

WINTER DIETS OF COYOTES IN RELATION TO PREY ABUNDANCE IN SOUTHERN TEXAS

LAMAR A. WINDBERG AND CARL D. MITCHELL

*Denver Wildlife Research Center, Animal and Plant Health Inspection Service,
U.S. Department of Agriculture, 319 Stowe Street, Laredo, TX 78041
Present address of CDM: U.S. Fish and Wildlife Service,
Red Rock Lakes National Wildlife Refuge,
Monida Star Route, Lima, MT 59739*

ABSTRACT.—Diets of coyotes (*Canis latrans*) and abundance of mammalian prey were estimated during 8 winters (1979–1986) in southern Texas. Lagomorphs (*Sylvilagus audubonii* and *Lepus californicus*) composed the greatest percentages of coyote diets (40–54%) in 6 of 8 winters; woodrats (*Neotoma micropus*) were staple prey; proportions of cotton rats (*Sigmodon hispidus*) in diets varied markedly in association with population irruptions; and small rodents and white-tailed deer (*Odocoileus virginianus*) were minor dietary components. The proportion of other minor prey items in coyote diets varied inversely with abundance of the five principal prey types. Although coyotes exhibited a general functional response to changes in abundance of prey types in the diverse prey community, evidence for selective feeding on cotton rats was revealed by regression analyses.

Coyotes (*Canis latrans*) are facultative predators that feed on a diversity of mammalian prey and other foods (Fichter et al., 1955; Gier, 1968; Johnson and Hansen, 1979; Korschgen, 1957; Meinzer et al., 1975; Niebauer and Rongstad, 1977; Sperry, 1941). A functional response by coyotes to cyclic fluctuation of snowshoe hares (*Lepus americanus*—Keith et al., 1977) and black-tailed jackrabbits (*L. californicus*—Hoffman, 1979) was reported in regions where those lagomorphs were dominant prey. However, predation by coyotes in a diverse prey community has not been evaluated in relation to fluctuations in abundance of prey.

In southern Texas, the coyote food base is broad and abundant, and coyotes attain high densities (Andelt, 1985; Bean, 1981; Knowlton, 1972; Knowlton et al., 1986). Based on dietary studies in the region, coyotes ate primarily mammalian prey in winter, and fed mainly on a variety of fruit, insects, and white-tailed deer (*Odocoileus virginianus*) fawns available during the warm season (Andelt, 1985; Andelt et al., 1987; Brown, 1977; Knowlton, 1964). Similar dietary shifts by coyotes from mammalian prey to seasonally available fruit and insects was reported for other regions (Harrison and Harrison, 1984; Horn, 1941; Litvaitis and Shaw, 1980; Meinzer et al., 1975; Nellis and Keith, 1976; Towell and Anthony, 1988). Although Bowen (1981) concluded that coyotes formed larger social groups to use large prey in Jasper National Park, Alberta, Andelt (1985) reported fewer large prey (deer) in coyote diets and no similar relationship with group size in southern Texas.

We measured coyote diets and relative abundance of mammalian prey during 8 consecutive winters from 1979 to 1986 in southern Texas. The objective was to relate changes in feeding patterns of coyotes to fluctuations in prey abundance during the season when food was assumed to have been most restricted.

METHODS

The study area of approximately 700 km² was located 5–40 km NE Laredo, Webb Co., Texas. Habitats and land use are typical of the South Texas Plains vegetational area (Gould, 1975; Windberg et al., 1985).

Four systematically spaced 24-km routes along unimproved ranch roads were used for sampling both coyote diets and prey abundance. We collected all coyote feces observed while driving the routes at 2–3-week intervals from early January to late March. Based on physical appearance or associated tracks, feces of other carnivores (<5%) were excluded from the samples.

Prey remains in dried feces were separated manually and identified by comparison with reference specimens. The volume of individual prey items was estimated visually to the nearest 5% of each fecal specimen. Minor food items were excluded from estimates of diet using the methods of Andelt (1985), Bowen (1981), and Knowlton (1964), in which the major item (>40% volume) of each fecal specimen was tallied as the sample unit. Estimates of diets are reported as percent distribution of the following prey categories: lagomorph, southern plains woodrat (*Neotoma micropus*), hispid cotton rat (*Sigmodon hispidus*), small rodents, white-tailed deer, and other prey. Rodents were separated into three categories for dietary analysis because they represented different values in terms of predatory effort and food intake: the relatively large woodrats typically inhabit areas of dense woody vegetation hence are probably more difficult to capture than other rodents (Gier, 1968); medium-size cotton rats exhibited erratic population irruptions; and all other rodents, collectively, were abundant but their relatively small size necessitated capture of substantially greater numbers to satisfy dietary requirements of coyotes.

Lagomorph abundance was estimated by flushing-transects (Gross et al., 1974). Forty permanently marked 1.6-km transects (in square configurations, 0.4 km per side) were spaced ≥ 3 km apart. Censuses were along transects between 2 h after sunrise and 2 h before sunset during January–February. Estimates of density for desert cottontails (*Sylvilagus audubonii*) and black-tailed jackrabbits were computed separately by use of program TRANSECT (Burnham et al., 1980).

We suspect that the reliability of density estimates for lagomorphs was inconsistent among years because variation in flushing behavior (Gross et al., 1974) and visibility (Wywiałowski and Stoddart, 1988) likely resulted from annual differences in the quantity of vegetative cover. Estimates of relative abundance of lagomorphs from visitations at scent stations for coyotes (Roughton and Sweeny, 1982) in the preceding fall (September) and following spring (May) were incorporated with flushing-transect data to reduce the assumed distortions in those estimates. There were 32 scent-station transects in 1979 and 72 per year during 1980–1986. The computation of indices of lagomorph abundance followed methods of Roughton and Sweeny (1982) and incorporated an adjustment for inoperable scent stations (Caughley, 1977). Annual estimates of lagomorph abundance in winter were weighted equally between flushing-transect and scent-station estimators. The estimate for 1979 was extrapolated from scent-station data because flushing-transects were not initiated until 1980.

Relative abundance of rodents was estimated from capture rates in kill-trap censuses conducted in January–February. Twenty-five permanent trap transects were spaced 1 km apart along each of the four routes used for sampling coyote diets. There were 10 M-4 Victor rat traps (Woodstream Corporation, Lititz, PA; identification of commercial products and companies does not constitute endorsement by the U.S. Government) with expanded treadles (5 by 5 cm) baited with a peanut butter-rolled oats mixture, spaced 10 m apart, per transect. The transects were operated for 4 consecutive nights and effective trap nights ranged from 2,782 to 3,309/year. Indices of relative abundance of rodents were derived from total captures per unit of trap effort and incorporated a correction for occupied and inoperable traps (Caughley, 1977).

Estimates of abundance for white-tailed deer were from aerial censuses for Webb Co. conducted in September–October by Texas Parks and Wildlife Department (H. G. Gore and W. F. Harwell, 1983, in litt.; H. G. Gore and J. M. Reagan, 1986, in litt.). We considered estimates of density in fall representative of relative abundance of deer on the study area during the subsequent winter. Percent survival of adult deer was estimated annually (fall-to-fall) by dividing population density at the beginning of the year into density of adults at end of the year; percent mortality was derived as 100% minus percent survival. Body condition of deer was estimated each winter by composite mean weights ($n = 35$ –334/year) of eviscerated mature males (5.5–7.5 years) and females (2.5–7.5 years) harvested during the preceding November–December on the southern portion of the study area (F. D. Matthews, III, pers. comm.).

Chi-square contingency tables were used to compare distribution of prey in coyote diets among sample periods, years, and prey types. The annual proportion of cottontails and jackrabbits also was compared by chi-square tests. The relationships between percent prey in coyote diets and estimates of prey abundance, and deer in coyote diets and deer weights were analyzed by linear correlation.

Optimal models were selected for regression of each prey type in coyote diets on abundance of the five principal prey types. Because some estimates of prey abundance were in different units of measurement, all received the standard normal transformation for regression analyses. Percentages of prey in diets (dependent variables) did not require transformation. Predictive models for multiple linear regression were identified by use of forward selection, backward elimination, and maximum R^2 procedures. The optimal model for each dependent variable was determined by Mallows' criterion C_p (Draper and Smith, 1981) and Akaike's information criterion (Akaike, 1969). The proportionate contribution of independent variables in the models to R^2 was calculated by systematically removing each from the equation and dividing its extra sum of squares by the regression sum of squares. Statistical significance was accepted at $P < 0.05$.

TABLE 1.—Percent prey in coyote diets among three randomly selected subsamples of 50 fecal specimens from two samples of 150 specimens, Webb Co., Texas, January–February, 1981.

| Sample group | n | Lagomorph | Woodrat | Cotton rat | Small rodents | Deer | Other prey |
|--------------|-----|-----------|---------|------------|---------------|------|------------|
| A | 150 | 62 | 10 | 1 | 5 | 8 | 15 |
| | 50 | 66 | 9 | 2 | 3 | 10 | 11 |
| | 50 | 62 | 7 | | 8 | 5 | 17 |
| | 50 | 59 | 13 | | 3 | 9 | 16 |
| B | 150 | 50 | 21 | 2 | 11 | 3 | 13 |
| | 50 | 53 | 21 | 3 | 11 | 1 | 10 |
| | 50 | 52 | 16 | 3 | 12 | 4 | 13 |
| | 50 | 47 | 25 | | 10 | 3 | 15 |

RESULTS AND DISCUSSION

Validation of estimates of diets.—Based on feeding trials with captive canids, fecal remains of small prey items were less detectable (usually underestimated) than larger prey (Floyd et al., 1978; Weaver and Hoffman, 1979). Our estimates of coyote diets were derived from the major prey item in each fecal specimen (73% of 2,335 specimens had only one item). We believe that exclusion of minor food items provided estimates that reflected the principal prey for each meal.

The number of fecal specimens collected ranged from 276 to 1,851/winter. Instead of examining all specimens, we selected a representative sample for each year. Preliminary analysis of 150 feces collected during each of two sample periods in January–February 1981 was conducted to establish a minimum sample size for estimating diets of coyotes. We first compared the percentages of prey types in the diet for cumulative subsamples, in increments of 10, from 10 to 150 fecal specimens. Because percentages of prey generally were similar with subsamples of ≥ 30 specimens, we hypothesized that minimum samples of 50 feces should provide adequate estimates of coyote diet. We validated that assumption by comparing the percent of prey types in three randomly selected subsamples of 50 fecal specimens from each of the two samples of 150 specimens (Table 1) and found similar distributions ($\chi^2 = 12.7$, *d.f.* = 15, $P = 0.63$; $\chi^2 = 8.3$, *d.f.* = 15, $P = 0.91$). Based on the validation, each winter sample comprised six subsamples of 50 feces collected at approximate 2-week intervals during the first 4 years of study. During the latter 4 years, sampling intensity was reduced to four comparable subsamples of 75 feces collected at approximate 3-week intervals. Equal numbers of fecal specimens were randomly drawn from the total number collected from each of the four routes during each subsample interval. Because fewer than the prescribed number of feces were available for three subsamples, annual samples ranged from 276 to 300.

Prey types.—Six prey categories were used for analysis of coyote feeding response (Fig. 1). Although there were differences in size, habitat use, and abundance of the two species of lagomorphs, we combined desert cottontails and black-tailed jackrabbits into one category because their remains often were difficult to distinguish in coyote feces. During 1980–1986, the lagomorph population averaged 83% cottontails and 17% jackrabbits with similar ($\chi^2 = 7.7$, *d.f.* = 6, $P = 0.26$) annual proportions of the two species. During the study, a four-fold fluctuation ($CV = 44\%$) in relative numbers of lagomorphs was observed with greater abundance during the first 5 years followed by relatively low abundance during the last 3 years (Fig. 1).

The largest rodents were woodrats ($\bar{X} = 265$ g, $n = 510$) and cotton rats ($\bar{X} = 87$ g, $n = 465$). Woodrats typically inhabit dense brushy cover with densities of 15–30/ha reported in optimum habitat in southern Texas (Raun, 1966). Woodrat abundance fluctuated five-fold ($CV = 49\%$) during the study (Fig. 1). Cotton rat abundance fluctuated dramatically and rapidly ($CV = 139\%$) with irruptions of 46-fold from 1981 to 1982 and 13-fold from 1985 to 1986.

Other species of rodents were relatively small and were combined as a prey category because, individually, they rarely composed a large volume in feces. Based on 4,409 captures during the 8-year study, composition of the small-rodent category included: *Peromyscus* sp. ($\bar{X} = 25$ g)—68.4%; *Onychomys leucogaster* ($\bar{X} = 38$ g)—18.1%; *Reithrodontomys fulvescens* ($\bar{X} = 12$ g)—

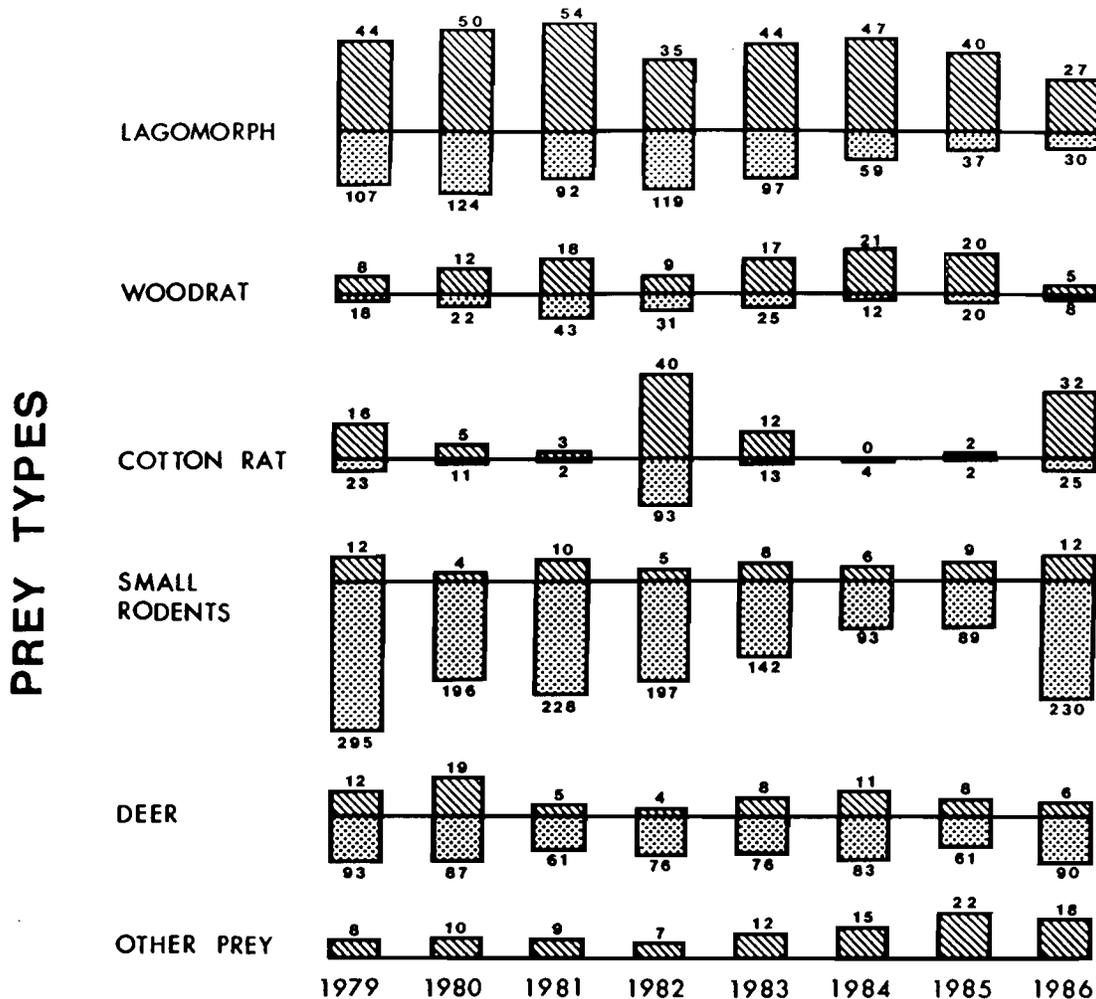


FIG. 1.—Percent distribution of six prey types in coyote diets (above line) and indices of prey abundance (below line) during 8 winters, Webb Co., Texas, 1979–1986. Lagomorph abundance is number/km²; rodent abundance is captures/1,000 trap nights; deer abundance is number/10 km².

6.5%; *Dipodomys ordii* (\bar{X} = 48 g)—4.3%; and *Chaetodipus* sp. (\bar{X} = 32 g)—2.7%. Abundance of small rodents varied three-fold (CV = 39%) during the study (Fig. 1).

We considered the indices of abundance for all rodents comparable based on the assumption that capture rates were similar. Kaufman et al. (1978) removed rodents from 12 grids (165 by 165 m) for 10 successive days in California and Nevada and reported similar percentages of captures (56–61%) after 4 days for four of the same genera (*Peromyscus*, *Chaetodipus*, *Dipodomys*, *Neotoma*) that we sampled.

Abundance of white-tailed deer was relatively stable (CV = 16%) except for 2 years (1981 and 1985) when the population declined following periods of below-average rainfall (Fig. 1). During the 8-year study, the other-prey category in coyote diets comprised: insects (predominantly Coleoptera)—24%; collared peccary (*Dicotyles tajacu*)—21%; unidentified large mammals (presumably flesh of deer, peccary, cattle, other carnivores)—21%; cattle—20%; vegetation—9%; unidentified birds—4%; and miscellaneous items—2%. We did not measure abundance of these components of coyote diets but assumed that it was relatively stable.

Dietary patterns.—We analyzed percent distribution of the six prey types among the subsamples for each winter sample. There was a numerical trend toward more deer in diets in early winter subsamples in 6 of 8 years. We believe that trend resulted from coyotes feeding on deer carrion available after the annual hunting season (November–December). Comparison of the

distribution of prey in diets of coyotes between the first (early) and second (late) halves of each winter sample indicated significant differences ($\chi^2 \geq 16.0$, $d.f. = 5$, $P < 0.01$) in 6 of 8 years. The differences were associated with more ($\chi^2 \geq 4.9$, $d.f. = 1$, $P = 0.03$) deer in diets during early winter in 1979, 1981, and 1986 and greater proportions of the other-prey category during late winter in 1983 and 1984. The latter was attributed primarily to greater consumption of insects when they became available with warmer temperatures in late winter. Comparison of dietary distributions between early and late winter for all years combined indicated no significant differences for the three principal prey types (lagomorphs, woodrats, cotton rats) that averaged 70% of the overall diet. From the overall comparison we also showed a greater proportion of small rodents ($\chi^2 = 6.8$, $d.f. = 1$, $P < 0.01$) and other prey ($\chi^2 = 4.2$, $d.f. = 1$, $P = 0.04$) in diets during late winter. Although these variations in diets occurred during the 8-year study, we combined all data for estimation of overall diet each winter for subsequent analyses. We believe that pooling data for estimates of winter diets was justified because the observed differences involved deer, small rodents, and other prey, which, collectively, represented only 30% of the overall diet and which were consistent annually.

During the 8-year period, diets of coyotes in winter averaged 95% mammalian prey. At least two prey types composed >15% of the diets each winter (Fig. 1). The principal prey type (lagomorph in 6 years and cotton rat in 2 years) composed 32–54% of the diets. The second most common prey type composed 16–35% of diets each winter and was woodrat in 3 years and four different prey types in the other 5 years. Each year, a third item composed 9–20% of diets and included all prey types except lagomorph.

The representation of two or three different prey types as major components of coyote diets each winter reflects the diverse prey base of the area. Nevertheless, lagomorphs were dominant prey in the diets (Fig. 1). Overall, woodrats were a staple prey composing 8–21% of the diets during 7 of 8 years. Dietary portions of cotton rats varied markedly (Fig. 1). They composed the greatest percentage (32% and 40%) of diets in 2 years but composed $\leq 5\%$ of diets in 4 years. Occurrence of small rodents and deer in coyote diets ranged from 4% to 12% except for 19% deer during drought conditions in winter 1980. The main components of the other-prey category were insects, peccary, unidentified mammal, and cattle, which composed 3.0%, 2.7%, 2.7%, and 2.5%, respectively, of the diet for the 8 years combined. The proportion of insects in diets during winter differed significantly among years ($\chi^2 \geq 37.4$, $d.f. = 7$, $P < 0.01$) with above-average percentages in 1983 (4%), 1984 (6%), and 1986 (7%). The proportion of peccary and cattle in diets did not differ significantly ($\chi^2 = 11.2$, $d.f. = 7$, $P = 0.14$; $\chi^2 = 7.4$, $d.f. = 7$, $P = 0.40$) among years.

Feeding response.—In evaluating feeding response of coyotes, we assumed that our estimates of diets were representative of coyotes on the study area and uninfluenced by variation in the age or social structure of the population. Inherent biases in estimates, including underestimation of small prey items (Floyd et al., 1978; Weaver and Hoffman, 1979), were assumed to have been similar among years, therefore, should not affect comparison of annual variation in coyote diets. Our census procedures for indices of prey abundance were standardized to assure comparable estimates among years. We employed a transformation (standard normal deviate) that eliminated the scale bias in estimates of prey abundance (Fig. 1) for multiple-regression analyses. Therefore, relationships between changes in coyote diets and fluctuations in prey abundances should be unaffected by biases in the estimators because they were assumed to be consistent among years.

Percentages of cotton rats in coyote diets fluctuated with their abundance ($r = 0.87$, $t = 4.3$, $d.f. = 6$, $P < 0.01$). There were positive correlations between dietary percentages of lagomorphs ($r = 0.47$), woodrats ($r = 0.26$), small rodents ($r = 0.47$), and deer ($r = 0.49$) with their respective abundance indices but the relationships were weak ($P \geq 0.25$). Totals for indices of abundance for the five principal prey types combined varied nearly three-fold during the 8 years of study and were correlated inversely ($r = -0.92$, $t = 6.6$, $d.f. = 6$, $P < 0.01$) with the percentage of other prey in diets of coyotes. Stenseth and Hansson (1979) developed a model for optimal selection of food and predicted that animals broaden their food niche during food scarcity.

TABLE 2.—Optimal models for regression of prey in coyote diets on abundance of prey types, Webb Co., Texas, 1979–1986.

| Prey in diet Prey abundance | Regression coefficients | Contribution to R^2 * | R^2 | F | P |
|--------------------------------|----------------------------|----------------------------|-------|------|------|
| Lagomorph | | | 0.87 | 9.0 | 0.03 |
| Intercept | 42.63 | | | | |
| Lagomorph | 5.19 | 0.27 | | | |
| Cotton rat | -6.89 | 0.62 | | | |
| Woodrat | 2.79 | 0.09 | | | |
| Woodrat | | | 0.92 | 15.0 | 0.01 |
| Intercept | 13.75 | | | | |
| Woodrat | 2.69 | 0.21 | | | |
| Cotton rat | -2.63 | 0.19 | | | |
| Small rodents | -4.38 | 0.52 | | | |
| Cotton rat | | | 0.91 | 15.5 | 0.01 |
| Intercept | 13.75 | | | | |
| Cotton rat | 13.84 | 0.78 | | | |
| Lagomorph | -6.02 | 0.13 | | | |
| Small rodents | 5.35 | 0.12 | | | |
| Small rodents | | | 0.75 | 7.6 | 0.03 |
| Intercept | 8.25 | | | | |
| Small rodents | 2.45 | 0.71 | | | |
| Lagomorph | -2.45 | 0.71 | | | |
| Deer | | | 0.83 | 6.7 | 0.05 |
| Intercept | 9.13 | | | | |
| Lagomorph | 4.86 | 0.73 | | | |
| Woodrat | -3.70 | 0.49 | | | |
| Cotton rat | -3.23 | 0.44 | | | |

* Contribution to R^2 was the quantity by which R^2 was reduced by removal of each independent variable (prey abundance) from the regression equation.

MacCracken and Hansen (1987) reported a negative correlation between diet diversity of coyotes and the abundance of black-tailed jackrabbits in Idaho. Similarly, Erlinge (1981) found that breadth of the food niche of stoats (*Mustela erminea*) was correlated inversely with density of their primary prey (voles).

The weak correlations between the proportion of prey in diets and their relative abundance for most individual prey types leads us to suggest that prey choice of coyotes involved differential responses to fluctuations among the diverse prey base. We assessed the influence of changes in abundance of the five principal prey types on dietary contributions of each prey by use of optimal models for multiple linear regression (Table 2). We assumed that the abundance of each prey type was a direct influence on its own dietary occurrence. If abundance of alternative prey types affected consumption of individual prey, we assumed that influence would be represented by a negative coefficient in the regression equation. We judged the relative contribution of independent variables (abundance of prey types) in the models by calculating the contribution of each to R^2 (Table 2).

The percent of each prey type, except deer, in diets of coyotes was correlated directly with its abundance (Table 2). Lagomorphs were the principal prey of coyotes (Fig. 1) and apparently were consumed in direct relation to their abundance. However, based on contributions to R^2 (Table 2), abundance of cotton rats had greater influence on consumption of lagomorphs than lagomorph abundance per se. Conversely, consumption of cotton rats was correlated mainly with their own abundance and was virtually unaffected by abundance of alternative prey. Occurrence of woodrats in the diets had a weak direct relationship with their abundance and was influenced negatively by abundance of cotton rats and small rodents (Table 2). The proportion of small rodents in diets was correlated, with similar strength, directly with their own abundance and inversely with abundance of lagomorphs.

The regression equation for deer in coyote diets was composed of three alternative prey and

excluded abundance of deer (Table 2). Therefore, estimates of abundance may not have reflected availability of deer as coyote food adequately. Deer typically were in poorer body condition during periods of drought when there was less plant forage. The percent of deer in diets of coyotes was correlated inversely ($r = -0.85$, $t = 4.0$, $d.f. = 6$, $P < 0.01$) with mean weights of adult deer during the 8 winters. During 5 winters when the percentage of deer (4–8%) in diets of coyotes was lowest ($\chi^2 = 14.7$, $d.f. = 1$, $P < 0.01$), estimated annual mortality of adult deer averaged 19%. During 2 winters of greater percentages of deer (11–12%), annual mortality of deer averaged 31%. In the winter (1980) of greatest ($\chi^2 = 10.3$, $d.f. = 1$, $P < 0.01$) occurrence of deer in diets (19%), annual mortality of deer was 40%. The trend for greater consumption of deer associated with lighter weights and greater mortality leads us to suggest that vulnerability of deer to coyote predation and availability of deer carrion varied among winters. Hence, consumption of deer by coyotes on the study area apparently was influenced more by body condition of deer than their abundance.

The positive correlations between proportions of prey in diets and relative abundance of lagomorphs and rodents (Table 2), and with availability (body condition) of deer, documented a general functional feeding response (Murdoch, 1973) by coyotes to the collective associated fluctuations of the five major prey types. However, the negative influence associated with abundance of some alternative prey types on consumption of all items (Table 2) indicated that the functional response may have been complicated either by prey selection or by differential availability of prey. Selective feeding on cotton rats was suggested by a stronger correlation with their own abundance than was indicated for other prey types and by their negative influence on consumption of two staple prey (lagomorphs and woodrats).

Optimal diet.—Among factors that influence prey choice by predators are absolute abundance, relative abundance, and relative value of potential prey types (Estabrook and Dunham, 1976). All three factors are interrelated. Models of optimal diet are used to predict that greater abundance of food results in greater specialization by increased foraging for the most profitable food (Pyke et al., 1977). Stenseth (1981) discussed some inconsistencies in current theory of optimal foraging and concluded that both relative and absolute densities of potential food items determine optimal diet. Erlinge's (1981) dietary analyses for stoats supported the concept that relative abundance of prey contributes substantially to feeding responses of some predators.

MacCracken and Hansen (1987) ranked profitability of prey items based on body size for assessment of optimal foraging by coyotes in Idaho. They concluded that coyotes selected prey as predicted by optimal-diet models because consumption of low-ranked foods was influenced by abundance of the most profitable prey (black-tailed jackrabbits).

Lagomorphs are primary prey for coyotes in many regions (Andelt et al., 1987; Gier, 1968; Hoffman, 1979; Keith et al., 1977; Korschgen, 1957; MacCracken and Hansen, 1987) and consistently composed a high percentage of coyote diets in winter on our study area (Fig. 1). When lagomorphs were relatively scarce in 1985 and 1986, their dietary proportions decreased (Fig. 1). Abundance of lagomorphs was similar in 1980 and 1982 (Fig. 1) but percent lagomorphs in diets of coyotes was significantly lower ($\chi^2 = 13.0$, $d.f. = 1$, $P < 0.01$) in 1982 because consumption of cotton rats, extremely abundant during that winter (Fig. 1), was greater ($\chi^2 = 98.7$, $d.f. = 1$, $P < 0.01$). That dietary shift represented a feeding response to marked differences in relative abundances of lagomorphs and cotton rats between 1980 (124:11) and 1982 (119:93). This was a clear case of prey selection associated with relative abundance as postulated by Stenseth and Hansson (1979). It also exemplifies a dietary shift away from a predominant prey type during a period when lagomorphs were most abundant, suggesting that cotton rats might represent a more profitable prey. In contrast to MacCracken and Hansen's (1987) assumption that handling cost of prey and resultant prey rank were directly proportional to relative body size, coyotes shifted from lagomorphs to the smaller cotton rats in response to change in relative abundance between those prey. In the diverse prey community on our study area, diets of coyotes generally reflected changes in the relative abundance of prey types with differentially greater consumption of cotton rats when they were abundant.

ACKNOWLEDGMENTS

We are grateful to J. B. Finley, Jr. and F. C. Turley of Callaghan Ranch Limited and D. W. Killam, F. D. Matthews, III, and W. S. Coston of Killam Ranch Company for granting access to private lands for this research. F. D. Matthews also provided weights of deer from 1978–1985. We thank B. G. Wagner, Jr. and C. E. Wahlgren for field assistance. Data analyses by R. M. Engeman, G. W. Smith, and L. C. Stoddart were greatly appreciated. We thank R. M. Engeman, F. F. Knowlton, and R. J. Taylor for helpful reviews of our manuscript. This study was partially conducted under the guidance and support of the U.S. Fish and Wildlife Service, U.S. Department of Interior. The Denver Wildlife Research Center transferred to the Animal and Plant Health Inspection Service, U.S. Department of Agriculture, on 3 March 1986.

LITERATURE CITED

- AKAIKE, H. 1969. Fitting autoregressive models for prediction. *Annals of the Institute of Statistical Mathematics*, 21:243–247.
- ANDELT, W. F. 1985. Behavioral ecology of coyotes in South Texas. *Wildlife Monographs*, 94:1–45.
- ANDELT, W. F., J. G. KIE, F. F. KNOWLTON, AND K. CARDWELL. 1987. Variation in coyote diets associated with season and successional changes in vegetation. *The Journal of Wildlife Management*, 51:273–277.
- BEAN, J. R. 1981. Indices of predator abundance in the western United States, 1981. United States Fish and Wildlife Service, Denver Wildlife Research Center, Denver, 103 pp.
- BOWEN, W. D. 1981. Variation in coyote social organization: the influence of prey size. *Canadian Journal of Zoology*, 59:639–652.
- BROWN, K. L. 1977. Coyote food habits in relation to a fluctuating prey base in South Texas. Unpubl. M.S. thesis, Texas A&M University, College Station, 58 pp.
- BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAKE. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, 72:1–202.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, 234 pp.
- DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis. John Wiley & Sons, New York, 709 pp.
- ERLINGE, S. 1981. Food preference, optimal diet and reproductive output of stoats *Mustela erminea* in Sweden. *Oikos*, 36:303–315.
- ESTABROOK, G. F., AND A. E. DUNHAM. 1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. *The American Naturalist*, 110:401–413.
- FICHTER, E., G. SCHILDMAN, AND J. H. SATHER. 1955. Some feeding patterns of coyotes in Nebraska. *Ecological Monographs*, 25:1–37.
- FLOYD, T. J., L. D. MECH, AND P. A. JORDAN. 1978. Relating wolf scat content to prey consumed. *The Journal of Wildlife Management*, 42:528–532.
- GIER, H. T. 1968. Coyotes in Kansas. *Kansas Agricultural Experiment Station Bulletin*, 393:1–118.
- GOULD, F. W. 1975. Texas plants—a checklist and ecological summary. *Texas Agricultural Experiment Station Miscellaneous Publications (Revised)*, 585:1–121.
- GROSS, J. E., L. C. STODDART, AND F. H. WAGNER. 1974. Demographic analysis of a northern Utah jackrabbit population. *Wildlife Monographs*, 40:1–68.
- HARRISON, D. J., AND J. A. HARRISON. 1984. Foods of adult Maine coyotes and their known-age pups. *The Journal of Wildlife Management*, 48:922–926.
- HOFFMAN, S. W. 1979. Coyote-prey relationships in Curlew Valley during a period of low jackrabbit density. Unpubl. M.S. thesis, Utah State University, Logan, 125 pp.
- HORN, E. E. 1941. Some coyote-wildlife relationships. *Transactions of the North American Wildlife Conference*, 6:283–287.
- JOHNSON, M. K., AND R. M. HANSEN. 1979. Coyote food habits on the Idaho National Engineering Laboratory. *The Journal of Wildlife Management*, 43:951–956.
- KAUFMAN, D. W., J. B. GENTRY, G. A. KAUFMAN, M. H. SMITH, AND J. G. WIENER. 1978. Density estimation of small mammals: comparison of techniques utilizing removal trapping. *Acta Theriologica*, 23:147–171.
- KEITH, L. B., A. W. TODD, C. J. BRAND, R. S. ADAMCIK, AND D. H. RUSCH. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. *International Congress of Game Biologists*, 13:151–175.
- KNOWLTON, F. F. 1964. Aspects of coyote predation in South Texas with special reference to white-tailed deer. Ph.D. dissert., Purdue University, Lafayette, Indiana, 189 pp.
- . 1972. Preliminary interpretations of coyote population mechanics with some management implications. *The Journal of Wildlife Management*, 36:369–382.
- KNOWLTON, F. F., L. A. WINDBERG, AND C. E. WAHLGREN. 1986. Coyote vulnerability to several management techniques. Pp. 165–176 in *Seventh Great Plains Wildlife Damage Control Workshop Proceedings*, San Antonio (D. B. Fagre, ed.). Texas A&M University System, College Station, 203 pp.
- KORSCHGEN, L. J. 1957. Food habits of the coyote in Missouri. *The Journal of Wildlife Management*, 21:424–435.
- LITVAITIS, J. A., AND J. H. SHAW. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. *The Journal of Wildlife Management*, 44:62–68.
- MACCRACKEN, J. G., AND R. M. HANSEN. 1987. Coyote feeding strategies in southeastern Idaho: optimal foraging by an opportunistic predator? *The Journal of Wildlife Management*, 51:278–285.

- MEINZER, W. P., D. N. UECKERT, AND J. T. FLINDERS. 1975. Foodniche of coyotes in the rolling plains of Texas. *Journal of Range Management*, 28:22-27.
- MURDOCH, W. W. 1973. The functional response of predators. *The Journal of Applied Ecology*, 10:335-342.
- NELLIS, C. H., AND L. B. KEITH. 1976. Population dynamics of coyotes in central Alberta, 1964-68. *The Journal of Wildlife Management*, 40:389-399.
- NIEBAUER, T. J., AND O. J. RONGSTAD. 1977. Coyote food habits in northwestern Wisconsin. Pp. 237-251 in *Proceedings of the 1975 Predator Symposium* (R. L. Phillips and C. Jonkel, eds.). Montana Forest and Conservation Experiment Station, University of Montana, Missoula, 268 pp.
- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, 52:137-154.
- RAUN, G. G. 1966. A population of woodrats (*Neotoma micropus*) in southern Texas. *Texas Memorial Museum Bulletin*, 11:1-62.
- ROUGHTON, R. D., AND M. W. SWEENEY. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. *The Journal of Wildlife Management*, 46:217-229.
- SPERRY, C. C. 1941. Food habits of the coyote. *United States Fish and Wildlife Service Wildlife Research Bulletin*, 4:1-70.
- STENSETH, N. C. 1981. Optimal food selection: some further considerations with special reference to the grazer-hunter distinction. *The American Naturalist*, 117:457-475.
- STENSETH, N. C., AND L. HANSSON. 1979. Optimal food selection: a graphic model. *The American Naturalist*, 113:373-389.
- TOWEILL, D. E., AND R. G. ANTHONY. 1988. Coyote foods in a coniferous forest in Oregon. *The Journal of Wildlife Management*, 52:507-512.
- WEAVER, J. L., AND S. W. HOFFMAN. 1979. Differential detectability of rodents in coyote scats. *The Journal of Wildlife Management*, 43:783-786.
- WINDBERG, L. A., H. L. ANDERSON, AND R. M. ENCEMAN. 1985. Survival of coyotes in southern Texas. *The Journal of Wildlife Management*, 49:301-307.
- WYWIALOWSKI, A. P., AND L. C. STODDART. 1988. Estimation of jack rabbit density: methodology makes a difference. *The Journal of Wildlife Management*, 52:57-59.

Submitted 20 March 1989. Accepted 17 October 1989.