

DISTANCES TRAVELED DAILY BY COYOTES, *CANIS LATRANS*, IN A PINE–OAK FOREST IN DURANGO, MEXICO

JORGE SERVÍN,* VÍCTOR SÁNCHEZ-CORDERO, AND SONIA GALLINA

Departamento de Desarrollo Sustentable, Instituto de Ciencias Sociales, Universidad Juárez del Estado de Durango, Apartado Postal 123, Durango, Durango 34001, Mexico (JS)

Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, Mexico DF 04510, Mexico (VSC)

Departamento de Ecología y Comportamiento Animal, Instituto de Ecología, AC Apartado Postal 63, Jalapa, Veracruz 18000, Mexico (SG)

Present address of JS: Instituto de Ciencias Sociales, Universidad Juárez del Estado de Durango, Apartado Postal 123, Zona Centro, Durango, Durango 34001, Mexico

Distances traveled daily by coyotes, *Canis latrans*, were monitored for 2 years (1990–1991) in an oak–pine forest (*Pinus* and *Quercus*) in Durango, Mexico. Fourteen adult coyotes (6 females and 8 males) were trapped, radiocollared, and monitored for 24-h periods during breeding, gestation, pup-rearing, and juvenile independence seasons. Mean distances traveled by day by males (16.47 km) were longer than those traveled by females (12.51 km). Mean distances traveled at night were longer (8.24 km) than distances traveled by day (6.51 km), for both sexes. Females and males traveled similar mean distances by day and by night during seasons of breeding, gestation, and juvenile independence. During the pup-rearing season, however, travel by males and females was predominantly nocturnal. Daily distances traveled by coyotes appear to be determined by energy demands imposed by these biological seasons.

Key words: *Canis latrans*, coyote, food availability, radiotelemetry, travel distances

The distance traveled daily by carnivores is an activity relatively less studied for many species. Individuals travel to meet biological requirements such as hunting for prey, mating, maintaining a territory, and caring for young. By determining individual daily movements, we can infer energy compromises imposed by breeding, gestation, pup rearing, and onset of juvenile independence (Krebs and Kacelnik 1991; Macdonald 1983; Pyke 1984; Schoener 1971).

The coyote, *Canis latrans*, is an abundant and widely distributed species in North America (Hall 1981). Several studies that have related distances traveled daily with food search and reproduction indicate that

individuals travel longer distances during breeding season and pup-raising season in regions where food is scarcer (Andelt and Gipson 1979; Bekoff and Wells 1986; Bowen 1982; Ozoga and Harger 1966). Distances traveled daily vary according to geographic location: larger distances have been recorded at higher latitudes, presumably as a result of patchier distribution of food resources (Bekoff and Wells 1986). Recent studies conducted at lower latitudes provide a baseline for identifying geographic patterns in distances traveled daily (Hernández and Delibes 1994; Servín and Huxley 1991, 1995; Servín 2000).

We conducted the 1st study determining movement patterns in coyotes inhabiting a pine–oak forest (*Pinus* and *Quercus*) in the Sierra Madre Occidental, Mexico. Our aims

* Correspondent: loboservin@prodigy.net.mx

were to determine distances traveled daily by individuals, to compare diurnal and nocturnal distances traveled by females and males, and to determine distances traveled daily by males and females throughout the biological seasons of breeding, gestation, pup rearing, and juvenile independence.

MATERIALS AND METHODS

This study was conducted at the Michilia Biosphere Reserve located in the municipality of Suchil, 154 km south-south-east of Durango City (between 23°30'N and 23°35'N latitudes and between 104°21'W and 104°15'W longitudes; altitudinal range, 2,000–2,950 m), on the Sierra of Michis, in the state of Durango, Mexico. This natural reserve is 250 km² in area. The climate is temperate and subhumid with a mean annual temperature of 12°C. The dry season is from February to May, heavy rainfall occurs between June and September, and light winter rains occur from December to January. Snowstorms also may occur in January or February. Mean annual rainfall fluctuates from 700 to 850 mm. The dominant vegetation types are pine–oak forest, pine forest, pinyon juniper forest (*Juniperus deppeana*), scattered woodlands, and grasslands. In shallow soils, the vegetation is primarily dry sherry (*Arctostaphylos pungens*) and oaks (*Q. rugosa* and *Q. potosina*). Natural grasses include *Aristida*, *Panicum*, *Bromus*, *Muhlenbergia*, and *Cistus*; principal herbaceous species are *Senecio* and *Stevia* (González-Elizondo et al. 1993).

Distances traveled daily.—Coyotes were trapped with padded leg-hold traps (Victor No. 3 Soft Catch, Woodstream Corporation, Lititz, Pennsylvania). Each individual was immobilized with an injected mixture of ketamine hydrochloride and xilacine hydrochloride for handling and processing (Servín and Huxley 1992; Servín et al. 1990), weighed, sexed, ear-tagged, radiocollared, and inspected for ectoparasites. Fourteen adult coyotes were captured, including 8 males (13.65 kg \pm 1.45 SE) and 6 females (11.0 \pm 2.21 kg). Males were significantly heavier than females ($t = 2.80$, $d.f. = 13$, $P = 0.007$). Radiocollars weighing less than 250 g were used (Telonics Inc., Mesa, Arizona). Radiocollared individuals were released at capture sites on the day of capture.

A directional 2-element H-antenna with a portable receiver TR-2 (Telonics Inc.) was used to

locate individuals. We applied triangulation for determining the location of radiocollared individuals by using 2 or more compass bearings with an intersecting angle $>20^\circ$ and $<160^\circ$ (Mech 1983). We established 75 stations for recording signals. Telemetry error was determined by reference transmitters to be $\pm 3^\circ$. Each location was plotted on a 1:10,000 map using the Universal Transverse Mercator grid system (White and Garrott 1990). Intensive 24-h tracking sessions, with hourly relocations, were conducted from 0000 to 2359 h (Smith et al. 1981). Male coyotes were monitored for 68 sessions and females for 23 sessions, totaling 91 sessions. Distances traveled daily were calculated as straight-line movement between each consecutive position. These distances were used as an index of activity.

Distances traveled daily were grouped into 4 biological seasons throughout the study: breeding, 1 January to March 15; gestation, 16 March to 31 May; pup rearing, 1 June to 15 September; and juvenile independence, 16 September to 31 December (Smith et al. 1981). Nocturnal samples included movements recorded from 1800 to 0659 h and diurnal samples, from 0700 to 1759 h.

Distances traveled daily were compared using Student's t -test (Zar 1999). The Wilcoxon non-parametric statistical test (Siegel 1986) was used to compare day and night nonindependent tracking data (Hulbert 1984). Diurnal and nocturnal traveled distances were compared between biological seasons and between sexes. Values are given as mean \pm SD.

RESULTS

Mean daily distances traveled by male coyotes were significantly longer (16.47 km \pm 4.95 SD; $n = 68$) than those traveled by females (12.51 \pm 3.52 km; $n = 23$; $z = 3.64$, $P < 0.001$). In both sexes, significant differences in daily traveled distances were observed between seasons: males traveled longer distances during the gestation season (19.04 km) and shorter distances in the season of juvenile independence (13.57 \pm 4.29 km; $t = 6.06$, $d.f. = 3$, $P < 0.05$), whereas females traveled longer distances during the pup-rearing season (16.68 km) and shorter distances during the breeding season (6.81 \pm 1.81 km; $t = 14.66$, $d.f. = 3$, $P < 0.001$; Fig. 1).

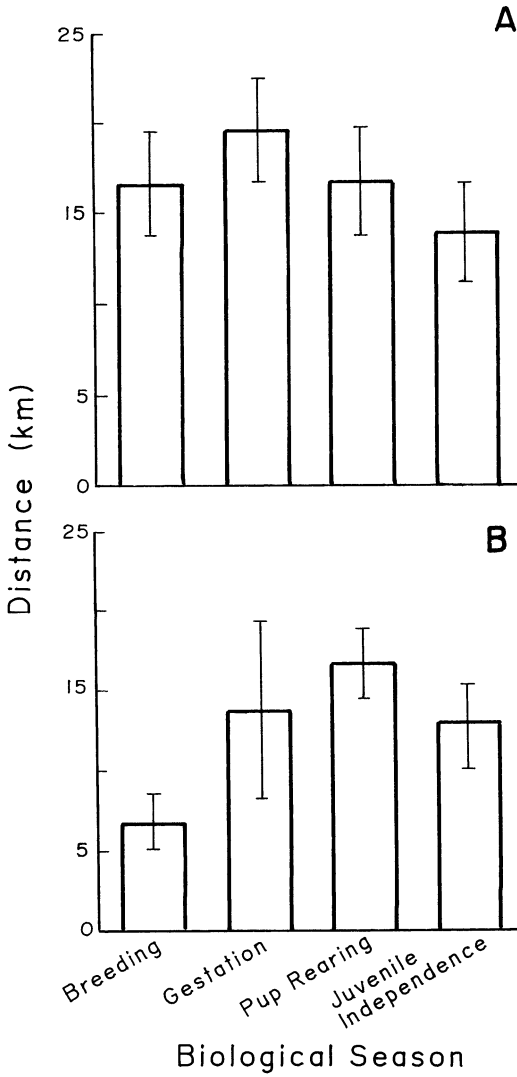


FIG. 1.—Distances traveled in 24-h periods by A) male and B) female coyotes in the Michilia Biosphere Reserve in Durango, Mexico. Bars indicate mean, vertical lines \pm *SD*.

Overall, mean male diurnal (7.44 km) and nocturnal (9.03 km) distances traveled were similar (Wilcoxon test, $z = 1.555$, $P = 0.119$, $n = 68$; Fig. 2A). No significant seasonal differences were observed during the breeding season (diurnal = 7.36 km, nocturnal = 9.1 km; $z = 0.902$, $P = 0.366$), gestation season (diurnal = 9.55 km, nocturnal = 9.49 km; $z = 0.0392$, $P = 0.96$), and season of juvenile independence (di-

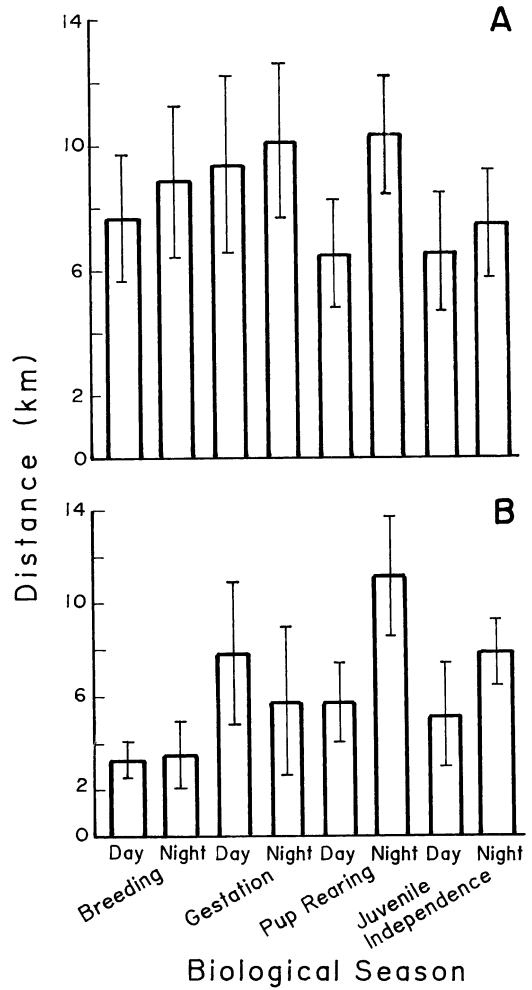


FIG. 2.—Distances traveled in 24-h periods by A) male and B) female coyotes at different biological seasons in the Michilia Biosphere Reserve, Durango, Mexico. Bars indicate mean, vertical lines \pm *SD*.

urnal = 6.35 km, nocturnal = 7.21 km; $z = 1.137$, $P = 0.255$), but during the pup-rearing season, males traveled longer distances (diurnal = 6.49 km, nocturnal = 10.32 km; $z = 2.86$, $P = 0.004$).

Overall, diurnal (5.61 km) and nocturnal (6.89 km) distances traveled by female coyotes were similar (Wilcoxon test, $z = 1.45$, $P = 0.146$, $n = 23$; Fig. 2B). No significant seasonal differences in distances traveled were observed during the breeding season (diurnal = 3.3 km, nocturnal = 3.5 km; z

= 0.059, $P = 0.610$), gestation season (diurnal = 7.8 km, nocturnal = 5.52 km; $z = 1.608$, $P = 0.107$), and season of juvenile independence (diurnal = 5.3 km, nocturnal = 7.91 km; $z = 1.60$, $P = 0.107$), but during the pup-rearing season, females traveled longer nocturnal distances (diurnal = 6.04 km, nocturnal = 10.64 km; $z = 2.31$, $P = 0.0206$).

DISCUSSION

Individuals monitored in this study were adults of a breeding group with defined home ranges. Our observations excluded transient individuals with undefined home ranges; thus, our results are comparable with similar studies conducted at higher latitudes (Andelt 1985; Andelt and Gipson 1979; Bekoff and Wells 1986; Bowen 1982; Petterson et al. 1999; Shivik et al. 1997; Smith et al. 1981).

Daily distances traveled in our study site were almost double those traveled by coyotes in mesquite grassland in Texas, where males traveled a mean of 8.1 km and females, 7.8 km (Andelt 1985). However, our results were similar to daily distances traveled in forested areas in Nebraska (Andelt and Gipson 1979) but were notably shorter than those reported in Nova Scotia, where daily distances traveled by coyotes reached an average of 20.2 km (Petterson et al. 1999). These findings suggest that habitat type rather than latitude influences individual distances traveled daily by coyotes. Preliminary evidence indicates that coyotes move longer distances in temperate than in dry habitats (Andelt 1985; Mace et al. 1984; Ozoga and Harger 1966).

Coyotes are highly cooperative breeders with a strong parental investment (Bekoff and Wells 1986). During the pup-rearing season, males forage more actively to gather enough food to feed the females and their pups (Andelt 1985; Harrison and Gilbert 1985). Females spend time teaching pups behavioral skills for foraging. Once pups are weaned, females and males forage independently. Our observations appear to fit

this pattern. Male and female nocturnal and diurnal distances traveled were similar. However, males and females traveled longer distances during the pup-rearing season, supporting the hypothesis of cooperative behavior and an increase in active foraging to provide enough food for pup rearing. This was particularly notable in males, which traveled significantly longer distances during the pup-rearing season. Moreover, nocturnal movements of males were longer than those of females during the breeding and gestation seasons, perhaps to provide more food to the female during reproductive periods when their energy demands are high (Fig. 2). During the pup-rearing season, males and females had longer nocturnal movements, perhaps to acquire more food resources for their young. Because pup survival depends on food resources provided by parents, cooperative feeding of pups results in higher pup survival (Bekoff and Wells 1986). Once pups are independent, male and female daily distances traveled decrease because they forage individually (Andelt 1985; Andelt and Gipson 1979; Bekoff and Wells 1986; Petterson et al. 1999; Shivik et al. 1997). Similar patterns in distances traveled by coyotes have been observed in Texas (Andelt 1985), forested areas in Maine (Harrison and Gilbert 1985), Nebraska (Andelt and Gipson 1979), California (Shivik et al. 1997), and Nova Scotia (Petterson et al. 1999).

Daily travel demands a high expenditure of energy (Gittleman and Harvey 1982; MacNab 1963). In coyotes, much of the metabolic energy available is invested in traveling within the home range. Feeding behavior is crucial to the energy intake required for maintaining a home range, feeding, mating, and pup rearing (Bekoff and Wells 1986; Gittleman and Harvey 1982; Pyke 1984; Schoener 1971).

Foraging behavior of coyotes at the Michilia reserve appeared to be related to energy demands imposed by the biological seasons. The breeding season is synchronized with greater and richer availability of

food resources. Coyotes at the Michilia reserve had a high consumption of rodents and lagomorphs during the breeding season (34%), including both high energy and protein values (Servín 2000; Servín and Huxley 1991). This suggests that the energy intake, consisting mostly of animal protein, is divided for breeding, home-range maintenance, mating, and scent marking among other functions. Conversely, during the seasons of pup rearing and juvenile independence, rodents and lagomorphs at the Michilia reserve are scarce, and coyote diet during this period consists predominately of pinyon juniper fruits (58.7%), with high availability but low energy and protein values (Servín 2000).

Daily distances traveled by coyotes may reflect an efficient use of energy related to food intake. These distances may be influenced by an individual's reproductive condition, age, sex, and biological season. An increase in energy intake by females during the breeding and gestation seasons is correlated with reproductive success (Harrison and Gilbert 1985; Mace et al. 1984). Thus, during the gestation season, distances traveled by individuals appear to maximize energy intake as compared with energy use. The breeding and gestation seasons demand high amounts of energy, and perhaps for this reason females traveled shorter distances during these seasons than during seasons of pup rearing and juvenile independence (Fig. 2B). Distances traveled daily by coyotes vary according to their biological season and food availability. Such behavioral plasticity allows coyotes to adjust successfully to a wide variety of environments.

RESUMEN

Se realizó el seguimiento de las distancias recorridas diarias de coyotes, *Canis latrans* durante 2 años (1990–1991) en un bosque de encino-pino (*Quercus* y *Pinus*) en Durango, México. Catorce coyotes adultos (6 hembras y 8 machos) fueron capturados, poniéndoseles radiocollares y seguidos por periodos de 24 horas durante los

periodos biológicos de reproducción, gestación, cría de cachorros e independencia de juveniles. Los promedios de las distancias recorridas diarias para los machos (16.47 km) fueron mayores que para las hembras (12.51 km). Los promedios de las distancias viajadas por los coyotes de ambos sexos por noche (8.24 km) fueron mayores que durante el día (6.51 km). Las hembras y los machos recorrieron distancias diarias similares durante el día y noche en los periodos biológicos de reproducción, gestación e independencia de juveniles. Sin embargo, durante el periodo de cría de cachorros, hembras y machos fueron predominantemente nocturnos. Las distancias recorridas diarias de los coyotes aparentemente están determinadas por las demandas energéticas impuestas por estos periodos biológicos.

ACKNOWLEDGMENTS

Field assistance in coyote trapping was provided by F. Alvarado, E. Contreras, R. Medina, J. A. Moreno, and J. Medina. We thank M. Huxley, J. García-Chavez, R. Rodriguez-Mazzini, E. Chacón, and M. Vences for field assistance in tracking coyotes. J. Laundré, B. Miller, B. Villa-Ramírez, Z. Tang-Martínez, S. Lindaker, and I. A. Rosen provided critical reviews of the manuscript. The study was funded by Consejo Nacional de Ciencia y Tecnología (project P220CCOR892158) and a sabbatical grant (990127) to J. Servín, the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO project P064) to J. Servín and V. Sánchez-Cordero, and the Departamento de Fauna Silvestre, Instituto de Ecología, A.C. (project 902-06) to J. Servín.

LITERATURE CITED

- ANDELT, W. F. 1985. Behavioral ecology of coyotes in South Texas. *Wildlife Monographs* 94:5–45.
- ANDELT, W. F., AND P. S. GIPSON. 1979. Home range activity, and daily movements of coyotes. *Journal of Wildlife Management* 43:944–951.
- BEKOFF, M., AND M. C. WELLS. 1986. Social behavior and ecology of coyotes. Pp. 251–338 in *Study of behavior* (D. S. Lerman, ed.). Academic Press, New York.
- BOWEN, W. D. 1982. Home range and spatial organization of coyotes in Jasper National Park, Alberta. *Journal of Wildlife Management* 46:201–216.
- GITTLEMAN, J., AND P. H. HARVEY. 1982. Carnivore

- home range size: metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10:57–63.
- GONZÁLEZ-ELIZONDO, S., M. GONZÁLEZ-ELIZONDO, AND A. CORTÉS-ORTIZ. 1993. Vegetación de la reserva de la biosfera la Michilía, Durango. *Acta Botánica Mexicana* 22:1–104.
- HALL, E. R. 1981. The mammals of North America. 2nd ed. John Wiley & Sons, Inc., New York 2:601–1181 + 90.
- HARRISON, D. J., AND J. R. GILBERT. 1985. Denning ecology and movements of coyotes in Maine during pup rearing. *Journal of Mammalogy* 66:712–719.
- HERNÁNDEZ, L., AND M. DELIBES. 1994. Seasonal food habits of coyotes, *Canis latrans*, in the Bolson de Mapimí, Southern Chihuahuan Desert, Mexico. *Zeitschrift fuer Säugetierkunde* 59:82–86.
- HULBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- KREBS, J. R., AND A. KACELNIK. 1991. Decision making. Pp. 105–136 in *Behavioural ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). Blackwell Scientific Publications, Oxford, United Kingdom.
- MACDONALD, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.
- MACE, G. M., P. H. HARVEY, AND T. H. CLUTTON-BROCK. 1984. Vertebrate home range size and energetic requirements. Pp. 31–53 in *The ecology of animal movement* (I. R. Swingland and P. J. Greenwood, eds.). Oxford University Press, Oxford, United Kingdom.
- MACNAB, B. K. 1963. Bioenergetics and the determination of home range size. *American Naturalist* 93:133–140.
- MECH, L. D. 1983. *Handbook of animal radio-tracking*. University of Minnesota Press, Minneapolis.
- OZOGA, J. J., AND E. M. HARGER. 1966. Winter activities and feeding habits of northern Michigan coyotes. *Journal of Wildlife Management* 30:809–818.
- PETTERSON, B. R., S. BONDRUP-NIELSEN, AND F. MESSIER. 1999. Activity patterns and daily movements of the eastern coyote, *Canis latrans*, in Nova Scotia. *Canadian Field-Naturalist* 113:251–257.
- PYKE, G. H. 1984. Animal movements: an optimal foraging approach. Pp. 7–31 in *The ecology of animal movement* (I. R. Swingland and P. J. Greenwood, eds.). Oxford University Press, Oxford, United Kingdom.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.
- SERVÍN, J. 2000. *Ecología conductual del coyote en el sureste de Durango*. Ph.D. dissertation, Universidad Nacional Autónoma de Mexico City, Mexico City, Mexico.
- SERVÍN, J., AND C. HUXLEY. 1991. La dieta del coyote en un bosque de encino-pino de la Sierra Madre Occidental. *Acta Zoológica Mexicana (Nueva Serie)* 44:1–30.
- SERVÍN, J., AND C. HUXLEY. 1992. Inmovilización de carnívoros silvestres con la mezcla de ketamina y xilacina. *Veterinaria Mexicana* 23:135–139.
- SERVÍN, J., AND C. HUXLEY. 1995. Coyote home range size in Durango, México. *Zeitschrift fuer Säugetierkunde* 60:119–120.
- SERVÍN, J., C. HUXLEY, AND M. VENCES. 1990. El uso combinado de hidrocloreto de ketamina (KHCL) e hidrocloreto de xilacina (XHCL) para inmovilizar coyotes silvestres. *Acta Zoológica Mexicana (Nueva Serie)* 30:27–37.
- SHIVIK, J. A., M. M. JAEGER, AND R. H. BARRETT. 1997. Coyote activity patterns in the Sierra Nevada. *Great Basin Naturalist* 57:355–358.
- SIEGEL, S. 1986. *Estadística no paramétrica, aplicada a las ciencias de la conducta*. Ed. Trillas, Mexico City, Mexico.
- SMITH, G. J., J. R. CARY, AND O. J. RONGSTAD. 1981. Sampling strategies for radiotracking coyotes. *Wildlife Society Bulletin* 9:88–91.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, Inc., New York.
- ZAR, J. H. 1999. *Biostatistical analysis*. 4th ed. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Submitted 17 December 2001. Accepted 29 September 2002.

Associate Editor was John G. Kie.