = 0.455$ ;  $P_{(0.05)} = 0.544$ )

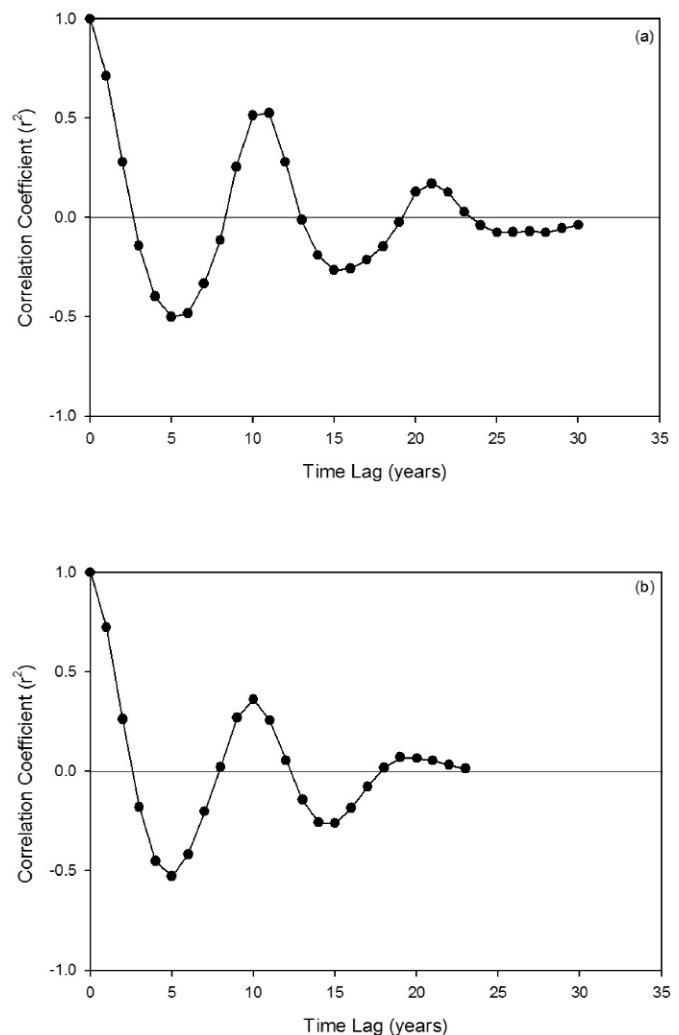
\*  $P \leq 0.10$ ; \*\*  $P \leq 0.05$ .

Lagomorph population cycles have been intensely studied, particularly those of *L. americanus* in relation to abundance of *L. canadensis* (see Hodges [2000] and Krebs et al. [1995] for reviews). Hare cycles with periods of 9–10 years and amplitude of 15- to 200-fold have been reported (Korpimaki and Krebs 1996). Like *L. americanus*, slight variations in synchrony in abundance of *L. californicus* between localized areas are sometimes reported (Gross et al. 1974). Causal factors for the cycles appear to be variations in mortality rates rather than changes in natality rates (Smith 1987; Wagner and Stoddart 1972). Knowlton and Stoddart (1992) suggested that predation may be an important factor influencing the cyclic pattern of abundance of *L. californicus*. Their empirical data-driven model of interactions between *C. latrans* and *L. californicus* indicated that such hypotheses warrant additional investigation.

One apparent anomaly in the data on abundance of *L. californicus* between our 2 study areas involves the relationship between spring and fall indices. In CV, abundance indices in spring were about one-half the indices of the preceding fall, reflecting the seasonal (spring–summer) pattern in reproduction accompanied by mortalities throughout the year. Because *L. californicus* in this area does not reproduce in fall and winter and 50% overwinter mortality is typical (Gross et al. 1974; Smith 1987; Stoddart 1987b), populations should be lower in spring. On INL, however, spring indices were typically much higher than indices the previous fall. Unlike the CV study population, which is demographically closed (Smith 1987; Smith et al. 2002), the INL study area probably did not include all seasonal areas used by that population. Appreciable numbers of *L. californicus* likely made significant migrational movements to historic wintering areas in northern portions of the INL site after our fall index period and remained there past our spring index period (Porth 1995; Smith et al. 2002). Fifty percent or more of the population of *L. californicus* on INL in spring may move onto the site between October and March, underscoring the need to understand movement patterns when trying to assess and interpret demographic data.

*Coyotes.*—On both study sites, abundance of coyotes in fall is typically twice that of the preceding spring, undoubtedly resulting from young born in the spring remaining close to their

natal territories before dispersing after our fall indices were obtained (Davison 1980). Our early concerns about low values of abundance for *C. latrans* in spring lead us to pursue an inventory in the fall when young of that year would be



**FIG. 6.**—Correlograms of abundances of *Lepus californicus* in a) fall and b) spring in Curlew Valley, Utah.

included. This proved inappropriate because population regulation of *C. latrans* has strong territorial and intraspecific dominance components. The data from spring provide a better assessment of the “stock” population without confounding it by including a highly variable reproductive component. Responses of populations of *C. latrans* to fluctuating food abundance have been assessed previously with respect to *L. americanus* (Keith 1963; O’Donoghue et al. 1997; Todd et al. 1981), *L. californicus* (Bartel and Knowlton 2005; Clark 1972; Hoffman 1979; Knudsen 1976), ungulate carrion (Weaver 1977, 1979), and arvicoline rodents (Todd et al. 1981). Although abundance of prey influences abundance of *C. latrans* in many studies, our correlogram analysis did not demonstrate a cyclic pattern within the CV population of coyotes, although linkage to prey populations (primarily *L. californicus*) seemed apparent. Such a relationship may be obscured in the CV data by delayed demographic responses, prey-switching on the part of coyotes, and substantial changes in the depredation management program for *C. latrans* during our study. The low exploitation rates of *C. latrans* by humans on INL (Davison 1980) may allow a more typical *C. latrans*–prey base response. However, the 2-year delay between peak prey abundance and numbers of *C. latrans* is curious. Intrinsic population limitations such as dominance and territoriality could dampen food-base–driven fluctuations in abundance of *C. latrans* and obscure cyclic behavior in demographic responses.

Abundance of *C. latrans* on INL may be 5 times that on CV. Weaver (1977, 1979) noted that the distribution of *C. latrans* within Jackson Hole in summer was correlated with the distribution of wild ungulates in winter, suggesting that because coyotes are territorial, they use habitats in summer where they also can survive in winter. This hypothesis may be relevant to populations on our study areas. During the first 20 years of our CV study, numbers of pronghorn and mule deer were very low and the population of *C. latrans* was primarily dependent upon *L. californicus* as a winter food resource and presumably responsive to changes in their abundance. On the other hand, INL was a wintering area for perhaps 7,000 pronghorn, which could have provided a substantial alternate food resource and the basis for a substantially higher density in the stock population of coyotes.

On INL, abundance of *C. latrans* also appeared to respond to increased abundance of *L. californicus* with a 1- to 2-year lag. Abundance of *L. californicus* peaked in 1981–1982, whereas that of *C. latrans* did not peak until 1983 (Fig. 3). The lag might result from adaptive foraging (Abrams 1992) or simply reflect accumulating changes in reproductive performance of populations of *C. latrans*. Inferring population responses of *C. latrans* to fluctuations in individual prey species solely from the data sets currently available is speculative. Data encompassing several prey cycles are needed before valid inferences are practical.

Although changes in abundance of *C. latrans* in CV reflected abundance of *L. californicus* through the 1960s, 1970s, and early 1980s, the population did not decrease when numbers of lagomorphs plummeted in 1982–1984 (Fig. 3). We propose 2

hypotheses for sustained higher abundance of *C. latrans* in CV during the latter part of our study. The 1st pertains to the development of alternative food sources such as ungulates (Knowlton and Gese 1995) or rodents (Bartel 2003; Bartel and Knowlton 2005). Identifying alternative food sources is confounded by our lack of information on the winter feeding patterns of *C. latrans* in CV, a period that may be critical for determining overall population levels (Weaver 1977, 1979). Although many rodents hibernate during the winter, *L. curtatus* (sagebrush voles) and *Dipodomys* (kangaroo rats) do not. We do not have data on their population trends because they were not accurately surveyed by our indexing procedures. Perhaps more important, populations of pronghorn and mule deer grew dramatically in CV during the latter portion of our study. Not anticipating such a development, we failed to monitor their abundance and can only speculate about implications.

A 2nd hypothesis for the patterns of abundance of *C. latrans* in CV proposes lower mortality rates associated with reduced exploitation by humans during the 1980s (Knowlton and Gese 1995). Mortality rates of *C. latrans* on the CV site are available for 1970–1979. During this period, mortality rates of adults were documented at 49–53% (Davison 1980; Knowlton and Stoddart 1983; Knudsen 1976), with mortality of juveniles approaching 77% (Davison 1980). Among the mortalities detected, 93% of mortalities of adults and 89% of those of juveniles were caused by human exploitation. Pelts of *C. latrans*, which sold for \$40–50 in the 1970s, declined to \$10–15 in value in the mid-1980s (Utah Department of Natural Resources, Division of Wildlife Resources 1997), presumably reducing incentives for human-induced mortality. Changes in the rate of human-induced mortality among *C. latrans* could confound our understanding of their response to reduced abundance of *L. californicus*. Thus, failure to detect an anticipated population decline in coyotes may have resulted from increased abundance of alternate foods or reduced human harvest due to decreasing pelt prices (Bartel 2003). Population responses of *C. latrans* to changing prey abundance may be more accurately portrayed in our data from INL where human exploitation rates were lower (Davison 1980).

*Rodents.*—We recognized 4 general patterns in multi-seasonal fluctuations in abundance among the 9 species of rodents in our study: relative stable numbers from year to year, 2 species with relatively low capture rates with irregular irruptions in abundance, several species with somewhat regular and repetitive patterns of increase and decline, and other species that displayed a general and systematic decline in abundance during the study. *S. townsendii* on INL was absent from all fall samples because these inventories occurred after these animals had aestivated for the year. Populations of *R. megalotis* and *O. leucogaster* appeared to fit the 2nd pattern.

The relative abundances of 3 species (*P. maniculatus*, *T. minimus*, and *A. leucurus*) appeared qualitatively cyclic, but cycles were not supported statistically by autocorrelation analyses. This is most evident with *P. maniculatus*, which appeared to peak at 2- to 3-year intervals. The paucity of data points within each “cycle,” as well as an apparent lack of

seasonal fidelity in peak abundances may preclude statistical cyclicality. The pattern of abundance for *P. maniculatus* on INL appears consistent with the pattern on CV but lapses in data collection preclude meaningful comparisons. Similarly, captures of *T. minimus* and *A. leucurus* on CV appear to peak at 2- to 3-year intervals, with higher numbers typically recorded in fall. Captures rates of *T. minimus* on INL were generally higher and the pattern appears similar to the CV pattern but missing data points constrain inferences. During the first 8 years of data collection, captures of *A. leucurus* also appeared to fluctuate cyclically at 2-year intervals, with peak abundances in fall. However, none were captured during the last 10 sampling periods, possibly as a result of habitat destruction by extensive range fires in 1983.

All 3 species of heteromyids captured on the CV site (*P. parvus*, *D. microps*, and *D. ordii*) declined dramatically in abundance between 1973 and 1984. The decline was most precipitous for *P. parvus*. However, the lower values in 1977–1984 were comparable to values observed on the INL site (Figs. 5a and 5b). Both species of *Dipodomys* also showed systematic declines between 1973 and the early 1980s. The initial declines preceded the 1983 range fire, seemingly discounting it as a significant causal factor. A decline in abundance was not observed among heteromyids on the INL site.

Combined indices of abundance for the 3 heteromyids on our CV site were correlated with the abundance of *C. latrans*, although the relationship was weak ( $R^2 = 0.287$ ,  $P = 0.018$ ; Fig. 7). The relationship seems especially evident at higher densities of *C. latrans* (Fig. 7). When the index of abundance of *C. latrans* was below 10, abundance of heteromyid rodents appears responsive to other factors, but above this threshold numbers of heteromyids remain consistently low. Our data from INL are consistent with this observation; indices of abundance of *C. latrans* were 5–10 times higher than in CV, whereas the index of abundance of *P. parvus* never exceeded 1.0 and only once did the abundance of *D. ordii* exceed 2. Henke and Bryant (1999) reported that while rodent density and diversity declined on study areas subjected to removal of *C. latrans*, *D. ordii* increased significantly in abundance on such sites in both shrubland and grassland communities. This was not the case for other heteromyids on their study sites. Alternate factors, including presence of other predators, also are likely to affect the abundance of small mammals. Although Stangl et al. (2005) suggested that heteromyids are underrepresented in pellets of barn owl and infer they may be able to evade capture by raptors, it seems unlikely that either *Dipodomys* or *P. parvus* could routinely evade attacks by agile terrestrial predators. We acknowledge several caveats associated with our population-monitoring procedures. Many of the methods are dependent on animal responses, which could vary among species or over time. For example, *L. curtatus* was commonly eaten by *C. latrans* in CV during some periods (Bartel and Knowlton 2005) but was strikingly absent from our monitoring samples. Their distribution may be concentrated in a few microhabitats that our trapping transects missed, our trap placements may have missed their runways, or these voles may

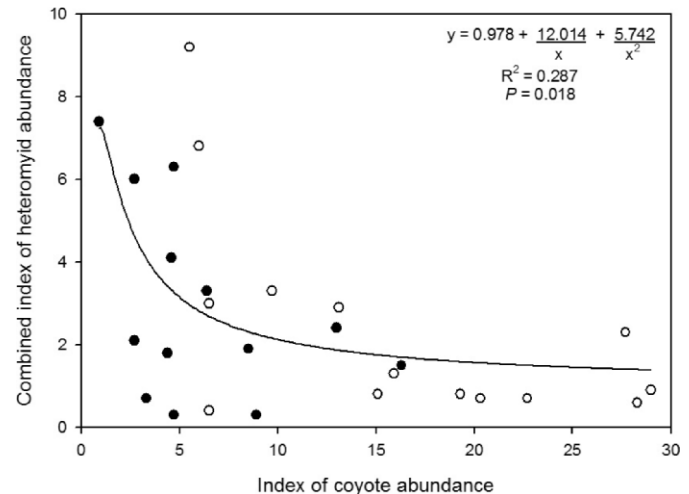


FIG. 7.—Combined indices of abundance for 3 species of heteromyids plotted against abundance indices for *Canis latrans* on Curlew Valley, Utah, study site, 1973–1986. Closed symbols represent spring values and open symbols represent fall values.

simply not respond to the baits we used. For other rodents, changes in production of plant seeds could affect population changes. Shifts in seed production also could influence the size of foraging areas that individual rodents scoured for resources, which, in turn, might change the size of areas that individual traps sampled, confounding population indices. In the case of *L. californicus*, season, as well as mean daily temperatures, influences jackrabbit flushing behavior (Eberhardt and Van Voris 1986) and resulting index values. Regardless of these limitations, long-term studies are clearly instrumental in examining abiotic and biotic relationships in community dynamics.

Compared to other long-term efforts of population monitoring, we found several similar patterns. First, we detected cycles in lagomorph populations with periods of 10–11 years, comparable to other studies on *L. americanus* (see Krebs et al. [1995] and Hodges [2000] for reviews) and hares (Korpimäki and Krebs 1996; Krebs et al. 2001). Second, in the beginning of the CV time series for *C. latrans*, we observed populations lagging behind changes in abundance of their main prey item, *L. californicus*, demonstrating similar cyclic trends. Third, although we did not directly evaluate abiotic influences on rodent species in the community, several long-term studies have shown that rodent populations respond independently to environmental variation (Brady and Slade 2004; Brown and Heske 1990; Friggens et al. 2003; Parmenter et al. 1993). However, we found qualitatively similar trends in multiannual cycles in *P. maniculatus*, *T. minimus*, and *A. leucurus*. Brady and Slade (2004) observed cycles in *P. maniculatus* with periods of 3.5 years, whereas Wolff (1985) found cycles with periods of 4–6 years. Last, many of the studies examining patterns of abundance in rodents detected seasonal fluctuations and many positive correlations between species (Brady and Slade 2004; Brown and Heske 1990; Parmenter et al. 1993). Although these interactions are difficult to separate from other

factors, it is evident that interspecific relationships are one of the major factors affecting community structure. Long-term studies such as ours emphasize the need for detailed investigations across temporal scales when determining the roles of individual species in ecological communities.

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