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Survival and Home Range Fidelity of Coyotes in Montana: Implications for Control

Abstract

Survival and home range characteristics of coyotes (Canis latrans) *were examined in the Missouri River Breaks of Montana during 1976-1992. Mean annual survival was greater* (P = 0.05) *for coyotes captured as adults (0.70-0.76) than those captured as juveniles (0.42). I attributed this difference to social status of individual coyotes and related habitat use. Survival of nomad-disperser adults (0.35-0.42) did not differ* (P>0.20) *from coyotes captured as juveniles. Survival of denning coyotes (0.82-0.85) was greater than either those captured as juveniles or nomad-disperser adults* (P<0.002). *Survival in this heavily exploited coyote population was similar to that reported for lightly exploited coyote populations. One male coyote lived for a minimum of 13.5 years. Three individual denning coyotes used the same home range for at least 5 years. Coyote populations increased despite fur prices ranging from $40-150 (in effect, a high bounty). High survival of an effective predator of mule deer on this area (denning coyotes) suggested that a general bounty system would not increase survival of deer.*

Key Words: Coyotes, *Canis latrans*, survival, longevity, home range fidelity, predation, coyote control, bounties, mule deer, *Odocoileus hemionus*.

Introduction

Concurrent with the mid-1990s decline in many mule deer *(Odocoileus hemionus)* populations in Montana, hunters have focused their interest on predation and its effect on deer populations. Requests to control predators, including coyotes, to increase survival of game animals have been made by hunters (Hamlin and Erickson 1996) and through them, by legislators. These requests have suggested direct control by government agencies and establishment of bounty systems funded by an earmarked increase in hunting license fees. For example, the Fish and Wildlife Conservation Predator Control Program (HB404) was introduced in the 55th (1997) Montana Legislative Session but died in Committee.

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Previously, a decline in mule deer populations in the mid-1970s occurred in Montana and throughout the western U.S. coincident and subsequent to a ban on use of compound 1080 (sodium monofluoracetate) and other toxicants for predator control on public lands by Executive Order No. 11643 (Connolly 1978). Controversy surrounding these events resulted in considerable research on coyotes and predation throughout the western U.S. Studies in Montana included those reported by Schladweiler (1980), Hamlin et al. (1984), Pyrah (1984) and Hamlin and Mackie (1989).

Information collected in the Missouri River Breaks (MRB) of Montana during these earlier studies is pertinent to current discussion and decisions about control of coyote populations to increase survival of mule deer populations. Some of the information presented here was reported earlier by Pyrah (1984) but his paper concentrated on social distribution and population estimates. Data on the fate, longevity, and movements of an additional seven coyotes were determined after that reported by Pyrah (1984). This provided the opportunity to report information on coyote longevity and home range fidelity not previously available and to discuss implications of that information to efficacy of coyote control to increase deer survival and hunting opportunity.

Study Area

Capture and marking of coyotes was conducted on or near a timbered 250 km^2 area in the MRB about 40 km northeast of Roy, Montana. This area was previously described by Mackie (1970), Hamlin et al. (1984) and Hamlin and Mackie (1989). Description of a larger coyote study area that included some plains habitat was provided by Pyrah (1984).

The MRB are a 6-15 km wide band of heavily dissected uplands that occur on both sides of the Missouri River in north-central Montana. Drainages become wider and deeper as they approach the river and are interspersed with open ridges extending toward the river from the rolling plains beyond the MRB. These ridgetops are dominated by big sagebrush (*Artemisia tridentata*) and wheatgrasses (*Agropyron spp.*). Side slopes of drainages are dominated by ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (*Juniperus scopulorum*). Climate is semiarid.

Livestock grazing was the major commercial land use, though recreational pursuits, including hunting, fishing, wildlife observation and sight-seeing also were major land uses. During this study, coyote pelts had substantial economic value and coyote hunting and trapping were major commercial land uses. The majority of land in this area is under Federal ownership and administered by the USDI, Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge (CMRNWR) and the USDI, Bureau of Land Management.

Methods

Thirty-seven coyotes were trapped, marked and released during 1976-1979 (Pyrah 1984). Twenty-three adult coyotes ($\geq$ 1-year-old) captured during 14 April - 10 July, 1976-1979 were equipped with radio-transmitter collars. Three radio-transmitter collars and 11 observation collars were placed on juvenile ($\leq$ 1-year-old) coyotes captured from 29 September - 16 October 1978 (Pyrah 1984). Aerial relocations of instrumented coyotes were made at an average interval of two weeks from a PA-18 Piper Super Cub aircraft during the life of the transmitter. Occasional relocations also were made from the ground (Pyrah 1984). Numbers of adults and pups were recorded for all visual observations of marked coyotes. Juvenile coyotes with observation collars provided information only on date and location of death when reported by hunters and trappers. More detailed descriptions of field methods were provided by Pyrah (1984).

Fate and date of death were determined for 17 of 23 adult and 11 of 14 juvenile coyotes. One adult was censored from analysis because death occurred within three days from probable capture-related injuries. One adult died prior to 1 October so was not included in the analysis that compared survival of adults to juveniles captured during autumn.

One adult coyote was trapped by a fur trapper aware of the study and released when he observed the radio-transmitter collar. For purposes of this analysis, that coyote was considered dead on the day he was trapped by the fur trapper.

Fate and date of death were undetermined for six adult coyotes after their transmitters ceased functioning or they dispersed beyond search range. Last relocations of those six coyotes were made from 54 to 2,356 days after capture. Because all but three deaths of the 16 other non-censored adult coyotes occurred after their transmitter ceased to function or they dispersed beyond search range, a method was devised to include these six coyotes in some of the analysis.

I calculated composite (weighted) mean annual survival using coyote death data as "band return" data in a cohort life table (Eberhardt 1969). Cohorts analyzed were those captured as adults and those captured as juveniles; specific ages were not used. The end product was average annual survival over the lifetime of the cohort. Survival rates and longevity were calculated by three different methods: 1) only those coyotes with a known date of death were used; 2) the six adult coyotes with unknown dates of death were assigned a death date on the last day a radio-relocation was made; and 3) each of the six coyotes of unknown fate was assigned a date of death based on the average date of death of all known fate coyotes that lived at least as long as that coyote. For example, Coyote N's transmitter functioned for 1,625 days. Known-fate coyotes that lived at least 1,625 days, lived from 1,626 to 4,489 days and an average of 2,703 days. Coyote N was assigned a longevity of 2,703 days after capture.

Method 1 does not provide maximal use of information. Method 2 underestimates longevity because 13 of 16 known fate adult coyotes lived longer than their transmitter functioned. Method 3 includes estimated data, but may be nearest to actual values.

To facilitate equal comparisons of longevity between autumn captured juveniles and spring-summer captured adults, starting date for comparative analysis was set at 1 October. Because of small samples and non-normal distributions, statistical tests of comparative longevity were made with nonparametric Mann-Whitney U tests (Zar 1984). Home range plots were made only for three coyotes that survived at least four denning seasons (minimum of 1,333 days of radio-transmitter contact). Perimeters of annual home ranges were established using the minimum convex polygon method (Mohr 1947). Age and social category were assigned as described by Pyrah (1984). These social categories were: den pairs (breeders), supernumary den adults (nonbreeders), nomads, and dispersers. Juveniles were a temporary nonbreeder social category.

Results and Discussion

Annual Survival

From 1 October, first year survival of adults was 0.67, 0.57 and 0.76 by Methods 1, 2 and 3, respectively. For juveniles (0.5 - 1.5 years), first year survival was 0.55 (6/11). Similar estimates of composite (averaged over their lifetime) mean annual survival rates were produced by all three methods (Table 1), but Method 2 produced minimal and Method 3 maximal estimates as expected. A substantial difference in mean annual survival between coyotes captured as adults and those captured as juveniles was observed (Table 1), but the difference appeared to be related to social status rather than age. Mean annual survival rates for adults in the nomad-disperser social category (0.35-0.42) were essentially the same as for coyotes captured as juveniles (0.42) (Table 1). Adult coyotes associated with dens had approximately twice the mean annual survival rates (0.82 - 0.85) as either nomad-disperser adults or coyotes captured as juveniles.

Expressed as average number of days survived after 1 October, survival of adults with known dates of death (Method 1) did not differ (Mann Whitney U=110, $P = 0.17$) from survival

Table 1. *Composite annual survival rate and average days of survival by age and social category for coyotes captured during 1976-1979 in the Missouri River Breaks, Montana*[a]

Age and Social Category [b]	Annual Period: 1 October to 1 October			Year starting date of capture		
	Annual Survival Rate					
	Method 1 [c]	Method 2 [d]	Method 3 [e]	Method 1	Method 2	Method 3
Adults	0.72 (15)(39/54) [f]	0.70 (21)(49/70)	0.76 (21)(68/89)	0.72 (16)(41/57)	0.71 (22)(53/75)	0.77 (22)(72/94)
Juveniles	0.42 (11)(8/19)	—	—	0.42 (11)(8/19)	—	—
Nomad Disperser Adults	0.39 (8)(5/13)	0.35 (11)(6/17)	0.42 (11)(8/19)	0.40 (9)(6/15)	0.37 (12)(7/19)	0.45 (12)(10/22)
Den Adults	0.83 (7)(34/41)	0.82 (10)(44/54)	0.85 (10)(55/65)	0.83 (7)(35/42)	0.82 (10)(46/56)	0.85 (10)(56/66)

	Beginning 1 October			Beginning date of capture		
	Average Number of Days Survived					
Adults	1,061(15) [g]	988 (21)	1,313 (21)	1,132 (16)	1,079 (22)	1,387 (22)
Juveniles	355 (11)	—	—	355 (11)	—	—
Nomad-Disperser Adults	319 (8)	279 (11)	374 (11)	420 (9)	365 (12)	454 (12)
Den Adults	1,908 (7)	1,767 (10)	2,142 (10)	2,047 (7)	1,904 (10)	2,282 (10)

[a] Composite annual survival for juveniles is for the category of coyotes captured as juveniles. It is an estimate of mean annual mortality throughout their life span. First year mortality (age 0.5-1.5) is reported in text.

[b] Adults = $\geq$ 1 year old at capture. Juveniles = <0.5 years old at capture. Social category as described in Pyrah (1984).

[c] Method 1 = only coyotes with known fate and date of death used.

[d] Method 2 = six adults with unknown fate and date of death included as deaths when radio transmitter ceased functioning.

[e] Method 3 = six adults with unknown fate and date of death included with average adjusted date of death as described in Methods Section.

[f] Annual survival rate (number of coyotes)(composite number of survivals/composite number of opportunities to survive).

[g] Mean number of days survived (number of coyotes)

of coyotes captured as juveniles. The difference was significant (Mann-Whitney U=167, $P = 0.05$) when Method 3 was used to calculate adult survival. Survival of adults associated with dens was different than for nomad-disperser adults whether only known date of death was used (Method 1, Mann-Whitney U=54, $P = 0.002$) or adjusted dates of death were included (Method 3, Mann-Whitney U = 127, $P < 0.001$). Survival of adults associated with dens differed from survival of coyotes captured as juveniles (Mann-Whitney U=75, $P < 0.001$) although survival of nomad-disperser adults was not different from survival of coyotes captured as juveniles (Mann-Whitney U = 53, $P > 0.20$).

Mean annual survival of coyotes with stable social status associated with den areas within timbered breaks habitat (0.82 - 0.85) was as high as any reported. Andelt (1985) reported annual survival of 0.68 for radio-transmitter collared adult coyotes on a Texas study area lightly exploited by humans. Annual survival there was 0.82 for residents (equivalent to denning coyotes in the MRB) and 0.51 for transients (equivalent to nomads in the MRB). Similarly, for another lightly exploited coyote population in south Texas, Windberg et al. (1985) found that annual survival of radio-transmitter collared adults ($\geq$ 1.5 - years) ranged from 0.68 to 0.70 and annual survival for juveniles (0.5 - 1.5 - years) was 0.42. In Maine, Harrison (1992) reported annual survival for radio-transmitter collared juveniles (0.5 - 1.5 - years) was 0.47 for dispersers and 0.74 for residents. Survival rates for these relatively lightly exploited coyote populations (0.68-0.70, all adults) were almost identical to those I report (0.70-0.77 all adults, Table 1) for a population subjected to relatively heavy harvest pressure by humans. I did not find published information on survival of instrumented coyotes for other heavily exploited populations.

Estimates of annual survival for adult coyotes based on age structure were 0.61 in Iowa (Boggess 1975), 0.59 in Texas as calculated by Bogess 1975 from Knowlton 1972 and 0.55 in Montana, based on my calculations using age structure data in Schladweiler (1980) and the equation of Chapman and Robson (1960). Nellis and Keith (1976) estimated adult coyote survival ranging from 0.58 - 0.64 from tag return data in Alberta. All these survival rates are from at least moderately exploited populations and are slightly lower than those reported here for the MRB. Use of age structure data to estimate annual survival may somewhat underestimate survival because it truncates maximal age and does not account for lesser vulnerability to harvest of older, experienced and socially stable coyotes.

Lack of stable, breeding social status often resulted in dispersal to non-timbered habitat with little topographic relief, and a lower life expectancy. Few juveniles were accepted into breeding units on this area (Pyrah 1984) which resulted in dispersal, nomadism and low survival. One of three radio-transmitter collared juveniles was a den supernumerary (extra adult) during its first year (Pyrah 1984). It dispersed in late July and was shot in December at 1.5-years-old. Social status at time of death for juveniles marked with observation collars was unknown, but most had dispersed from the area where marked. Coyotes first captured as juveniles probably were less likely to end up in timbered breaks habitat than coyotes that were established denning adults when captured.

A minimum of 85 percent of 27 deaths of coyotes were human-caused; 67 percent were shot and 18 percent were trapped. One of these was trapped in a control action by the U.S. Fish and Wildlife Service after it had dispersed from the area. Eighty-one percent of coyotes were taken from October through February; 59 percent were taken from December through February.

Longevity

Juvenile coyotes lived an average of about one year ($\bar{x}$= 355 days; range, 76-793 days) after capture on 1 October (Table 1). Longevity of adult coyotes in the nomad-disperser social category was similar to coyotes captured as juveniles (range 160-910 days) (Table 1). Adults in a stable, breeding social unit (denners) lived an average of six years after capture or 5.5 years after 1 October of the year of capture (range 614-4,624 days) (Table 1).

Greatest longevity observed was for an adult male captured by a fur trapper 4,624 days after initial capture. This coyote, a minimum of 1-year-old at initial capture, was a minimum of 13.5-years-old at death. Canine teeth were recovered from two other radio-transmitter collared adult coyotes at death and they were aged by tooth cementum layers (Linhart and Knowlton 1967) as 9.5-and 12.5-years-old. The oldest wild coyotes reported elsewhere were a 14.5-year-old female in Colorado and a 13.5-year-old male in Texas (Knowlton 1972).

Home Range Fidelity

Few studies continued long enough or had coyotes survive long enough to determine fidelity to home range. Others have reported coyotes occupying the same home range for periods of 3-4 years (Camenzind 1978, Bowen 1982, Andelt 1985).

Two coyotes in the denner social category in the MRB occupied the same home range for five years (Female C and Male M), (Fig. 1). Another coyote (Male L) occupied the same general area for at least five years, but a shift occurred after three years to an overlapping adjacent area (Fig. 1). The fate of the female mate of L was unknown because she was not marked with a radio-transmitter collar. She might have died and male L found another mate in the adjacent area. When male L occupied his new adjacent home range (Fig. 1), another denning pair used the original denning area in 1983. Although home range area was stable through the years for these denning coyotes, den sites changed (Fig. 1). All three coyotes were killed outside their traditional den areas (Fig.1).

Death occurred for most denning coyotes after they left the original denning area. Five coyotes that were originally one of a denning pair became nomads. Four of these were shot or trapped outside their original den area and fate of the other was unknown. Two of these coyotes had feet damaged by trapping which may have made them less competitive in social conflicts and led to their shift to nomadism (Pyrah 1984). Older coyotes also might become less socially competitive and eventually be forced from their den area, increasing their risk of death. Final fate of three of ten coyotes that remained denners was unknown and location of death for another was unknown. Of the other six, three were slightly outside their traditional home range at death, one each was shot and trapped within their home range and one appeared to have died a natural death within its home range. It appeared that coyotes in the MRB maintained strong fidelity to home range as long as they remained socially competitive members of denning pairs.

Implications for Coyote Control

Coyotes have been killed for years in the western U.S. because of their real and perceived depredations on domestic animals and wildlife. Control efforts were by individuals, through state and local bounties, and by direct government programs such as the Federal Animal Damage Control Program (ADC) (Connolly 1978). In Montana, state bounties on coyotes were in place in the late 1800s. In 1929 the Montana Fish and Game Department had 14 employees solely dedicated to predator control (Smith 1929). Additionally, 11 hunters were employed by the Federal Government and 13 by the Montana Livestock Commission (Smith 1929). A brochure published by the Montana Fish and Game Department ca. 1927 entitled "Sportsmen's Dollars Destroy Coyotes" above a picture of "a month's catch of coyotes and other predatory animals . . ." extolled the program as follows: "The Fish and Game Department of Montana is rendering service to this great Treasure State in ways and to an extent few of its people realize. The cut on the title page of this folder shows what just one man in the employ of the Department accomplished for the protection not only of the game in which our sportsmen are interested, but also for the protection of the livestock, poultry and songbirds; $42,943.46 were expended by the Department during the years 1925 and 1926 in the destruction of these common enemies of domestic and wild life (sic). This fund is created by the setting aside of 25c from each hunting and fishing license for this purpose. . ."

Although millions of coyotes were killed in Montana and the Western U.S. during the last hundred years, of the control measures used, only toxicants were effective in reducing coyote populations (Cain et al. 1972). The most effective toxicant, Compound 1080, may have been relatively effective in reducing coyote populations where it was intensively used in northwestern states (Wagner 1972, Hamlin and

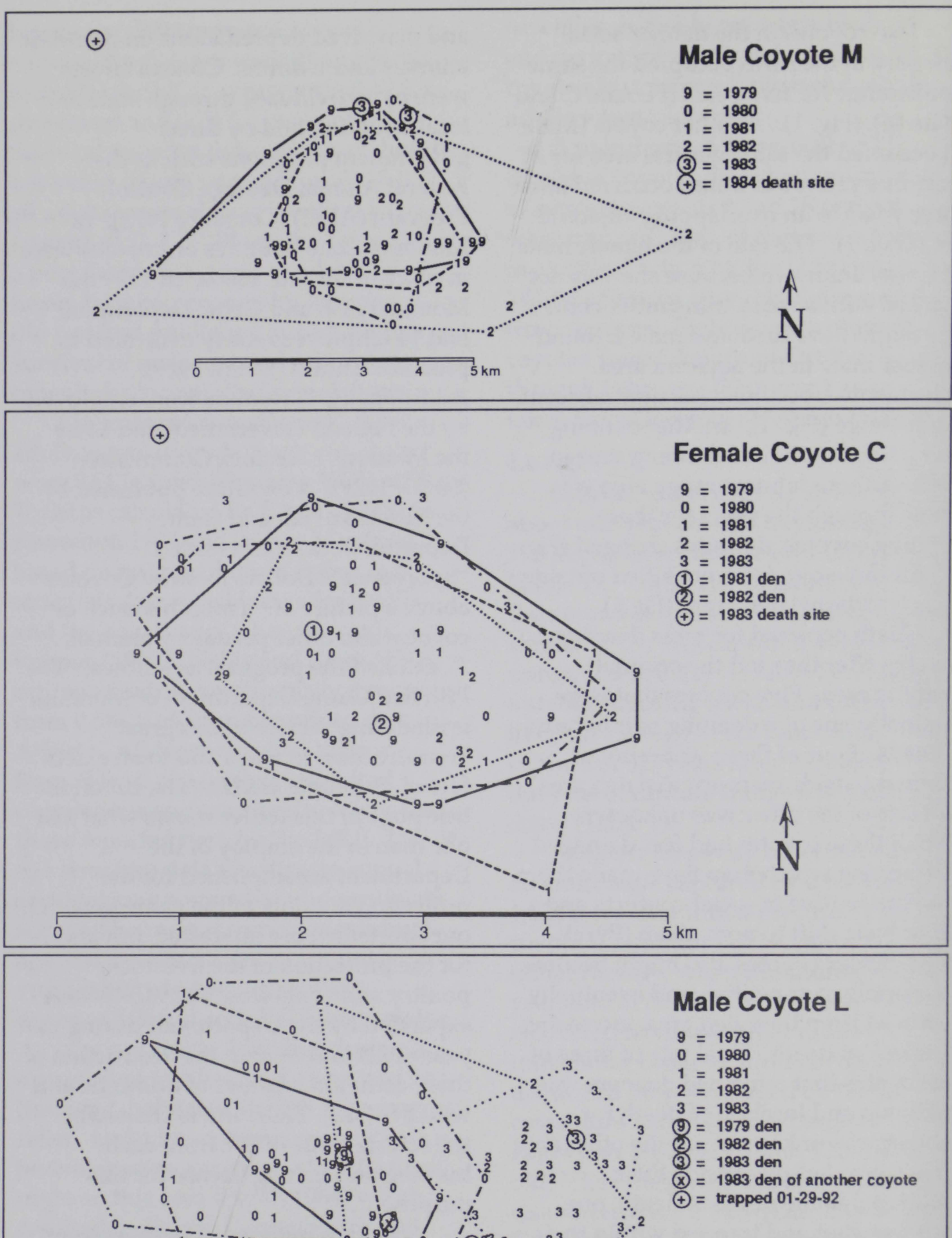

Figure 1. *Annual home range polygons and relocation sites for three coyotes in the Missouri River Breaks, Montana, 1979-1983. Known den sites and death sites included. Letter designations for coyotes are those used by Pyrah (1984).*

Mackie 1989). The use of toxicants for predator control on public lands was banned in 1972 (Connolly 1978) because of increasing public distaste for government killing of predators and the deaths of many nontarget mammals and birds.

There are two general approaches to predator control: 1) overall reduction of numbers on the assumption that depredation losses correlate directly with predator abundance and 2) selective control of the depredating individual or local populations (Connolly 1978). Bounty programs, government hunters, and toxicants are examples of the first approach, and except for the use of toxicants, have generally been unsuccessful. Latham (1951) summarized numerous studies and concluded that the bounty system failed for a variety of social, economic, and ecological reasons. Connolly and Longhurst (1975) concluded that a simulated coyote population could survive an annual control kill of 70 percent. At a 75 percent level of control, the population still persisted for more than 50 years. This model assumed compensatory reproduction, however, and control could be achieved at lower kill levels if compensatory reproduction did not operate or did so at a lower level.

It should be noted that generalized reductions in numbers of coyotes or long-term reduction in numbers is not necessary to reduce some depredations. Reductions in coyote numbers or removal of individual coyotes immediately prior to the time of birth for livestock or game may reduce losses of newborns in small areas (second approach). This approach to concentrate selective control on severe problem areas is currently used by ADC. The goal now is not to control coyote numbers, but to selectively kill depredating individuals or local populations. This approach has evolved because of limited resources, public concerns, the withdrawal of toxicants as a tool, and probably because of some increased ecological knowledge.

Information presented here clearly indicates the ineffectiveness of a general bounty system or other methods of general hunting and trapping to control coyotes, particularly in secure habitats. Average statewide prices of coyote pelts from Montana fur dealer surveys (Giddings 1995) rose from $8.30 in 1971-72 to $37.12 in 1975-76, $54.00 in 1977 and 1978, and $80.95 in 1978-79. Coyote pelt prices remained between $42.53 and $66.22 during 1979-80 through 1987-88. Prices "crashed" in 1988-89 and averaged between $13.00 and $25.00 through 1994. Harvest estimates for coyotes generally coincided with pelt price level (Giddings 1995). Prices for coyote pelts from the study area and vicinity were generally higher than those reported above. Many of these "pale northern pelts" were sent to fur auctions in Canada, and during the peak of prices in 1977-82, prices often averaged over $100.00 per coyote pelt. This price incentive was substantially more than any bounty offered or proposed. The fur price incentive resulted in substantial trapping and hunting from the ground and intensive aerial hunting of coyotes from fixed-wing aircraft and helicopters. Shooting coyotes from the ground was the only legal form of coyote harvest on the CMRNWR, but illegal aerial hunting and illegal trapping occurred there.

Despite intense hunting and trapping, coyote populations on the MRB study area, especially within the timbered breaks habitat increased from 1977 through 1983-84 (Pyrah 1984, Hamlin and Mackie 1989). Survival of coyotes associated with dens in timbered breaks habitat was as high or higher than reported elsewhere, including protected populations on refuges. Fur harvest was limited almost entirely to dispersing juveniles and adult nomad-dispersers. These nomad adult coyotes were often old or injured coyotes, at a disadvantage in social competition or as predators of deer. Fur harvest did not exceed annual recruitment because the coyote population in timbered breaks habitat increased during the period of high pelt prices. Thus, harvest level based on fur price incentives was compensatory to other forms of mortality in timbered breaks habitat during 1977-1984.

Denning pairs and associated den supernumeraries (Pyrah 1984), were the coyotes most likely to effectively prey on deer fawns (Hamlin and Schweitzer 1979) and adults (Knowles 1976) and also were least vulnerable to harvest by fur hunters. Consequently, the coyote harvest that occurred was not likely to be effective in reducing coyote predation on deer in timbered breaks habitat. Predation rate on mule deer fawns was related to level of alternate prey populations but not to size of coyote population (Hamlin et al. 1984, Hamlin and Mackie 1989).

Fur harvest will remove the most easily trapped or shot coyotes with effort appropriate to an economic return. Assuming that toxicants are not a politically viable alternative in coyote control, only intensive hunting and trapping after the period of prime fur associated with intimate knowledge of denning areas are likely to effectively reduce local predation on deer or other game animals. It is unlikely that these conditions could be met except on a limited number of small areas. Targeted control efforts may be successful in some situations of depredations on domestic animals. They are less likely to be successful for widely dispersed wildlife populations. In either case, substantial knowledge about local coyote territories - denning areas and intensive effort beyond that resulting from fur price incentives will be necessary to reduce losses of game animals to coyote predation.

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Literature Cited

Andelt, W.F. 1985. Behavioral ecology of coyotes in south Texas. Wildl. Monogr. 94. 45 pp.

Boggess, E.K. 1975. Some population parameters of Iowa coyotes, and an analysis of reported livestock losses. M.S. Thesis, Iowa State Univ., Ames. 94 pp.

Bowen, W.D. 1982. Home range and spatial organization of coyotes in Jasper National Park, Alberta. J. Wildl. Manage. 46:201-216.

Cain, S.A., J. A. Kadlee, D. L. Allen, R.A. Cooley, M.G. Hornocker, A.S. Leopold and F.H. Wagner. 1972. Predator Control-1971. Rep. To Council Environ. Qual. Dep. Inter., by Advis. Comm. Predator Control. Univ. Of Michigan Press, Ann Arbor. 207 pp.

Camenzind, F.J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pp. 267-294 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y. 384 pp.

Chapman, D.G., and D.S. Robson. 1960. The analysis of a catch curve. Biometrics. 16:354-368.

Connolly, G.E., and W.M. Longhurst. 1975. The effects of control on coyote populations. Univ. California, Davis, Div. Agric. Sci., Bull. 1872. 37 pp.

Connolly, G.E. 1978. Predator Control and Coyote Populations: A Review of Simulation Models. Pp. 327-345 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y. 384 pp.

Eberhardt, L.L. 1969. Population analysis. Pp. 457-495 *in* R.H. Giles, Jr., ed. Wildl. Manage. Tech., The Wildl. Soc., Wash., D.C. 623 pp.

Giddings, B. 1995. Statewide furbearer program annual management and harvest report, 1993-1994, Montana. Montana Dept. Fish, Wildl. and Parks, Helena. 51 pp.

Hamlin, K.L., and L. L. Schweitzer. 1979. Cooperation by coyote pairs attacking mule deer fawns. J. Mammal. 60:849-850.

Hamlin, K.L., S.J. Riley, D. Pyrah, A.R. Dood, and R.J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. J. Wildl. Manage. 48:489-499.

Hamlin, K.L., and R.J. Mackie. 1989. Mule deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. Fed. Aid in Wildl. Restor., Job Compl. Rept., Proj. W-120-R, Montana Dept. Fish, Wildl. and Parks, Helena. 401 pp.

Hamlin, K.L., and G.L. Erickson. 1996. Draft environmental assessment of proposed changes in hunting season structure for mule deer in southwestern Montana. Montana Dept. Fish, Wildl. and Parks, Helena. 124 pp.

Harrison, D.J. 1992. Dispersal characteristics of juvenile coyotes in Maine. J. Wildl. Manage. 56:128-138.

Knowles, C.J. 1976. Observations of coyote predation on mule deer and white-tailed deer in the Missouri River Breaks, 1975-1976. Pp. 117-138 *in* Montana Deer Studies, Job Prog. Rept., P-R Proj. W-120-R7. Montana Fish and Game Dept., Helena. 170 pp.

Knowlton, F.F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. J. Wildl. Manage. 36:369-382.

Latham, R.M. 1951. The ecology and economics of predator management. Final Report, P-R Proj. 36-R. Report II. Penn. Game Comm., Harrisburg. 96 pp.

Linhart, S.B., and F.F. Knowlton. 1967. Determining age of coyotes by tooth cementum layers. J. Wildl. Manage. 31:362-365.

Mackie, R.J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. No. 20. 79 pp.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

Nellis, C.H., and L.B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-68. J. Wildl. Manage. 40:389-399.

Pyrah, D. 1984. Social distribution and population estimates of coyotes in north-central Montana. J. Wildl. Manage. 48:679-690.

Schladweiler, P. 1980. The effects of coyotes on big game populations in Montana. Fed. Aid Job Final Rept., Proj. W-120-R, Montana Dept. Fish, Wildl. and Parks, Helena. 78 pp.

Smith, F.L. 1929. Hunters war on predatory animals. Montana Wildlife. 2(7):9.

Wagner, F.H. 1972. Coyotes and Sheep. 44th Fac. Honor Lect., Utah State Univ., Logan.

Windberg, L.A., H.L. Anderson, and R.M. Engeman. 1985. Survival of coyotes in southern Texas. J. Wildl. Manage. 49:301-307.

Zar, J.H. 1984. Biostatistical analysis, second edition. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.