A comparison of coyote ecology after 25 years: 1978 versus 2003[1]

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Abstract: Most ecological studies of coyotes are of short duration and studies are generally never repeated, thus the opportunity to compare changes in coyote (*Canis latrans* Say, 1823) ecology over time is rare. We compared coyote home ranges, activity patterns, age, and diet at the Welder Wildlife Refuge in south Texas between 1978–1979 and 2003–2004 (25 years later). The Minta index of overlap between 1978 and 2003 home ranges was 51.7 ± 7.0 ($n = 7$), much greater than the Minta index value based on randomized tests (28.7 ± 8.6), indicating similar spatial patterns between time periods. The Minta index was 12.3 ± 6.2 ($n = 7$) for core areas, whereas the Minta index value based on randomized tests was 4.0 ± 3.0. Although overall diets were similar between 1978 and 2003, we detected some differences in prey species consumed. Activity patterns were similar between the two study periods, with peaks in movement occurring around sunrise and sunset. There was no difference in the mean age between the two populations ($P = 0.44$, $n = 68$, $t_{[66]} = 2.00$). Our findings suggest that population features, such as home-range position and age structure, are similar between extended time periods, while individual-level patterns, such as the prey species consumed and distribution of locations within a home range, are dynamic and may reflect changes in the local environment.

Résumé : La plupart des études écologiques sur les coyotes (*Canis latrans* Say, 1823) sont de courte durée et ne sont généralement pas répétées; il y a donc peu d'occasions de comparer les changements au cours du temps dans l'écologie des coyotes. Nous avons comparé les aires vitales, les patrons d'activité, l'âge et le régime alimentaire des coyotes du Welder Wildlife Refuge dans le sud du Texas en 1978–1979 et en 2003–2004 (25 ans plus tard). L'indice de Minta qui mesure le chevauchement entre les aires vitales entre 1978 et 2003 est de $51{,}7 \pm 7{,}0$ ($n = 7$), ce qui est de beaucoup supérieur à un indice calculé à partir d'essais aléatoires ($28{,}7 \pm 8{,}6$); il y a donc des structures spatiales similaires durant les deux périodes. L'indice de Minta pour les aires centrales est de $12{,}3 \pm 6{,}2$ ($n = 7$), alors qu'il est de $4{,}0 \pm 3{,}0$ pour les essais aléatoires. Bien que les régimes alimentaires globaux soient similaires en 1978 et en 2003, il y a des différences dans les espèces de proies consommées. Les patrons d'activité sont semblables dans les deux périodes d'étude, avec des maximums des déplacements vers l'aube et le coucher du soleil. Il n'y a pas de différence dans l'âge moyen entre les deux populations ($P = 0{,}44$, $n = 68$, $t_{[66]} = 2{,}00$). Nos résultats indiquent que les caractéristiques démographiques, telles que la position de l'aire vitale et la structure en âge, sont semblables sur de longues périodes, alors que les patrons d'ordre individuel, comme les espèces de proies consommées et la répartition des positions au sein de l'aire vitale, sont dynamiques et peuvent refléter les changements dans l'environnement local.

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Introduction

Typically, animal home ranges are spatially segregated by geographically (e.g., rivers) and behaviorally (e.g., scent marks) defined boundaries within the landscape. Factors intrinsic to the home range, including prey availability (Patterson and Messier 2001) and suitable den sites (Doncaster and Woodroffe 1993), may influence the size and geography of home ranges, but social factors, such as pack size, also influence home-range size (Bowen 1981). For coyotes (*Canis latrans* Say, 1823), home-range positions regularly follow natural landscape features, including roads, fences, and rivers (Andelt 1985; Gese et al. 1996*a*, 1996*b*), but are not typically influenced by pack size (Andelt 1985; Patterson and Messier 2001).

Information on home-range boundaries and within-home-range spatial patterns between generations is rarely available for carnivores. A study on female spotted hyenas (*Crocuta crocuta* (Erxleben, 1777)) showed that individual home-range patterns were diverse, but territorial boundaries of clans remained constant over time (Boydston et al. 2003*a*). Most carnivore studies have examined spatial patterns in populations that experienced population fluxes (i.e., Packer et al. 2005). For example, after a population of badgers (*Meles meles* (L., 1758)) was eradicated, others recolonized the area and established similar home-range boundaries to those observed before the eradication (Cheeseman et al. 1988; Doncaster and Woodroffe 1993). Similarly, gray wolves (*Canis lupus* L.,

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1758) showed relatively stable home-range positions even when the population was rapidly growing (Hayes and Harestad 2000). When alpha coyote mortalities occur, neighboring packs rarely expand their home ranges into the newly available space (but see Gese 1998); instead, new individuals establish a home range within the available space and home-range boundaries remain stable between years (Althoff and Gipson 1981).

Although home-range positions and size often remain constant for specific coyote pairs or packs (Althoff and Gipson 1981; Bowen 1981; Bekoff and Wells 1982; Andelt 1985), these studies were limited to a few years, and little information is available regarding spatial patterns between generations. Kitchen et al. (2000a) examined the spatial structure of coyote packs between multiple generations and observed similar boundary and core-area patterns, but found changes in the distribution of coyote locations. Coyotes also altered their temporal activity patterns across this same time period following a change from high to low human exploitation (Kitchen et al. 2000b). Whether similar spatial patterns will be observed within a coyote population in a more stable environment after several decades is unknown.

In addition to spatial patterns, few studies have been able to measure other ecological parameters between coyote generations but instead have focused on seasonal or annual patterns. Coyotes may alter their social organization based on annual reproductive success (Kleiman and Brady 1978) and seasonal changes in prey availability (Bowen 1981). Changes in prey availability will likely be expressed in coyote dietary patterns as well. In fact, coyotes demonstrate plasticity in diets (Andelt et al. 1987; Lingle 2000; Sacks and Neale 2002), behaviors (Shivik et al. 1997), activity patterns (Bekoff and Wells 1981), and spatial patterns (Gese 1998). Specifically, coyotes may change diet when prey base changes (Lingle 2000), expand pack territorial boundaries when an alpha from a neighboring territory dies (Gese 1998), and change activity patterns in response to changes in disturbance levels by humans (Kitchen et al. 2000b) or the reintroduction of gray wolves (Arjo and Pletscher 1999; Switalski 2003). Although these studies have provided useful information on coyote responses to environmental changes, no information is available that compares coyote populations in relatively stable environmental conditions until now.

Our main objective was to compare home-range positions and size, activity patterns, ages, and diets of coyotes on the same study area from two time periods separated by 25 years. We specifically addressed the following questions. (1) Did home-range positions and size, space use within home ranges, and diet remain unchanged after 25 years? (2) Did the age structure of the coyote population remain similar? (3) Did changes in the environment (e.g., prey) influence coyote space use within home ranges and diet? We hypothesize that home-range and core-area positions, diets, and age structure of coyotes will be similar between the two study periods because of the environmental stability at the study area.

Materials and methods

Study area

The study was conducted on the 3157 ha Welder Wildlife Refuge (WWR) and adjacent ranches in San Patricio County, Texas. The northern border of the WWR is the Aransas River. The WWR is located in a transition zone between the gulf prairie and marshes and the south Texas plains (Gould 1975). Vegetation consists of mixed grasslands and shrubs (see Drawe et al. 1978). An abundant diversity of mammals, birds, and reptiles live at the WWR (Knowlton 1964). The main mammalian predators are coyotes and bobcats (*Lynx rufus* (Schreber, 1777)). Since the establishment of the WWR in 1954, coyotes have not been controled except within a small area of the refuge in the 1970s (Andelt 1985; Kie and White 1985; D.L. Drawe, personal communication). A 391 ha coyote exclosure was built in 1973 and maintained throughout the 1970s for an experiment (Kie and White 1985). The exclosure area was likely part of a coyote home range, as five coyotes were removed at the beginning of this experiment and additional coyotes were removed over the next decade (Teer et al. 1991). Coyote control on adjacent ranches has been minimal. No records are available on prey abundances during the initial 1978–1979 study period, although an increase in feral pigs since that period has been observed. Additionally, the WWR has experienced almost no changes in management practices since the 1978–1979 study (D.L. Drawe, personal communication).

Data collection and analysis

To allow for direct comparison, field methods used during 2003–2004 (hereinafter referred to as 2003) followed techniques used during the 1978–1979 study (Andelt 1985; hereinafter referred to as 1978). Fieldwork began in January 2003 and continued into January 2004. We captured adult coyotes using no. 3 Soft Catch® padded leg-hold traps with attached tranquilizer tabs (Balser 1965). Each captured coyote was immobilized (Cornerly 1979) to remove the first premolar for aging and to attach a VHF radio collar. All handling procedures for the 2003 study were approved by Utah State University and Colorado State University animal care and use committees and follow the *Canadian Journal of Zoology* guidelines.

We located radio-collared coyotes via triangulation a minimum of once every 1–3 days, although most were found daily. We obtained three or more bearings, 20°–160° of one another, within 20 min or less for each coyote location. Point locations were obtained using the maximum-likelihood estimator in program Locate™ II (Nams 1990). Radio tracking occurred at all hours of day and night. Additionally, we obtained hourly locations for each radio-collared coyote during two night-time and one day-time 12 h tracking sessions per month. Coyotes within the same group were regularly located within 0–5 min of each other to determine associations. Coyotes found <100 m apart were defined as together (Andelt 1985). Animals typically found together were defined as belonging to the same pack. We recorded information on location, movement, and inter- and intra-specific interactions for all telemetry and visual observations.

We calculated home ranges and core areas using an adaptive kernel algorithm (Worton 1989). Home ranges (90% isopleth) and core areas (30% isopleth) were determined with CALHOME (Kie et al. 1996) and ArcView® version 3.2 (Environmental Systems Research Institute, Inc. 1999). Locations were pooled for all coyotes belonging to the

same pack to obtain one home-range estimate and one core-area estimate for each pack. We compared home-range and core-area sizes between the two study periods with a Student's t test. We calculated the centers of activity for all home ranges in 1978 and 2003. We then matched 2003 and 1978 home ranges that had the closest center of activity points to create a paired set of home ranges. We compared the spatial overlap of the matched home ranges and core areas observed in 2003 with those observed in 1978 (Andelt 1985). We calculated percent overlap both proactively and retroactively (i.e., 2003 over 1978 and 1978 over 2003) and obtained a single percent overlap value using the Minta index (Minta 1992):

$$\text{Percent overlap} = \frac{\text{HRoverlapAB} \times 100}{\sqrt{\text{AB}}}$$

where home ranges (HR) A and B are the matched home-range pairs from (A) 1978 and (B) 2003.

We performed a randomization test by simulating Minta index values for randomly placed home ranges to determine if home range and core overlap was greater or less than expected. That is, we created an ArcView® version 8.3 Avenue script that randomly distributed 1978 home ranges across the study area (i.e., constrained by the study-area boundaries). Home ranges were randomly moved in X and Y coordinate directions using the Transform2D object with the Move and Transform commands, but rotation around the center of the home range was not possible in Avenue. The program then identified the original 1978 home range that was closest to each simulated home range and calculated the Minta index of overlap value. A simulation consisted of randomly moving all home ranges and determining the overlap with their original 1978 home range. We ran 1000 simulations for home ranges and repeated this procedure using core areas. Our simulations produced expected null distributions with which we compared observed overlap values.

We also calculated the percentage of 2003 coyote location points within the home range of the matched pair from 1978. We compared this value with the percentage of 2003 location points that fell within all other 1978 home ranges. For a final and very conservative estimate of spatial overlap, we used multiple response permutation procedures (MRPPs; Mielke et al. 1976) to compare the distribution of coyote point locations in 2003 with point locations from the matched 1978 home range. MRPPs were included because, unlike our other methods of spatial analyses, they evaluate point location data (Mielke et al. 1976).

Age of captured coyotes was determined by analyzing the cementum annuli of the first premolar or canine pulled at the initial time of capture (Roberts 1978; Matson's Laboratory, Milltown, Montana). To evaluate the adult population, coyotes that were classified within the 0 age class (i.e., <1 year old) were considered dependents and were excluded from the statistical analysis. We used a Student's t test to compare the mean age of the coyote population in 1978 with that in 2003. We also used a Pearson χ^2 exact test to compare the age structure between 1978 and 2003.

As in 1978, we calculated activity patterns from the 12 h tracking sessions in 2003. Straight-line distances were calculated between all hourly locations. Similar to 1978, we divided time into four categories in 2003: morning (0501–1000), day (1001–1700), evening (1701–2200), and night (2201–0500). We also divided hourly distance data into four biological seasons in 2003: nursing, early post nursing, late post nursing, and pre-breeding (Andelt 1985). We compared hourly distance traveled by time of day, season, and the interaction of time of day and season using a two-way factorial ANOVA in a blocked design.

Similar to 1978, fecal samples were collected at least two times each month, from January to December 2003, for dietary analysis on all paved and mowed, unpaved roads in the WWR. During sampling, we drove or walked transects and collected all coyote feces. We also collected scat opportunistically while in the field. Feces were oven dried and stored until they could be washed for dietary analysis. Scat analysis for identification and quantity of prey items followed methods in Andelt (1985). We identified prey items to species when possible, but first placed each item into one of five major prey categories: mammal, reptile, bird, fruit, and insect. We further classified the size of mammalian prey items as large (e.g., white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780)), medium (e.g., cottontail rabbit, *Sylvilagus floridanus* (J.A. Allen, 1890)), or small (e.g., hispid cotton rat, *Sigmodon hispidus* Say and Ord, 1825) (Andelt 1985). Dietary overlap (O) of the five major categories was compared using Pianka's (1973) equation:

$$O_{pq} = \frac{\sum p_i q_i}{\sqrt{\sum p_i^2 \sum q_i^2}}$$

where p_i is the proportion of food item i in the diet of predator p and q_i is the proportion of food item i in the diet of predator q. For our analysis, predator p represents coyotes in 1978 and predator q represents coyotes in 2003. A value of 1 signifies complete dietary overlap, whereas a value of 0 indicates no overlap. We also used logistic regression to compare the frequency of occurrence of specific prey items in the diet of the 2003 coyote population with the diet of the population at the WWR in 1978. We re-scored all scat data as presence/absence of each species and each scat was treated as an independent observation for the logistic regression. We did not include reptile and bird categories in the logistic regression analysis because they were rarely found in scat. We conducted statistical analyses in SAS® (SAS Institute Inc. 1988). Values presented are means ± SE.

Results

We found some differences in the sex and number of radio-collared coyotes in the two study periods (Table 1). In 1978, 48 adult coyotes were radio-collared. Twenty-four of these adults (10 females, 14 males) were residents, comprising seven distinct social groups and home ranges (Fig. 1; Andelt 1985). Two of the resident breeding females and two apparent breeding males used the same home range in succession (Andelt 1985). A total of 17 adult coyotes (11 females, 6 males) were radio-collared in 2003. Thirteen of these coyotes (7 females, 6 males) were residents, comprising eight distinct social groups and home ranges (Fig. 1). Two of the resident males used the same home range in succession. The first male died of heartworms and a new male occupied the same site following

Table 1. Number and sex (M, male; F, female) of radio-collared coyotes (*Canis latrans*) located to define each home range at the Welder Wildlife Refuge (WWR), Texas, during the 1978 and 2003 study periods.

	Home range							
Year	A	B	C	D	E	F	G	H
1978	3M–2F	2M–1F	3M–2F	3M–2F	1M*–1F	2M*–2F	1M	—
2003	1F	1M	2F	2F	1M–1F	1M–1F	1M	2M

*One male observed with two different packs (see Andelt 1985).

Fig. 1. The 3157 ha Welder Wildlife Refuge (WWR), Texas (in light gray), with coyote (*Canis latrans*) home ranges and core areas shown for 1978 and 2003. A coyote exclosure was in use during 1978 (darker gray patterned trapezoid) and, therefore, the 2003 home range H was excluded from the overlap analysis so that home ranges could be matched.
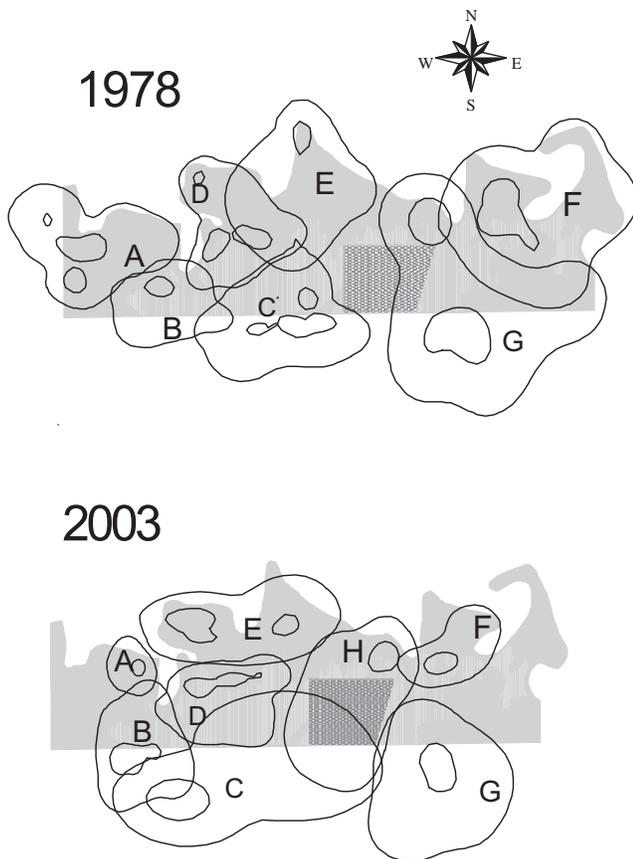
the first one's death. Although the number of radio-collared coyotes was lower in 2003 than in 1978, this is unlikely to represent differences in density because more coyotes were observed with un-radio-collared coyotes in 2003 than in 1978. For example, one female was pregnant at time of capture in 2003, but we failed to capture another adult coyote in her home range.

Home-range analysis

Although un-radio-collared coyotes were observed during both study periods, only data on radio-collared coyotes are included in the home-range analyses. There was no significant difference in home-range sizes between 1978 (0.76 ±

0.15 km^2) and 2003 (0.62 ± 0.14 km^2; $t_{[13]} = -0.68$, $P = 0.51$, $n = 15$) or in the core-area sizes between 1978 (0.07 ± 0.02 km^2) and 2003 (0.05 ± 0.01 km^2; $t_{[13]} = -1.00$, $P = 0.34$, $n = 15$).

Unlike 1978, the coyote exclosure area was available to coyotes in 2003 (Fig. 1). To enable direct comparisons, we excluded the home range that existed in the former coyote exclosure space and, therefore, only 7 of the 8 home ranges observed in 2003 were used in spatial analyses involving matched pairs. Arithmetic centers of activities were 0.9 km (±0.1 km) apart between matched pairs from the two study periods (Fig. 1). Our assignment of matched pairs was confirmed because 82.8% ± 5.6% of the 2003 locations fell within the 1978 matched home ranges, whereas only 37.1% ± 7.4% fell within other 1978 home ranges.

Home ranges showed considerable overlap between the two time periods. The mean percent overlap of home ranges observed in 2003 and those in 1978 was 65.7% ± 11.9% and the mean percent overlap of home ranges observed in 1978 and those in 2003 was 55.1% ± 11.3%. There was no significant difference in the percent overlap of home ranges between the two study periods ($t_{[12]} = 0.65$, $P = 0.53$; Fig. 2). The Minta index value was 51.7 ± 7.0 ($n = 7$). The Minta index value based on the randomized tests was 28.7 ± 8.6 and 96.6% of the random Minta index values fell below the observed Minta index value (Fig. 3; range = 2.6–52.8, $n = 1000$). MRPPs resulted in a significant difference in the distribution of locations between the two periods for all seven pairs of overlapping home ranges ($P < 0.0001$ in all seven cases).

The 30% core areas also showed overlap (Fig. 2). The mean percent overlap of core areas in 2003 with those in the 1978 study was 20.8% ± 11.1% and the mean percent core-area overlap in 1978 with those in the 2003 study was 7.6% ± 3.6%. There was no significant difference in percent core-area overlap between 1978 and 2003 ($t_{[12]} = 1.13$, $P = 0.28$). The Minta index was 12.3 ± 6.2 ($n = 7$) for core areas, whereas the Minta index value based on randomized tests was 4.0 ± 3.0 and 96.8% of the simulated Minta index values fell below the observed Minta index value (Fig. 3; range = 0.0–15.3, $n = 1000$).

Age structure

We were unable to extract or analyze a premolar from all captured coyotes, but we were able to successfully determine the age of 47 coyotes in 1978 and 21 coyotes in 2003. Coyote age classes ranged from 0 to 10 years old in 1978 and from 0 to 9 years old in 2003. We found no difference in the mean age of the adult coyote populations between 1978 (2.95 ± 0.31, $n = 44$) and 2003 (3.43 ± 0.75, $t_{[56]} = 2.00$, $P = 0.50$, $n = 14$) or in age structure ($\chi^2_{[2]} = 4.32$, $P = 0.12$).

Fig. 2. Overlap of home ranges between the 1978 (thin outline) and the 2003 (thick outline) study periods at WWR. In 1978, the coyote exclosure (patterned trapezoid in *c*, *g*, and *h*) formed the west border of home range G. Only one of the two packs in 2003 was used for direct comparisons, although a combination of 2003 home ranges G and H showed the most overlap with the 1978 home range G (*h*).
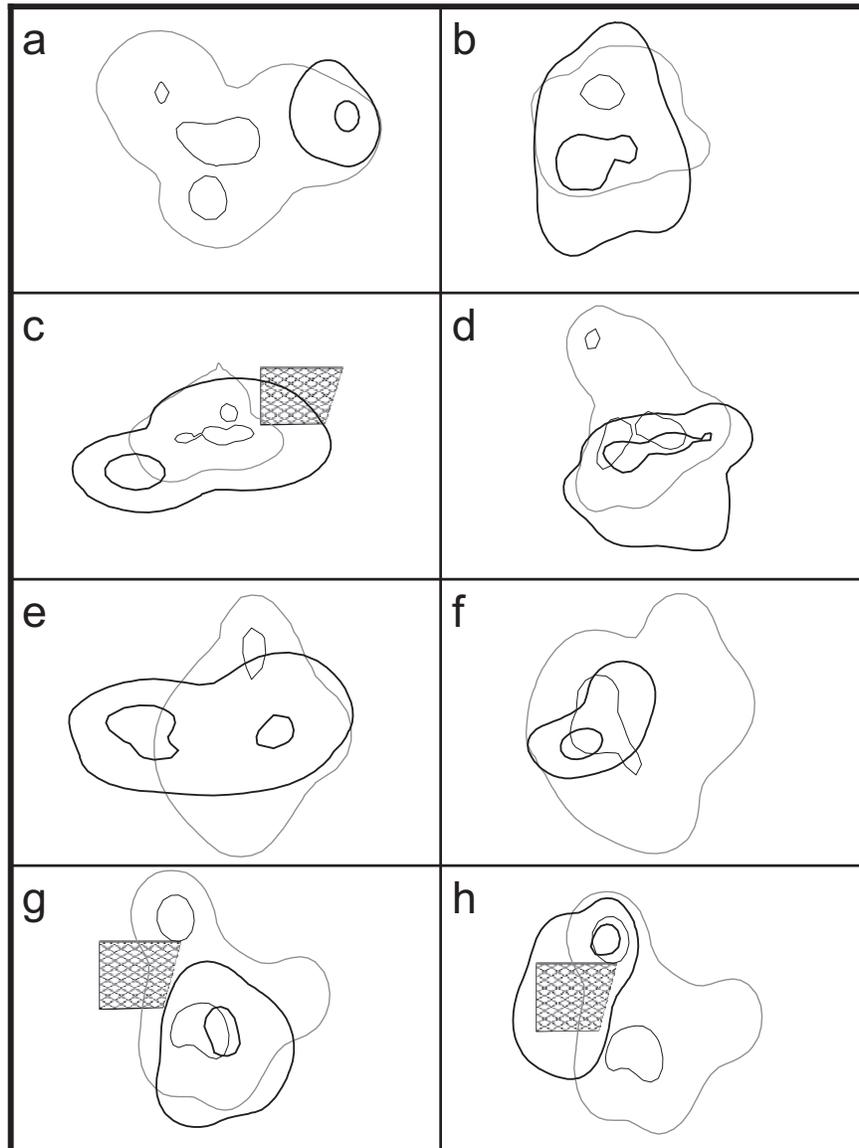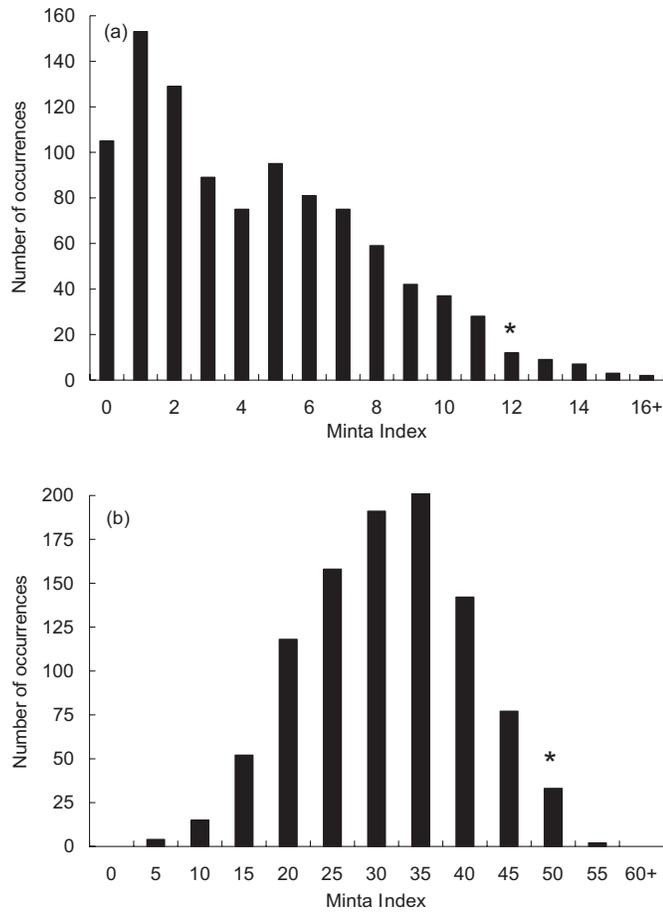

Activity patterns

All 17 radio-collared coyotes were observed during ≥1, 12 h tracking session. Coyotes were active at all times in 2003, but were most active around sunrise and sunset, similar to those in 1978 (Fig. 4). There was a significant difference in the hourly distance traveled by time of day in 2003 ($F_{[3,125]}$ = 7.87, $P < 0.001$, $n = 126$), but, unlike in 1978, no significant difference in hourly distance traveled by season ($F_{[3,125]}$ = 1.71, $P = 0.20$, $n = 126$). The interaction of season and time of day for hourly distance traveled was significant in 2003 ($F_{[9,125]} = 2.03$, $P = 0.05$, $n = 126$). Straight-line distance traveled by all coyotes over all times and seasons in 2003 was more than 7 km within a 24 h period ($n = 126$), which was similar to the 8 km traveled by coyotes in 1978 (Andelt 1985).

Scat analysis

A total of 1235 coyote scats were collected and analyzed in 2003 and compared with 2715 scats collected and analyzed in 1978. Of the total scats collected in 2003, 113 were excluded from analysis because no prey item made up at least 40% of the scat or the sample was destroyed when a drying oven malfunctioned. Of five major prey categories, mammals made up the majority of coyote diet in both 1978 (61.5%) and 2003 (57.9%; Fig. 5). During both study periods, mammalian prey items included white-tailed deer, cottontail, feral pig (*Sus scrofa* L., 1758), javelina (*Tayassu tajacu* L., 1758), cattle (*Bos taurus* L., 1758), and a variety of rodent species. Fruit was the second most common dietary item in 1978 (31.9%) and in 2003 (28.1%; Fig. 5). The most common types of fruit were Texas persimmon (*Diospyros texana* Scheele), agarito barberry (*Mahonia trifoliolata* (Moric.) Fedde), southern dewberry (*Rubus trivialis* Michx.), and prickly pear cactus (*Opuntia engelmannii* var. *lindheimeri* (Engelman.) Parfitt & Pinkava). Most of the re-

Fig. 3. Frequency of Minta index values of overlap based on randomization tests ($n = 1000$) for core areas (*a*) and home ranges (*b*). Asterisks indicate observed Minta index values of 12.3% ± 6.2% for core-area overlap (*a*) and 51.7% ± 11.3% for home-range overlap (*b*).

Fig. 4. Activity patterns, as measured by hourly, straight-line distance traveled, of adult male (*a*) and female (*b*) coyotes at WWR in 1978 and 2003. Sunrise occurred between 0530 and 0730 and sunset between 1730 and 1930.
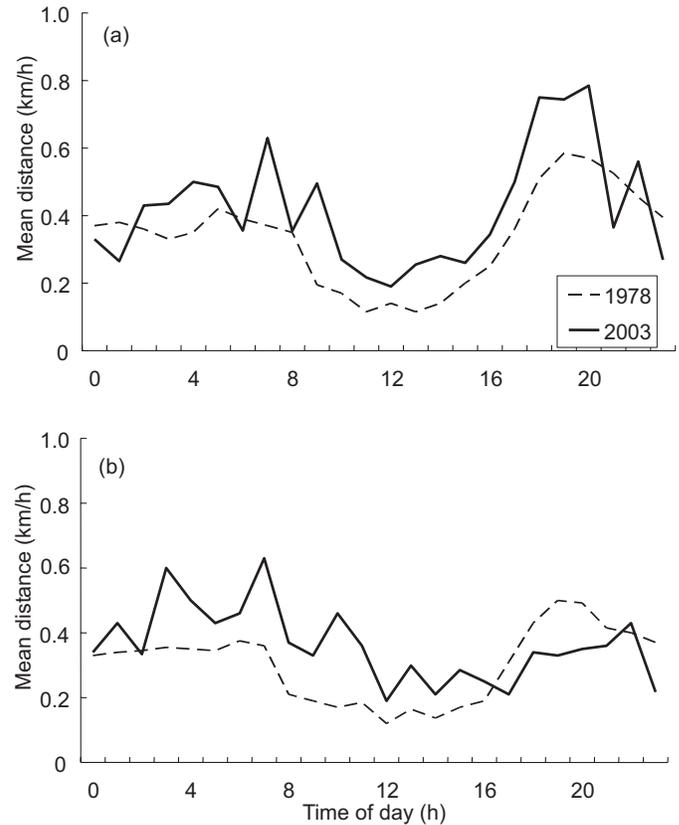
maining prey items were insects in both 1978 (5.6%) and 2003 (13.2%; Fig. 5), which included grasshoppers and beetles.

Pianka's index of overlap, for the five major prey categories, showed an overlap index value of 0.91 between 1978 and 2003. There was a significant difference in dietary composition of the five major prey categories between months within a given year ($\chi^2_{[66]} = 986.78$, $P < 0.0001$) and between years ($\chi^2_{[6]} = 54.80$, $P < 0.0001$), but there was no significant difference for the interaction of month and year ($\chi^2_{[66]} = 73.41$, $P = 0.25$). Although both study periods showed similar variation in monthly trends for the percent occurrence of the major prey categories (Fig. 6), the magnitude of differences were evident when comparing the presence or absence of insects, fruits, and mammals independently, and some differences were significant (Fig. 6, Table 2).

We analyzed mammalian prey items in more detail and found that the size class of mammalian prey items in scat differed significantly by month, year, and the interaction of month and year (Table 3). There was a significant difference in the presence of cottontail rabbits and white-tailed deer in scat among months and years (Table 3, Fig. 7). There was also a difference in the presence of cattle in scat between years (Fig. 7), although there was no interaction between
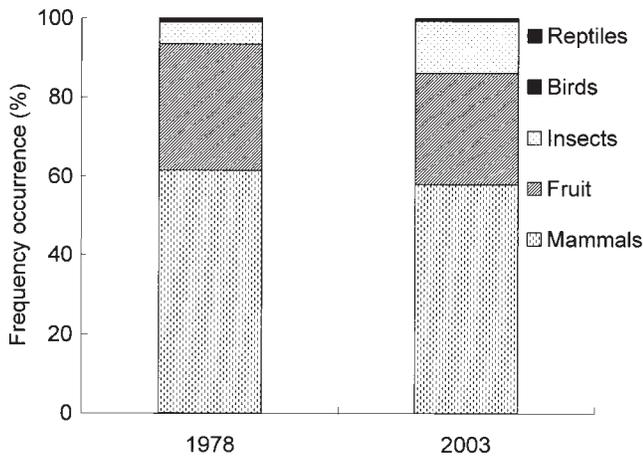
month and year (Table 3). Small-mammal presence differed significantly by month and in the interaction of month and year, but not between years (Table 3, Fig. 7). Feral pigs made up to 34% of the 2003 monthly diet, but was only found in one coyote scat during all of 1978 (Fig. 7).

Discussion

Our findings of similar diet, age structure, and size and position of coyote home ranges and core areas between the two study periods, separated by 25 years, support our hypothesis. Similarity of coyote home-range positions at the WWR is indicated by the high percent overlap between matched home ranges in the 2003 and 1978 studies and greater than expected Minta index value based on randomization tests.

Although we found a high percentage of home-range overlap between the two study periods, two matched pairs of home ranges showed variation in size. For example, the 2003 home range A was much smaller than the 1978 home range A. Gese (1998) observed an incident of a coyote pack expanding its boundaries when the social dynamics of a neighboring pack changed. A similar event may have created the observed size differences for home ranges A and F between the two study periods. The cause of observed size differences is unclear because no data are available during the succession of home ranges that occurred over the 25-year period and further studies that experimentally investi-

Fig. 5. Percent frequency of occurrence of five major prey item categories found in coyote scat at WWR over 12 months in 1978 (November 1978 – October 1979) and 2003 (January–December 2003).

Fig. 6. Percent frequency of occurrence of fruit (*a*), mammals (*b*), and insects (*c*) in coyote scat collected at WWR in 1978 and 2003.

Table 2. The three major categories of prey items found in all coyote scat collected at WWR in 1978 and 2003 (*n* = 3837).

| Prey type	Variable	χ^2	df	*P*
Insect	Year	0.00	1	0.998
	Month	226.24	11	<0.0001
	Year × month	11.77	11	0.381
Mammal	Year	2.40	1	0.121
	Month	451.65	11	<0.0001
	Year × month	56.04	11	<0.0001
Fruit	Year	2.49	1	0.114
	Month	697.15	11	<0.0001
	Year × month	37.93	11	<0.0001

Note: Chi-square values from logistic regressions are shown.

gate the causes of changing spatial patterns of coyote home ranges are still needed. Even with the observed differences in the size of two home ranges, however, our overall conclusion of a high degree of spatial overlap between a 25-year time period is still evident.

Fewer animals were trapped and radio-collared in 2003 than in 1978. In 2003, radio-collared coyotes were often observed with 1–3 unknown coyotes. These observations make it unlikely that the difference in the number of radio-collared coyotes represents different densities between the two study periods. A slight decrease in density, however, could have occurred and we are currently attempting to evaluate population densities using genetic samples collected during the two study periods.

The differences observed by MRPPs are reflected in the low core-area Minta index values that we observed. Although the Minta index value was small for core areas, we observed greater overlap than expected based on our randomized tests. Of the seven matched home-range pairs, there was no core-area overlap in four matched pairs (Fig. 2). Home ranges A and B (Fig. 1) showed a shift in core areas from areas outside of the WWR in 1978 to areas within the boundaries of the WWR in 2003. The core area
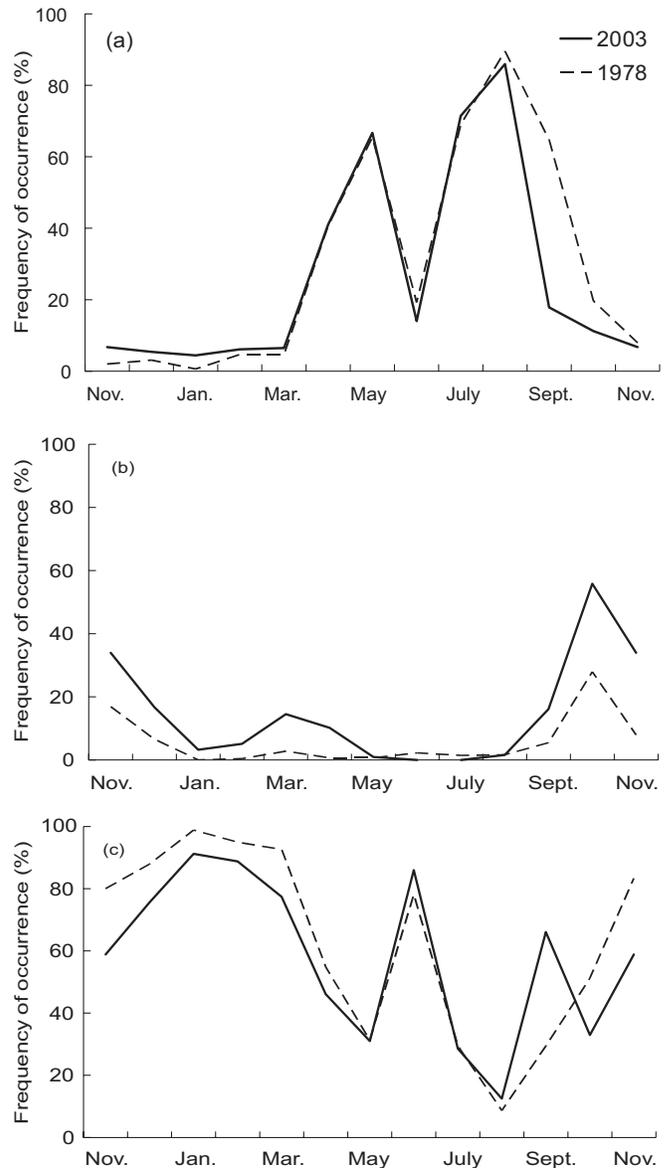
of home range C, on the southern section of the WWR, changed from an area that included part of the edge of the WWR in 1978 to one that was farther from the WWR in 2003 (Fig. 1). Home range E was the fourth and final home range that did not have core-area overlap between the two study periods (Fig. 1). It is unclear what caused these shifts and our post hoc visits to core areas revealed no obvious habitat or other differences between areas that overlapped with 1978 core areas and core areas that did not. Changes may be related to prey distribution, den-site selection, successional changes in vegetation, or other causes. Although absolute amount of core overlap was low, the usefulness of our simulations was apparent; in the large amount of available space we found that coyotes overlapped core areas more often than expected.

As described above, coyotes were excluded from a small area of the WWR for a deer project during the 1978 coyote study (Kie and White 1985). The area of exclusion overlaps

Table 3. Mammalian prey items found in coyote scat ($n = 2142$) collected at WWR in 1978 and 2003.

Prey type	Variable	χ^2	df	P
Mammals (by size type)	Year	46.11	6	<0.001
	Month	221.11	66	<0.001
	Year × month	148.36	66	<0.001
Rodent	Year	0.00	1	0.995
	Month	65.59	11	<0.001
	Year × month	91.71	11	<0.001
Cottontail rabbit	Year	31.17	1	<0.001
	Month	73.14	11	<0.001
	Year × month	21.75	11	0.026
Cattle	Year	0.01	1	0.925
	Month	14.07	11	0.229
	Year × month	24.60	11	0.010
White-tailed deer	Year	9.10	1	0.003
	Month	180.24	11	<0.001
	Year × month	32.30	11	<0.001

Note: Chi-square values from logistic regression are shown.

Fig. 7. Percent frequency of occurrence of rodents (*a*), cottontail rabbits (*Sylvilagus floridanus*) (*b*), cattle (*Bos taurus*) (*c*), white-tailed deer (*Odocoileus virginianus*) (*d*), and feral pigs (*Sus scrofa*) (*e*) in coyote diet collected at WWR in 1978 and 2003.

with the eighth 2003 home range (Fig. 1; home range H). The area outside of the historical coyote exclosure partially overlaps with a 1978 home range used in the above comparisons. In fact, 73% of all home range H locations fell within the northern section of the 1978 home range G, and the other locations are within the coyote exclosure area. Combining the two 2003 home ranges includes the majority of the 1978 home range and the coyote exclosure (Fig. 2*h*). Home ranges overlap by 52.4% when the two 2003 home ranges are considered alone, but the overlap increases to an average of 69.7% when the home ranges are combined. It is therefore likely that the coyote exclosure reduced the number of home-range spaces available and influenced space use of all neighboring territorial coyotes at the WWR. We may have found even greater spatial stability if the coyote exclosure had not existed during the initial study period.

Like Kitchen et al. (2000*a*), we found similar home-range positions between coyote generations, but unlike Kitchen et al. (2000*a*), we found no difference in home-range sizes between the two study periods. Our findings of similarly sized home ranges and core areas between the two study periods may reflect relatively stable prey availability (except for feral hogs, see below) and habitat at the WWR or result from similarities in the mean age and age structure between the two time periods. Unfortunately, no quantifiable measurements of habitat and prey were taken during the 1978 study period. Although direct comparisons cannot be made, anecdotal evidence suggests relative stability of both. The observed similarities in age are probably a result of a relatively stable coyote population that does not experience human persecution or extreme fluctuations in environmental conditions.

Similar to the 1978 study period, activity and distance traveled peaked around sunset and sunrise, although coyotes moved at all times of the day and night. Our results are consistent with other studies that found no difference between activity patterns of individual coyotes, but found a difference in activity based on the time of day (Holzman et al. 1992; Shivik and Crabtree 1995; Shivik et al. 1997).

Andelt (1985) found no difference in the distance traveled by coyotes in different biological seasons except that coy-

otes traveled greater distances during the breeding season (16 Jan. – 15 Feb.) and females reduced their distance traveled during the nursing season (16 Apr. – 15 June). During the 2003 study period, trapping began during the breeding season. We, therefore, could not collect information to evaluate activity patterns during the breeding season. Similar to the 1978 study, we did not observe differences in the hourly distance traveled during the remaining biological seasons in 2003. The weak difference in the interaction of season and time in 2003 may reflect the limitations of the data because few of the same coyotes were observed at all times during all seasons. The observed differences in activity by time of day are commonly observed in other coyote studies. Our results differ from observations of gray wolves, where seasonal and sex differences in movement and activity patterns were observed (Jędrzejewski et al. 2001). These differences may reflect how the variation in social structures and seasonal prey base of gray wolves and coyotes influence activity patterns. In fact, coyote activity is related to searching
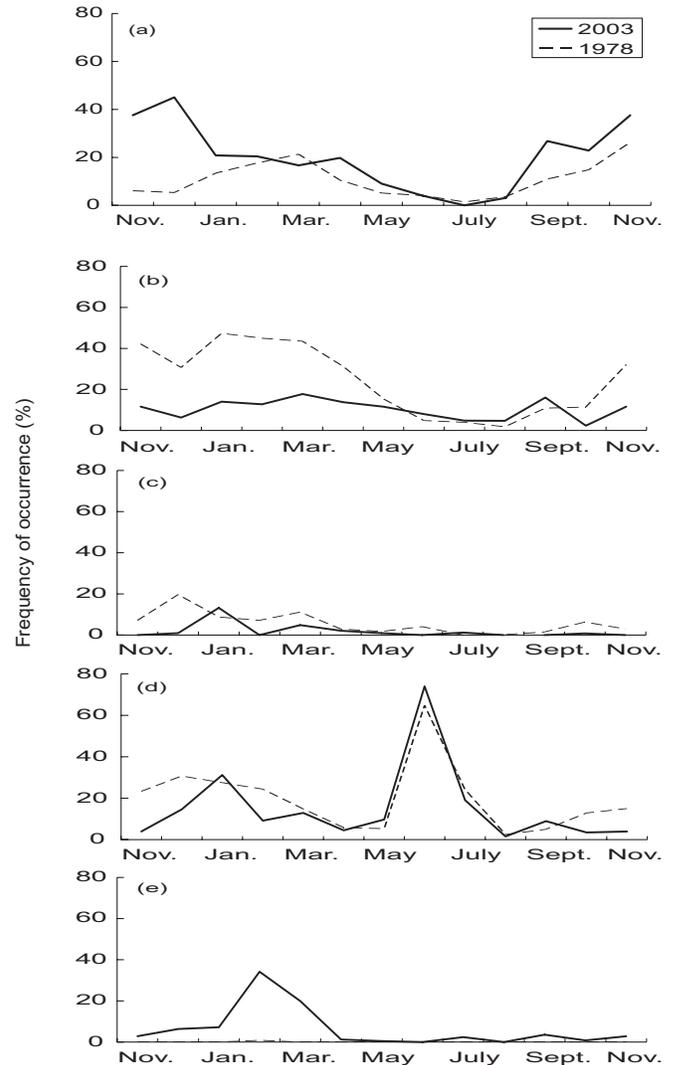
for prey items (Bekoff and Wells 1981; Gese et al. 1996a), vigilance (Switalski 2003), scent marking (Bowen and McTaggart Cowan 1980), and interaction with pack members (Laundré and Keller 1981). Coyotes can change activity patterns relative to changes in the local environment. Activity patterns of coyotes have changed in response to gray wolf re-introductions in Yellowstone National Park (Switalski 2003) and western Montana (Arjo and Pletscher 1999), providing additional support that similarities observed in coyote activity patterns at the WWR likely reflect long-term stability in the local environment.

Our results indicate that coyote diets varied seasonally during both study periods. This is consistent with other studies that found coyote diet varied in response to seasonal changes in prey availability (Bekoff and Wells 1981; Bowyer et al. 1983; Andelt et al. 1987). We found a high degree of dietary overlap between the two studies, with Pianka's index of overlap near one. Although the percentages of occurrence in the category of prey items were similar between the two study periods, some changes in the type of prey within a category were observed. In 2003, coyotes increased the amount of rodents in their diet while reducing the amount of cottontails and cattle compared with those in 1978. Similar to other regions, cottontail rabbit population levels typically fluctuate in southern Texas (Windberg and Mitchell 1990). Cottontail surveys at the WWR indicated low density levels in 2003 (T. Blankenship, unpublished data). Unfortunately, no data are available on cottontail density from the 1978 study, so direct comparisons cannot be made. There was an increase in the feral pig population between the two study periods (D.L. Drawe, personal communication). As the feral pig population increased, coyotes used feral pigs as a more regular prey item. It is, therefore, unclear if a reduction in cottontails in the 2003 diet is related to a reduction in availability, an increase in use of other prey items, such as feral pigs, or a combination of these factors.

Annual changes in prey items by coyotes have been related to changes in prey availability, successional changes in the vegetation, and interspecific competition (Hamlin et al. 1984; Andelt et al. 1987; Windberg and Mitchell 1990; Arjo and Pletscher 1999; Neale and Sacks 2001). The small changes we observed in coyote diet may reflect changes in prey distribution or availability, and these changes may have influenced how coyotes used space within territories.

Our findings suggest that population features, such as home-range position and age structure, are similar between extended time periods. Long-term stability in home-range positions likely reflects the influence of neighboring, tenured coyote home ranges, the relative stability of the environment, and the high density of coyotes at the WWR (Andelt 1985). During both study periods, individual coyotes died or dispersed from home ranges and new individuals established home ranges that followed similar spatial patterns of the former occupant(s). Established neighboring coyotes likely created boundaries that restricted space use by new coyotes.

If environmental conditions at the WWR were not relatively stable during changes of tenure, however, it is unlikely that the observed patterns would have emerged (McNicholl 1975). Changes in space use by gray wolves have been attributed to food shortages (Mech 1977; Messier 1985) and population fluxes resulting from intensive har-

vesting (Fritts and Mech 1981). Space use and activity patterns were significantly different in spotted hyenas relative to changes in anthropogenic activity levels (Boydston et al. 2003b). Similarly, if coyotes experienced dramatic shifts in environmental conditions or were intensively removed, as they experience in much of their range, similarities may not have occurred. Boundary shifts were evident in a coyote population that experienced high levels of mortality from canine hepatitis (Camenzind 1978) and territory size fluctuated with prey abundance when coyotes experienced high levels of human exploitation (Mills and Knowlton 1991).

It is interesting that after 25 years, coyotes exhibit similar space use, activity patterns, age structure, and overall diet in a relatively stable environment. Coyotes are frequent targets of control programs, creating unstable environments in which coyotes must exhibit behavioral and spatial plasticity to thrive. Our study, however, found that this plasticity is not expressed in coyotes that experience relatively stable conditions.

Acknowledgements

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