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# Functional feeding responses of coyotes, *Canis latrans*, to fluctuating prey abundance in the Curlew Valley, Utah, 1977–1993

Rebecca A. Bartel and Frederick F. Knowlton

**Abstract:** We investigated interactions between coyotes (*Canis latrans* Say, 1823) and prey in the Curlew Valley, Utah, by comparing prey abundances with prey consumption rates. Previous studies reported a cyclic trend in black-tailed jackrabbit (*Lepus californicus* Gray, 1837) density with a period of 10 years and >150-fold amplitude, as well as short-term fluctuations among some rodent species that exceeded an 8-fold difference in amplitude over 2 years. Our results suggest changes in coyote diets mainly reflect the fluctuations in jackrabbit abundance. Prey switching to rodents during periods of low jackrabbit abundance also was evident. We used the initial feeding pattern analysis to compare prey consumption rates to prey abundance. Coyotes demonstrated a type II (hyperbolic) functional feeding response to changes in jackrabbit abundance. Functional feeding responses to rodent abundances were more difficult to assess because of the strong influence of jackrabbits. In most comparisons, we visually detected a linear functional feeding response to varying rodent abundances; yet this was not statistically supported by Akaike's Information Criterion corrected for small sample sizes (AICc) to assess different models.

**Résumé :** Nous avons étudié les interactions entre les coyotes (*Canis latrans* Say, 1823) et leurs proies dans la vallée Curlew, Utah, en comparant l'abondance des proies et les taux d'ingestion de ces proies. Des études antérieures ont signalé des tendances cycliques dans la densité des lièvres de Californie (*Lepus californicus* Gray, 1837) avec une période de 10 années et une amplitude de >150 fois, ainsi que des fluctuations à court terme de certaines espèces de rongeurs avec des différences d'amplitude de plus de 8 fois sur 2 années. Nos résultats indiquent que les changements dans le régime alimentaire des coyotes reflètent surtout la fluctuation d'abondance du lièvre. Il y a aussi des indications de changement de proies favorisant les rongeurs durant les périodes de faible abondance des lièvres. Une analyse des patrons d'alimentation initiale (initial feeding pattern analysis) nous a permis de comparer les taux de consommation des proies et l'abondance de celles-ci. Les coyotes ont une réponse fonctionnelle alimentaire de type II (hyperbolique) en réaction aux changements d'abondance des lièvres. Les réponses fonctionnelles aux abondances de rongeurs sont plus difficiles à déterminer à cause de la forte influence des lièvres. Dans la plupart des comparaisons, nous détectons visuellement une réponse fonctionnelle alimentaire linéaire aux variations d'abondance des rongeurs, mais ce n'est pas appuyé statistiquement par le critère d'information d'Akaike (corrigé pour les petits échantillons; AICc) utilisé pour évaluer les différents modèles.

## Introduction

Food-habit studies have been used to assess the role that animals play in ecosystems. In the case of coyotes (*Canis latrans* Say, 1823), understanding food habits provides a basis for insights regarding habitat selection (Murray et al. 1994), population density (Clark 1972; Hoffman 1979; Knowlton and Stoddart 1992), movement patterns and home-range size (Litvaitis and Shaw 1980; Mills and Knowlton 1991), reproductive rates (Gier 1968 in Knowlton 1972), social organization (Bowen 1981; Gese et al. 1996), behavioral budgeting and activity patterns (Bekoff and Wells 1981; Gese et al. 1996), as well as livestock depredation rates (Stoddart et al.

2001). Using a long-term prey abundance data set and a collection of coyote scats from Curlew Valley, Utah, we examined coyote functional feeding responses to fluctuating prey abundances of multiple species.

Feeding patterns can be compared to prey abundances to assess functional feeding responses. A functional response is defined as the change in the number of prey consumed in relation to prey abundance (Soloman 1949; Holling 1959). Holling (1959) quantified these functional responses in three mathematical equations. Type I (or linear) has caused some confusion because it refers to two different curves. Originally, Holling (1959) showed type I to be linearly increasing with prey density until it reaches some asymptote. This

depiction is similar to type II (hyperbolic), except that the intersection of the increasing line and horizontal line is sharp versus the smoother transition in type II. Most authors refer to type I as linear without the asymptote (Turchin 2003). It has been suggested that this type of response is rare and only occurs when prey handling time is trivial or predation is a matter of chance encounter (Knowlton and Stoddart 1992; Messier 1995). In a type II response, the number of prey killed increases, but the proportion of overall prey consumed per predator decreases at higher densities (Murdoch 1973; O'Donoghue et al. 1998). This deceleration may result from predator satiation (Murdoch 1973) or an adaptive adjustment of search rates (Abrams 1990). Type II responses have been previously suggested to describe one of the relationships between coyotes and black-tailed jackrabbits, *Lepus californicus* Gray, 1837 (Hoffman 1979; Stoddart et al. 2001). Type III responses are sigmoidal in shape and are typical of generalist predators (Keith et al. 1977). Type III responses could result from a number of possible interactions: (i) predators learning to recognize, capture, and (or) handle prey more efficiently as prey density increases; (ii) predators switching prey types; (iii) adaptive variation in foraging rates; or (iv) changes in prey behavior or vulnerability (O'Donoghue et al. 1998).

### Study area

We worked within a 700-km<sup>2</sup> portion of the Curlew Valley located in Box Elder County, Utah. The valley is a semi-arid intermountain basin formed by Pleistocene Lake Bonneville (Gross et al. 1974; Hoffman 1979). Beyond the southern limits of the study area lie mud flats of the Great Salt Lake (Gross et al. 1974). The most prominent features of the area are two isolated, remnant volcanic cones: Wildcat Hills (maximum elevation 1553 m) and Cedar Hill (maximum 1585 m) (Gross et al. 1974; Hoffman 1979). Valley-floor elevations at the southern end of the valley are approximately 1280 m, with an average rise of 5.7 m/km from south to north (Gross et al. 1974).

Climate is characteristic of Bailey's (1998) Temperate Desert Division Ecoregion. Climate data were recorded at the Snowville Station of the National Climatic Data Center, about 15 km northeast of the study site (NOAA 2002). Average annual temperatures for the study area (1977–1991) were stable with little variation, from 6.1 to 10.0 °C (mean 7.9 °C). Mean annual spring temperatures in May ranged 8.3–13.3 °C (mean 11.3 °C). Mean annual fall temperatures in October ranged 6.7–11.7 °C (mean 8.7 °C). Mean total precipitation ranged 20–56 cm (mean 31.8 cm). Precipitation usually occurred as snow between November and March and rain in late spring and early summer.

Vegetation is characteristic of the Intermountain Semidesert and Desert Province (Bailey 1998) and the Northern Desert Shrub Biome (Fautin 1946). Generally, one or two types of shrubs or trees dominate the vegetation zones, being limited by soil moisture and salinity (Gross et al. 1974; Hoffman 1979). Sage-annuals were the principal type composing 49% of the study area. Agricultural crops present included crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and alfalfa (*Medicago sativa* L.). Some areas of sagebrush were

plowed and seeded with crested wheatgrass as a range improvement practice (Hoffman 1979). After an extensive fire in 1983, additional areas were reseeded (Booth 2001).

Multiple rodent species occur in the area including the deer mouse (*Peromyscus maniculatus* (Wagner, 1845)), western harvest mouse (*Reithrodontomys megalotis* (Baird, 1858)), Great Basin pocket mouse (*Perognathus parvus* (Peale, 1848)), Ord's kangaroo rat (*Dipodomys ordii* Woodhouse, 1853), chisel-toothed kangaroo rat (*Dipodomys microps* (Merriman, 1904)), least chipmunk (*Tamias minimus* Bachmann, 1939), northern grasshopper mouse (*Onychomys leucogaster* (Wied-Neuwied, 1841)), and sagebrush vole (*Lemmyscus curtatus* (Cope, 1686)). Lagomorphs include black-tailed jackrabbit, mountain cottontails (*Sylvilagus nuttallii* (Bachman, 1837)), and pygmy rabbits (*Brachylagus idahoensis* (Merriman, 1891)). Mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) and pronghorn (*Antilocapra americana* (Ord, 1815)) are present. Several carnivores inhabit the study area, including coyotes, badgers (*Taxidea taxus* (Schreber, 1777)), long-tailed weasels (*Mustela frenata* Lichtenstein, 1831), bobcats (*Lynx rufus* (Schreber, 1777)), and striped skunks (*Mephitis mephitis* (Schreber, 1776)). Occasionally, kit fox (*Vulpes macrotis* Merriman, 1888), mountain lion (*Puma concolor* (L., 1771)), and red fox (*Vulpes vulpes* (L., 1758)) have been documented (Hoffman 1979).

Most of the study area (60%) is public land managed by the Bureau of Land Management. The remainder of the area is privately owned. The area is grazed by domestic sheep in the winter and by cattle seasonally (Hoffman 1979; Booth 2001).

### Methods

#### Abundance measurements

Long-term monitoring of coyote demography and coyote-prey interactions occurred in Curlew Valley from 1963 through 1993. We used predator and prey abundance data collected in previous studies (Stoddart 1987; Bartel 2003; Bartel et al., 2005). Abundance data were collected each spring and fall for jackrabbits from fall 1962 through spring 1993. Rodent abundance indices were recorded from fall 1973 through fall 1986 for eight species. Coyote scats provided measurements of prey consumption and were used from fall of 1977 through fall of 1993 (for details see Bartel et al. 2005).

#### Coyote feeding patterns

Scat analysis was used to assess coyote diet patterns. Sixty scats were randomly selected from each spring and fall season of years for which scats were available. All available scats were used if 60 scats were not available. Scat-analysis techniques followed Kelly (1991).

Scat samples containing mammalian prey are composed of two parts: residue (namely, bone, hair, teeth, and other diagnostic parts) and fecal matrix (non-skeletal and non-hair remains) (Kelly 1991). Most of the fecal matrix was removed in the washing process. Since we were primarily interested in the residue portion of the sample, the scats were further separated from the remains of the fecal ma-

trix through a sieve system. Each diagnostic part was identified to species if possible. Hairs were identified using both a reference collection and the key in Adorjan and Kolenosky (1969). Bones and teeth were classified according to a reference collection and guide provided by Gilbert (1990). Numbers of teeth and claws were recorded by species when possible. Visual estimates of occurrence were assigned for each species present in an individual scat. Non-mammalian prey items were not identified to species but noted as present when recognized. To ensure consistent identification of prey items, the first 480 scats (42% of total scats) were reanalyzed. Three percent of identifications were changed. Most of these changes were “unknown” samples eventually identified as a recognizable species.

Fall and spring sampling periods were analyzed separately. Measurement totals of mass of bone, hair, and other; number of teeth; mass of teeth; number of claws; mass of claws; and number of jaws for each species present were recorded for each scat. Percentage of bone, percentage of hair, number of occurrences of a prey item, number of teeth per scat, percentage of scats, percentage of occurrence of a prey item, and mean proportion of a prey item were calculated for each scat. Number of occurrences reported the number of scats in which a prey item occurred within a sampling period. Mean numbers of teeth per scat were used instead of total number of teeth to correct for varying sample sizes among sampling periods.

Three different consumption estimates were used to evaluate feeding patterns: number of teeth per scat, percentage of scats, and percentage of occurrences. Number of teeth per scat gave the most basic information with the least error when reporting how common an item is in the diet. Percentage of scats is the fraction of a sample of scats in which a prey species occurs, and is a measure of how common a food item is in the diet of the animals (Kelly 1991). Percentage of occurrence is the number of times one prey species occurs as a fraction of the total number of prey occurrences for all prey species (Ackerman et al. 1984; Kelly 1991). Percentage of occurrence is 100% for a single food item only when all occurrences are from one prey species, but using percentage of scats could yield 100% occurrence for each species of prey. Percentage of occurrence is most commonly reported in other studies and is useful for comparisons.

Initially, all food items identified in scats were reported as the number of occurrences. Non-mammalian food items found in scats were classified in a general grouping (bird, reptile, etc.). Lagomorphs and rodents were identified to the finest taxonomic grouping practical, typically to species. The two kangaroo rat species were indistinguishable and, consequently, grouped together. Species for which we did not have abundance measurements or species that were not prevalent in the coyote diets were grouped as “other rodents.” Birds were identified by the presence of quills, feathers, claws, or beaks. Insects generally included grasshoppers, crickets, and in one instance, bees. The “other” category contained non-vertebrate items such as vegetation, invertebrates, remaining fecal matrix, and in one case, glass. “Unknown” items included shards of bone without diagnostics. Most of the food items identified in coyote scats were mammalian.

## Functional feeding response

We evaluated 72 models for coyote functional feeding responses. Initially, all functional feeding response models were assessed separately for each season, but because relationships were similar the data were combined. To assess functional response, two components were necessary: abundance measurements and consumption measurements of the prey species. These requirements were met for six prey groups: jackrabbits, deer mice, Great Basin pocket mice, western harvest mice, combined kangaroo rats, and all combined rodents. Abundance measurements were not available for sagebrush voles possibly because they were not vulnerable to methods used to assess abundance. Northern grasshopper mice, least chipmunks, or white-tailed antelope squirrels (*Ammospermophilus leucurus* (Merriam, 1889)) were not detected in coyote diet results. An earlier study on coyote food habits in Curlew Valley (Hoffman 1979) also did not find the latter species prevalent in the coyote diet. As a result, functional feeding responses could not be assessed for these four species.

Four functional feeding models were tested: (1) null,  $y = b$ ; (2) linear,  $y = a + bx$ ; (3) hyperbolic Michaelis–Menton function,  $y = ax/(b + x)$ , which is similar to Holling’s (1959) type II curve (Patterson et al. 1998); and (4) sigmoidal,  $y = (b + x)^c/ax^c$ , which is similar to Holling’s (1959) type III response (Real 1977). The variable  $x$  in all models represents the abundance of the species of interest. In the null models,  $b$  is the mean of the predictor variable (in this case, a consumption measurement). In the hyperbolic and sigmoidal models, parameter  $a$  is the asymptotic consumption rate when predators are satiated and parameter  $b$  is prey density at half the maximum consumption rate (Patterson et al. 1998). Variable  $b$  was constrained as a positive number and limited consumption to zero when prey abundance was zero. Then using PROC NLIN in SAS<sup>®</sup> version 8.2 (SAS Institute Inc. 2002), two linear (null and linear) and two nonlinear (hyperbolic and sigmoidal) regression models were fitted to the consumption data sets. PROC NLIN converged the parameters to find the lowest sum of squares error. To compare among the four models we used maximum log-likelihood values to calculate Akaike’s Information Criterion adjusted for small sample sizes ( $AIC_c$ ), and then evaluated  $AIC_c$  weights.

## Results

### Feeding patterns

Twenty-two samples totaling 1140 scats (mean 52) were used to evaluate coyote feeding patterns by scat analysis. Samples were available for fall periods of 1977, 1979–1989, and 1991–1993 ( $N = 15$ ), and for spring periods of 1981–1983, 1985–1986, and 1992–1993 ( $N = 7$ ) (Table 1). Seasons were tabulated and analyzed separately.

Jackrabbits contributed the majority of teeth per scat in the majority of samples, excluding fall periods of 1983–1988 and spring periods of 1985–1986, when rodents, predominantly sagebrush voles, contributed the majority of teeth per

Table 1. Mean number of teeth per scat of prey items in coyote scats from Curlew Valley, Utah, 1977–1993.

| Season and prey item             | 1977<br>(56) | 1979<br>(28) | 1980<br>(58) | 1981<br>(56) | 1982<br>(57) | 1983<br>(53) | 1984<br>(52) | 1985<br>(39) | 1986<br>(56) | 1987<br>(55) | 1988<br>(55) | 1989<br>(57) | 1991<br>(56) | 1992<br>(53)* | 1993<br>(55)† |
|----------------------------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|---------------|---------------|
| <b>Fall</b>                      |              |              |              |              |              |              |              |              |              |              |              |              |              |               |               |
| <i>Lepus californicus</i>        | 2.38         | 2.36         | 3.16         | 1.84         | 2.46         | 1.26         | 1.10         | 0.51         | 0.54         | 2.65         | 2.04         | 0.88         | 2.25         | 1.89          | 1.33          |
| Rodents                          |              |              |              |              |              |              |              |              |              |              |              |              |              |               |               |
| <i>Peromyscus maniculatus</i>    | 0.00         | 0.00         | 0.00         | 0.00         | 0.09         | 1.87         | 0.00         | 2.31         | 0.70         | 0.05         | 0.16         | 0.11         | 0.14         | 0.00          | 0.00          |
| <i>Reithrodontomys megalotis</i> | 0.09         | 0.04         | 0.00         | 0.16         | 0.04         | 0.47         | 0.00         | 0.05         | 2.79         | 0.24         | 0.33         | 0.05         | 0.09         | 0.00          | 0.05          |
| <i>Lemmus curtatus</i>           | 0.02         | 0.00         | 0.00         | 0.07         | 0.02         | 16.09        | 28.63        | 8.21         | 1.16         | 6.98         | 12.53        | 0.25         | 0.00         | 0.08          | 0.00          |
| <i>Perognathus parvus</i>        | 0.18         | 0.00         | 0.02         | 0.00         | 0.44         | 0.89         | 0.02         | 1.00         | 2.48         | 0.02         | 0.29         | 0.18         | 0.32         | 0.06          | 0.65          |
| <i>Dipodomys</i> spp.            | 2.02         | 0.00         | 0.19         | 0.41         | 0.00         | 0.00         | 0.00         | 0.23         | 0.25         | 0.00         | 0.27         | 1.11         | 1.32         | 1.02          | 2.40          |
| Other rodents                    | 0.00         | 0.29         | 0.00         | 0.00         | 0.00         | 0.00         | 0.00         | 0.15         | 0.00         | 0.00         | 0.13         | 0.00         | 0.16         | 0.00          | 0.00          |
| Unknown rodents                  | 0.02         | 0.07         | 0.03         | 0.02         | 0.00         | 0.02         | 0.04         | 0.64         | 0.14         | 0.11         | 0.07         | 0.07         | 0.02         | 0.02          | 0.05          |
| <b>Spring</b>                    |              |              |              |              |              |              |              |              |              |              |              |              |              |               |               |
| <i>L. californicus</i>           |              |              |              | 3.42         | 2.33         | 4.45         |              | 1.30         | 1.05         |              |              |              |              | 3.14          | 1.85          |
| Rodents                          |              |              |              |              |              |              |              |              |              |              |              |              |              |               |               |
| <i>P. maniculatus</i>            |              |              |              | 0.31         | 0.00         | 0.00         |              | 0.32         | 0.19         |              |              |              |              | 0.12          | 0.13          |
| <i>R. megalotis</i>              |              |              |              | 0.04         | 0.00         | 0.00         |              | 0.00         | 0.35         |              |              |              |              | 0.00          | 0.00          |
| <i>L. curtatus</i>               |              |              |              | 0.00         | 0.33         | 4.31         |              | 29.38        | 6.60         |              |              |              |              | 0.04          | 0.29          |
| <i>P. parvus</i>                 |              |              |              | 0.00         | 0.07         | 0.24         |              | 0.23         | 3.07         |              |              |              |              | 0.18          | 0.06          |
| <i>Dipodomys</i> spp.            |              |              |              | 0.13         | 0.67         | 0.00         |              | 0.00         | 0.02         |              |              |              |              | 2.98          | 1.00          |
| Other rodents                    |              |              |              | 0.00         | 0.00         | 0.10         |              | 0.00         | 0.00         |              |              |              |              | 0.00          | 0.00          |
| Unknown rodents                  |              |              |              | 0.25         | 0.04         | 0.07         |              | 0.00         | 0.11         |              |              |              |              | 0.00          | 0.02          |

Note: Sample sizes are in parentheses.

\*Sample size was 51 teeth per scat for the Spring prey items in 1992.

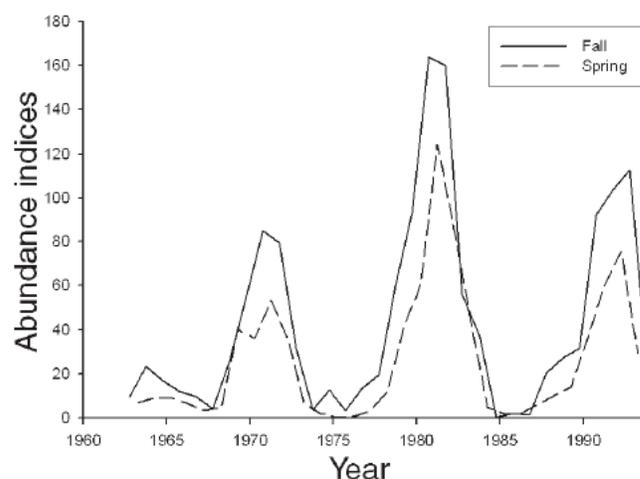
†Sample size was 52 teeth per scat for the Spring prey items in 1993.

scat (Table 1). The largest mean number of sage-brush vole teeth per scat was documented in fall of 1984 and spring of 1985 (28.63 and 29.38 teeth per scat, respectively).

**Jackrabbits**

Abundance indices for jackrabbits were available from 1962 to 1993 for fall ( $N = 32$ ) and from 1963 to 1993 for spring, with missing values for 1987–1988 ( $N = 29$ ). Fall jackrabbit abundance varied from 0.4 to 163.8, and spring abundance measurements fluctuated between 0.5 and 124.4 (Fig. 1). A cycle in the jackrabbit population seemed evident, with a period of approximately 10 years and amplitude reaching 325. Spring abundance was typically half the preceding fall abundance throughout most of the series. Using  $AIC_c$  values, hyperbolic functional feeding responses were most parsimonious for the number of teeth per scat model and the percentage of scat model, while sigmoidal responses were chosen for the percentage of occurrence model (Table 2). Hyperbolic models best fit the number of teeth per scat and the percentage of scat consumption data because they had higher  $AIC$  weights (Figs. 2a, 2b; Table 2). Sigmoidal models best fit the percentage of occurrence consumption data (Fig. 2c, Table 2). Sigmoidal models converged optimally only for the percentage of occurrence consumption data.

**Fig. 1.** Relative abundance of *Lepus californicus* in Curlew Valley, Utah, 1962–1993.



**Table 2.** Models of coyote functional feeding responses for six prey groups.

| Prey                   | Variable* | Model                  | <i>N</i> | <i>K</i> | Maximum log-likelihood | $AIC_c$ | $AIC$ weights |
|------------------------|-----------|------------------------|----------|----------|------------------------|---------|---------------|
| <i>L. californicus</i> | TPS       | Null                   | 22       | 1        | -36.499                | 75.198  | 0.000         |
|                        | TPS       | Linear                 | 22       | 2        | -27.243                | 59.117  | 0.228         |
|                        | TPS       | Hyperbolic             | 22       | 2        | -26.024                | 56.679  | 0.772         |
|                        | TPS       | Sigmoidal <sup>†</sup> | 22       | 3        | -40.767                | 88.868  | 0.000         |
|                        | PS        | Null                   | 22       | 1        | -111.706               | 225.612 | 0.000         |
|                        | PS        | Linear                 | 22       | 2        | -94.334                | 193.300 | 0.000         |
|                        | PS        | Hyperbolic             | 22       | 2        | -86.523                | 177.678 | 1.000         |
|                        | PS        | Sigmoidal <sup>†</sup> | 22       | 3        | -100.179               | 207.690 | 0.000         |
|                        | PO        | Null                   | 22       | 1        | -104.230               | 210.661 | 0.000         |
|                        | PO        | Linear                 | 22       | 2        | -90.307                | 185.246 | 0.001         |
|                        | PO        | Hyperbolic             | 22       | 2        | -84.270                | 173.172 | 0.399         |
|                        | PO        | Sigmoidal              | 22       | 3        | -82.512                | 172.357 | 0.600         |
| <i>P. maniculatus</i>  | TPS       | Null                   | 14       | 1        | -16.219                | 34.771  | 0.381         |
|                        | TPS       | Linear                 | 14       | 2        | -15.185                | 35.461  | 0.270         |
|                        | TPS       | Hyperbolic             | 14       | 2        | -15.079                | 35.249  | 0.300         |
|                        | TPS       | Sigmoidal              | 14       | 3        | -15.226                | 38.852  | 0.050         |
| <i>Dipodomys</i> spp.  | TPS       | Null                   | 14       | 1        | -12.268                | 26.869  | 0.282         |
|                        | TPS       | Linear                 | 14       | 2        | -10.670                | 26.432  | 0.351         |
|                        | TPS       | Hyperbolic             | 14       | 2        | -10.761                | 26.612  | 0.321         |
|                        | TPS       | Sigmoidal <sup>†</sup> | 14       | 3        | -11.055                | 30.510  | 0.046         |
| <i>P. parvus</i>       | TPS       | Null                   | 14       | 1        | -17.132                | 36.597  | 0.629         |
|                        | TPS       | Linear                 | 14       | 2        | -16.927                | 38.944  | 0.195         |
|                        | TPS       | Hyperbolic             | 14       | 2        | -17.132                | 39.354  | 0.159         |
|                        | TPS       | Sigmoidal <sup>†</sup> | 14       | 3        | -17.676                | 43.752  | 0.018         |
| <i>R. megalotis</i>    | TPS       | Null                   | 14       | 1        | -16.046                | 34.425  | 0.374         |
|                        | TPS       | Linear                 | 14       | 2        | -15.011                | 35.112  | 0.265         |
|                        | TPS       | Hyperbolic             | 14       | 2        | -14.864                | 34.819  | 0.307         |
|                        | TPS       | Sigmoidal <sup>†</sup> | 14       | 3        | -14.968                | 38.335  | 0.053         |
| Combined rodents       | TPS       | Null                   | 14       | 1        | -28.769                | 59.871  | 0.460         |
|                        | TPS       | Linear                 | 14       | 2        | -28.046                | 61.183  | 0.239         |
|                        | TPS       | Hyperbolic             | 14       | 2        | -27.986                | 61.063  | 0.253         |
|                        | TPS       | Sigmoidal              | 14       | 3        | -27.984                | 64.368  | 0.049         |

\*TPS is the number of teeth per scat, PS is the percentage of scats, and PO is the percentage of occurrence of a prey item.

<sup>†</sup>Model failed to converge.

## Rodents

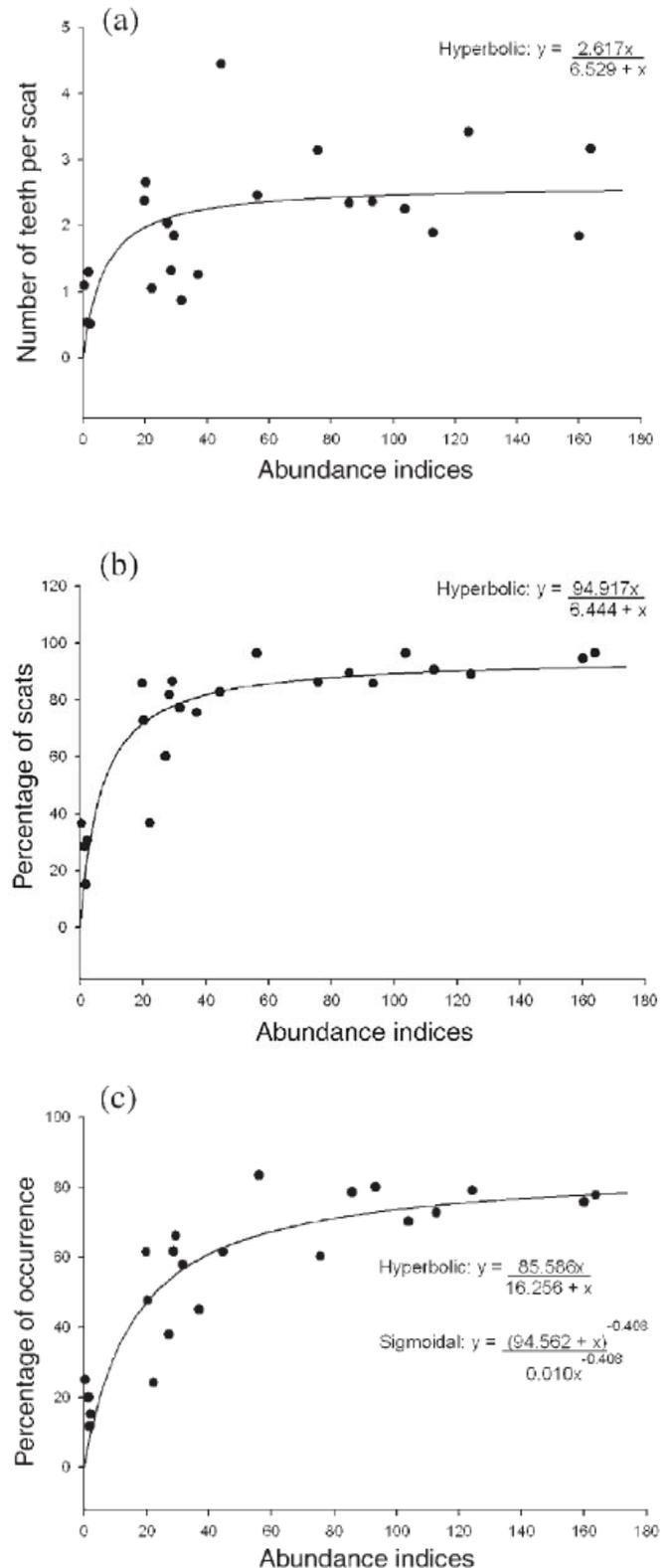
Coyote functional feeding responses to rodents were examined with the same consumption measurements used for jackrabbits, but herewithin only the relationships derived from the number of teeth per scat data are presented. Overall, rodents (excluding voles) did not compose a large fraction of the coyote diet. The combination of rodents comprising a small proportion of the diet, cases of zero detection of abundance, and reduced sample size ( $N = 15$ ) complicated fitting many functional feeding models. Number of teeth per scat data provided the consumption measurement with the smallest associated error. The deer mouse appeared to exhibit a cycle with a 2-year period and relative amplitude of 34 in both seasons (Fig. 3a). Among trapped rodents, deer mice provided the highest reported abundance values (range 3.0–36.7). Evidence of an initially strong but declining kangaroo rat population is demonstrated by abundance indices of 6.0 in 1974, which decreased to very low numbers by 1982 and remained low through 1986 (Fig. 3b). Abundance indices of the Great Basin pocket mouse suggested a decreasing population from an index of about 4.7 in 1974, until 1978 when it stabilized between 0.0 and 1.0, with a slight rebound in 1985–1986 (Fig. 3c). Indices of western harvest mouse abundance suggest irregular fluctuations. Overall abundance values are low, from 0.0 to 2.0 (Fig. 3d). The best coyote functional feeding response models to each rodent group were null models, with the exception of the linear model for kangaroo rat consumption (Table 2). Many of the sigmoidal models failed to converge. Within the rodent groups, many of the models had similar  $AIC_c$  values (Table 2). Functional feeding responses are presented with the best two models for each rodent group (Fig. 4a–4e). In addition to analyzing relationships between coyote and individual rodent species, functional feeding responses of coyotes to all consumed rodents were also evaluated. Only the numbers of teeth per scat were used because percent data of individual rodents were not additive and would result in a value  $>100\%$ . Again, the null model was found to be the most parsimonious using  $AIC_c$  values (Table 2, Fig. 4e).

## Discussion

### Feeding patterns

Coyote consumption of jackrabbits followed jackrabbit abundance trends closely in all years except the falls of 1987–1988. All rodents were an important part of coyote diets during periods of low jackrabbit abundance (1985–1986). Coyote diet data suggest selective feeding on voles when available. This can only be speculated because vole abundance data were not available. Microtine rodents, sagebrush voles in particular, were usually present in the diet in all sampling periods. Voles are common coyote prey (Weaver 1977; Johnson and Hansen 1979; Todd et al. 1981; O'Donoghue et al. 1998). Microtines were believed to be rare in the study area, but may have occurred in high densities locally in alfalfa fields (Hoffman 1979; Knowlton and Gese 1995) or in other preferred habitats with sagebrush and crested wheatgrass (Carroll and Genoways 1980). Vole populations appear to have experienced irruptions rather than a cyclic pat-

**Fig. 2.** *Canis latrans* functional feeding response to *L. californicus* abundance in Curlew Valley, Utah, 1977–1993. The responses number of teeth per scat (a), percentage of scats (b), percentage of occurrence of a prey item (c) were fitted to hyperbolic functions.



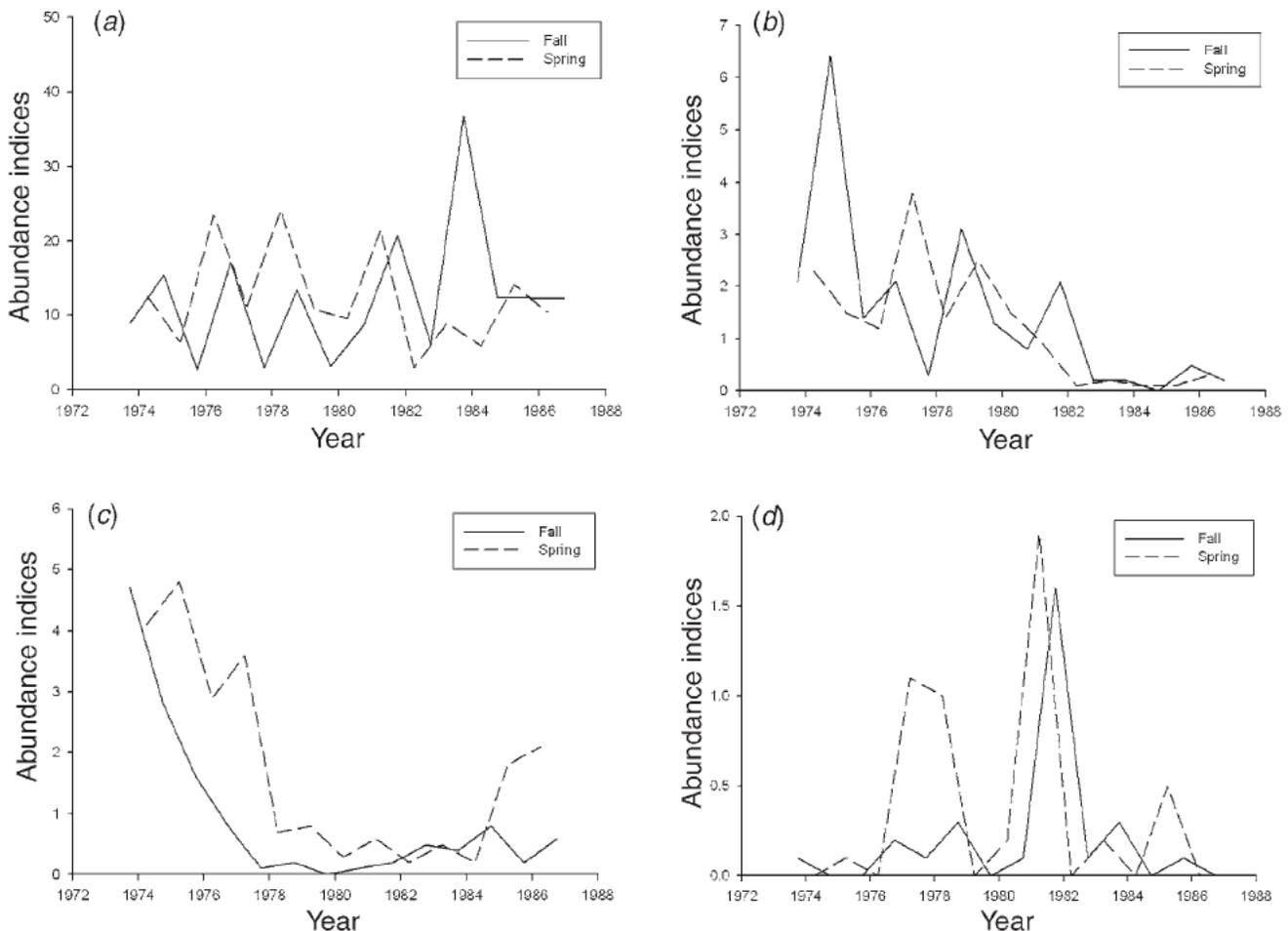
tern, possibly as a result of a post-fire reseeded of crested wheatgrass effort in 1983. Voles were most prevalent in coyote diets in fall of 1984. Prey switching is difficult to quantify with these data and most of the proposed behaviors are only speculation. Typically prey switching is documented by comparing relative use versus availability of alternative prey types (Greenwood and Elton 1979; Patterson et al. 1998). Without accurate abundance measurements for voles, assessments provide an incomplete story.

Functional feeding responses were evaluated using the abundance data and feeding pattern analysis. Initially, all functional feeding response models were assessed separately for each season, but because relationships were similar, spring and fall data were combined. Coyote functional feeding responses to jackrabbits were hyperbolic (or type II; Holling 1959) for most consumption measurements (Fig. 2). This suggests coyotes increasingly fed on jackrabbits as prey numbers increased, but reached an asymptote at prey abundances of ~60 jackrabbits. This response is typical of specialist predators or when there are few alternative prey (O'Donoghue et al. 1998). This response may also indicate adaptive foraging (i.e., adjusting search rates and behavior to the costs of foraging) (Abrams 1992). Although these two explanations may not be mutually exclusive, we believe it

is an effect of the former phenomenon rather than adaptive foraging. Adaptive foraging is not instantaneous and would usually involve a lag time (Abrams 1992). Sufficient evidence of a lag time during the study period was not found, but this could be a consequence of only acquiring data at 6-month intervals. More precise abundance measurements may be necessary to demonstrate a time lag. The asymptote suggests a satiation level (Holling 1959; Murdoch 1973). This is consistent with the coyote functional feeding response to jackrabbits that Hoffman (1979) derived for Curlew Valley, 1970–1975. A similar curve has been suggested to describe the relationship between coyotes and snowshoe hares (O'Donoghue et al. 1998; Patterson et al. 1998) and between coyotes and white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780) (Patterson et al. 1998).

Sigmoidal models only converged for the jackrabbit percentage of occurrence data, and it was chosen as the best fit model based on AIC weight. For the number of teeth per scat and percentage of scat consumption data, sigmoidal models did not converge and were not more parsimonious than hyperbolic models. Functional feeding curves using the number of teeth per scat data fit less well than the curves using percent data. This probably reflects variances in the numbers of teeth per scat. Percent data are constrained in that the con-

Fig. 3. Relative abundances of *Peromyscus maniculatus* (a), *Dipodomys* spp. (b), *Perognathus parvus* (c), and *Reithrodontomys megalotis* (d) in Curlew Valley, Utah, 1973–1986.

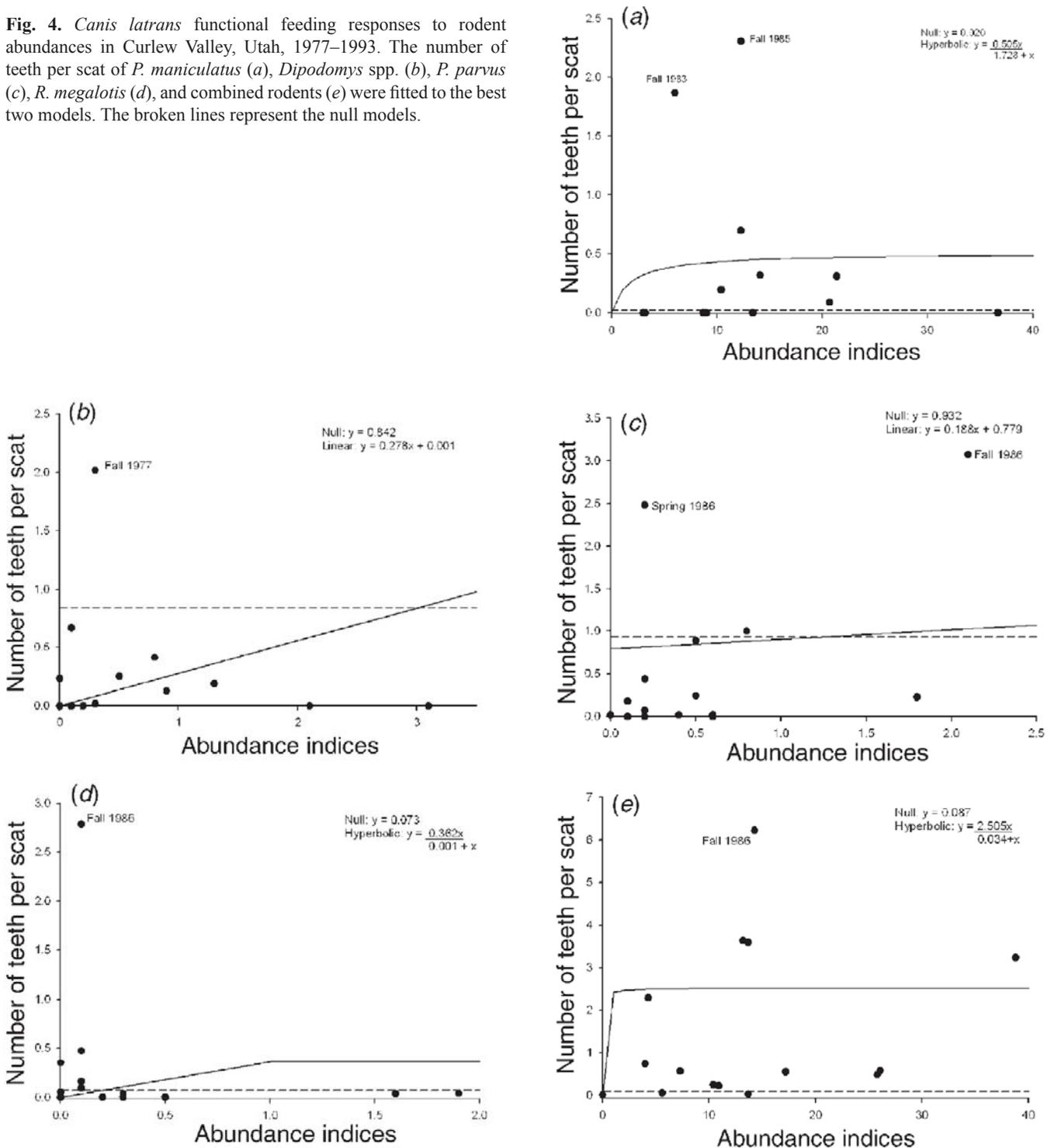


sumption measurements are converted to a proportion of a prey species present in the diet, resulting in less spread, and hence, a tighter fitting curve.

Several issues may confound model selection to describe functional feeding relationships between coyotes and the rodent groups. Coyotes may have not been heavily feeding on rodents (excluding voles). In several sampling periods, consumption of various rodents was not detected. Hoffman

(1979) suggested a linear functional feeding response of coyotes to different rodent groups in Curlew Valley, 1973–1975. There are three interpretations of linear models: (1) predators feed directly proportional to prey density (Holling 1959), (2) handling time is trivial, or (3) prey encounters are a matter of chance (Knowlton and Stoddart 1992; Messier 1995). It is more likely that rodent encounters were a matter of chance. Although visually many of the coyote feeding re-

**Fig. 4.** *Canis latrans* functional feeding responses to rodent abundances in Curlew Valley, Utah, 1977–1993. The number of teeth per scat of *P. maniculatus* (a), *Dipodomys* spp. (b), *P. parvus* (c), *R. megalotis* (d), and combined rodents (e) were fitted to the best two models. The broken lines represent the null models.



sponses to rodent abundances appeared linear, this was not supported using AIC model selection methods. This may have occurred for several reasons. First, in many of the rodent groups, the various models had similar AIC<sub>c</sub> values. Using AIC weights, the models were compared with the best model with the lowest AIC<sub>c</sub> value. In addition, many of the rodent consumption data had high outlier points. The difficulty in deriving functional feeding responses of coyotes to rodents in Curlew Valley was also influenced by the strong feeding preference of coyotes for jackrabbits and voles during periods of high abundance. We chose not to exclude these outliers because they are important in describing a complete coyote functional feeding response by indicating coyote feeding behavior during periods of low abundance of their main prey item. If a longer data series was available that overlapped more than one jackrabbit cycle, there may be more points with higher values (indicating higher consumption), and consequently, better fitting curves.

There are several biases associated with scat analysis that could affect functional feeding response results: sampling biases, the amount of diagnostic material a prey species contributes to a scat (differential detectability), and equating occurrences of more than one prey item in a scat (effects of prey and meal size) (Mech 1970; Floyd et al. 1978; Weaver and Hoffman 1979; Weaver 1993; Kelly and Garton 1997). These biases are not mutually exclusive. We acknowledge such biases even though this study did not specifically address most of them. The main goal was to use measurements of consumption from scat analysis to reveal changes in coyote diets and use that information to explore functional feeding patterns. Changes in diet composition in conjunction with changes in prey availability provide one measure of the shape of functional responses; they do not require knowledge of actual number of prey consumed (Boutin 1995). Since we were more interested in assessing feeding patterns in response to several prey species, an index of consumption (mean number of teeth per scat) was used within each taxonomic group.

Several assumptions and biases exist when developing and interpreting functional feeding responses. Functional feeding response data are difficult to collect in the field, especially for carnivores using more than one prey species. Direct measures of variables used in functional response equations are difficult to obtain in the field such as prey handling time, search rate, wasted time, encounter rates, predator interference, etc. Functional feeding response relationships were defined solely by comparing prey consumption (number of teeth per scat) to prey availability. There are errors associated with prey availability that could affect the results, mainly detecting prey abundance. The differences between "low" and "high" abundance estimates of rodents are numerically small and could have a large effect on the functional feeding response models. Absence is difficult to prove even though there were cases of zero consumption detected and zero abundance detected. These difficulties illustrate the need for a long time series of well-measured data. Even though rodent abundance measurements were intensive (3000 trap-nights per sample period), the series is still small when compared with the jackrabbit abundance measurements.

It would be more beneficial to have rodent abundance and consumption data for more than one jackrabbit cycle. This may lessen the effects of the functional feeding response models attempting to fit a few outlier points when coyotes consume higher numbers of rodents. A larger trapping effort could also reduce the effects of stochastic events on rodent abundance trends.

The statistical models selected to test consumption data could introduce error into model selection and interpretation. Very few sigmoidal models converged using PROC NLIN procedures (SAS Institute Inc. 2002). Small sample sizes of scats (50–60 scats per season) and of prey abundance measurements (through one jackrabbit cycle) combined with instances of zero detection for rodent abundance and zero consumption detected exaggerated the convergence issue. Consequently, it was difficult to identify a best fit model for many of the rodent consumption measurements. This is a result from the large variance in rodents consumed; the greater the variance, the less power there is to distinguish between competing models (Trexler et al. 1988). In addition, sigmoidal models have been suggested to show effects of learning to recognize, capture, or kill prey. Our results propose coyotes are eating rodents opportunistically, suggesting few effects of behaviors associated with a sigmoidal response. Understanding functional feeding responses of a predator with multiple prey options in field situations can be challenging, especially when one prey source, in our case jackrabbits, overwhelmingly predominates.

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