DEER-PREDATOR RELATIONSHIPS

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Abstract: Deer (*Odocoileus* spp.) populations in the western United States and Canada have declined in many areas in recent years. Causes of the decline have not been identified, but predation by coyotes (*Canis latrans*), mountain lions (*Puma concolor*), and wolves (*Canis lupus*) has been proposed as 1 of many factors. Ballard et al. (2001) reviewed 40 studies involving deer:predator relationships to determine if predation could be implicated in the deer declines. Reviews of the individual studies are provided herein. Ballard et al. (2001) suggested that predation by any of these species could be a significant mortality factor in some cases under certain conditions. A herd's relation to habitat carrying capacity, weather, human-use patterns, number and type of predator species, and habitat alterations all affect predator:prey relationships.

In recent years mule (*Odocoileus hemionus*) and black-tailed (*O. h. columbianus*) deer appear to have declined in many areas of the western United States and Canada, causing concern for population welfare and continued uses of the deer resource. Causes of the decline have not been identified, but predation by coyotes (*Canis latrans*), mountain lions (*Puma concolor*), or wolves (*Canis lupus*) has been proposed as one of many factors. Ballard et al. (2001) assessed results of published studies conducted since the mid-1970s concerning predator:deer relationships to determine if predation could be a factor in the apparent deer population declines, and whether there was evidence that predator control could be a viable management tool to restore deer populations. This paper presents case histories that Ballard et al. (2001) used as the basis for their findings concerning deer:predator relationships.

METHODS

I reviewed studies conducted since the mid-1970s and, where applicable to deer, included some studies summarized by Connolly (1978, 1981). I used selected abstracting services and searched for literature pertaining to deer:predator relationships. I searched all major biological and wildlife journals and reviewed literature citations within articles for additional references. I purposefully excluded predator diet studies because these do not allow assessment of effects of predation on prey populations.

CASE HISTORIES

I review case histories by deer species and location where studies examined the role of predation in limiting or regulating mule or black-tailed deer population growth. Because many such studies were conducted on white-tailed deer (*O. virginianus*) and those could have implications for mule and black-tailed deer management, a number of these studies were included in this review.

Mule deer

Arizona. Smith and LeCount (1979) found strong correlations in Arizona between mid-winter fawn:doe ratios and both winter forb yields and October to April rainfall prior to fawning. However, within a 244-ha predator-free enclosure, the aforementioned correlations were not apparent. The deer population within the enclosure increased rapidly with annual finite rates of increase ranging from 1.0 to 1.6 from 1970-71 through 1975-76. After 1975-76, the herd declined when deer densities reached 18/km^2. The deer population outside the enclosure was thought to be stable with densities ranging from 3-5/km^2 during the study. Fawn/doe ratios during 1970-71 through 1975-76 (prior to decline in enclosure) averaged 80 fawns per 100 does and 50 per 100 does outside the enclosure. Researchers indicated predators were abundant outside the enclosure. Although rainfall had profound effects on fawn:doe ratios, predation also had a large impact. Despite these differences, the deer population outside the enclosure increased when favorable weather conditions returned.

North Kings River, California. Salwasser et al. (1978) examined fawn production and survival in the North Kings River herd during 1971-1975. Similar to other mule deer herds, this herd declined during the 1950s and 1960s.

Fetal rates per adult female were high during 1971-1975 with averages for 2, 3, and 4 year-old and older deer of 1.68, 1.53, and 1.85, respectively. They concluded that initial productivity was not the cause of low fawn recruitment.

By comparing fetal rates with autumn sex-age surveys, they determined most fawn mortality occurred prior to winter, and that only 25-49% of fawns survived. Winter fawn losses reportedly were low. Earlier, Salwasser (1974) determined most fawn losses occurred during and immediately after fawning. The deer herd declined at recruitment rates of 20%, but apparently stabilized with recruitment rates of 23-32%. He speculated a decline in nutritional condition of summer range was the ultimate factor even though coyote predation was probably the proximate agent.

Western Great Basin, California. Bleich and Taylor (1998) investigated survival and cause-specific mortality rates of radio-collared adult deer among 5 populations within the western Great Basin during 1986-1994. The 5 populations were located on winter ranges in eastern California and western Nevada. They monitored 168 adult deer (27 males, 141 females); 13 males and 54 females died. Cause of mortality was determined for 76% (41 of 54) of females and 85% (11 of 13) of males. For females (n = 41), predation, human-induced mortality, and malnutrition accounted for 83.0, 4.8, and 12.2% of mortalities, respectively. Of the 11 males for which cause of death could be determined, 4 were attributed to mountain lion predation and 7 to hunting. There was no evidence of malnutrition among any deer killed by mountain lions or human-induced causes.

Predation by mountain lions accounted for >70% of adult female deer mortality on winter range and proportions of deaths did not differ among the 5 populations. Of 34 female deer killed by predators, mountain lions killed 91%. Overall, the proportion of female deer killed by lions was greater than that of male deer killed by lions.

Bleich and Taylor (1998) indicated that not enough was known about influences of predation, nutrition, and climate to factor out relative roles of these variables. However, they suggested that because few animals died of starvation, mountain lion predation did not appear to be a compensatory form of mortality in these 5 deer populations. They speculated that mountain lion predation may regulate deer numbers in similar ecosystems where droughts and severe winters occur unpredictably.

Colorado, Idaho, and Montana. Unsworth et al. (1999) examined survival rates of radiocollared mule deer fawns and adult females over a large geographic area to describe the influence of survival rates on deer population dynamics. Survival estimates were based on 1,875 radiocollared fawns captured in late autumn to early winter, and on 1,536 radiocollared adult females.

Over-winter fawn survival rates did not vary among states, but did vary among years (Unsworth et al. 1999). Female fawns exhibited higher average survival rates than male fawns. Adult female survival rates did not differ among states or years. Their results suggested that survival rate estimates for fawns and adults were common to mountain environments of the 3 states. Heavier fawns had higher survival rates than fawns that weighed less. Fawn weights varied among states and years, and reflected variations in summer condition and possibly lag effects from the previous winter. They suggested increased fawn weights prior to winter may increase fawn survival.

Causes of mortality differed by state, but there were large annual differences within each state. Predation was responsible for 0-83% of all mortalities across all years in Colorado, 3-100% in Idaho, and 62-86% in Montana. Winter starvation varied among states and years, and ranged from 0 to 82% of total mortality.

Fawn and adult female survival rates across all states and years averaged 0.444 and 0.853, respectively. Through modeling, they estimated 66 fawns per 100 does in early winter were necessary to maintain deer populations. Because fawn:doe ratios had been below this value, they suggested the proximate factor responsible for the deer population decline was low December fawn:doe ratios, or ultimately, low recruitment to the yearling age class. Causes of fawn mortality for fawns <6 months of age were not reported.

Piceance Basin, Colorado. Bartmann et al. (1992) conducted an in-depth analysis of the role of compensatory mortality in population dynamics of mule deer within 2 areas of the Piceance Basin, Colorado during 1981 through 1988. By using treated and untreated areas, they determined that when deer populations were at habitat carrying capacity, predation by coyotes was compensatory to starvation mortality. Deer densities ranged from 61 to 80 deer per km^2. Coyote densities were not estimated as they only were concerned with reducing coyote predation rates. They reported December fawn:doe ratios were relatively high with low variance, and suggested magnitude of density-dependent mortality effects were greatest for overwinter fawn mortality. They also suggested that density-dependent mortality often goes undetected in many mule deer populations because of highly variable environments (e.g., severe winters) that would mask such effects and make testing difficult. They concluded that, in established mule deer populations where abiotic factors such as severe winters do not overshadow biotic factors, high overwinter fawn mortality should be viewed as a symptom of density-dependent population regulation.

Montana. Mackie et al. (1998) summarized research that was conducted in Montana on both mule and white-tailed deer since 1975, while Hamlin and Mackie (1989) summarized mule deer research in the Missouri River Breaks area over a 27-year period. Reproductive rates of adult female mule deer were relatively high throughout Montana and ranged from 1.25 to 1.76 fawns per doe, whereas rates for white-tailed deer ranged from 1.5 to 2.0 fetuses per adult doe. However, there were significant differences by age class; fawns of either deer species rarely produced young. Recruitment rates for mule deer were lower and more variable than those for white-tailed deer.

Mackie et al. (1998) indicated fawn mortality in both deer species was relatively high (i.e., ≥75% annually). Approximately 66% of mule deer fawn mortality occurred during summer and about 25% during winter, but there was wide variation among years, particularly during winter (Hamlin and Mackie 1989). Similarly, approximately 66% of white-tailed deer fawn mortality occurred during summer, but winter mortality was only 3 to 10% annually.

Mackie et al. (1998) indicated there was no consistent factor affecting fawn mortality. In the Missouri River Breaks, productivity and survival of mule deer fawns was correlated with summer forage production and condition, but fawn recruitment appeared to be related to forage quality and the length of time that green, succulent forage was available. They found no evidence of a compensatory relationship between forage supply and fawn mortality. During 1975-1987 coyotes accounted for 88% of deaths of radiocollared fawns. During winters of 1976 through 1986, coyote predation accounted for 95% of fawn mortality, but they indicated other factors were involved that predisposed some fawns to predation. There was no correlation between fawn mortality and coyote density, and they indicated other factors such as availability of alternate prey, habitat and forage conditions, and winter severity influenced coyote predation rates. In comparison, numbers of adult female white-tailed deer during spring were correlated with number of fawns recruited the following spring. They suggested fawn limitation was behavioral and involved resource partitioning during summer rather than amount of available forage.

Mackie et al. (1998) suggested winter mule deer fawn mortality was related to a number of factors including fawn condition prior to and during winter. Winter severity did not always predict fawn mortality and other interactions were involved. They suggested summer forage condition prior to winter was an important factor.

Hunting was the largest cause of adult female mule deer mortality; mortality from natural causes ranged from 0 to 25%. They suggested human harvest and other forms of mortality were not compensatory and these causes varied independently of deer density (Mackie et al. 1998:106). Although coyote predation on adults was low, it was the largest cause of natural mortality and second highest cause of mortality behind hunting mortality. Coyote predation on adult mule deer was highest during winter and spring and included adults in poor as well as good condition. Natural mortality rates in adult female white-tailed deer were <16% annually.

Hamlin and Mackie (1989) and Mackie et al. (1998) suggested there was a potential for predation to influence deer population trends in mountainous areas of Montana and that combined effects of multiple predator species could exert greater and more consistent predation pressure than that exerted by single predator systems. Hamlin and Mackie (1989) indicated predation, combined with even low-moderate levels of other mortality could be sufficient to further reduce low density deer populations, or at least keep them from increasing.

North-central Montana. Hamlin et al. (1984) reported coyote populations increased in north-central Montana following a ban on use of compound 1080 in 1972 and deer populations declined. Consequently, they studied timing, extent, and causes of mule deer fawn mortality from summer to early winter during 1976-1981.

Initial fawn production based on fawn-at-heel counts was high, ranging from 1.50 to 1.76 fawns per doe. Deer densities apparently were well below habitat carrying capacity as the deer population was 40 to 45% of previous highs (Mackie et al. 1982:872). Changes in age ratios indicated annual summer fawn mortality rates ranged from 4 to 56%, and averaged 32%. Mortality rates appeared higher during late- rather than early-summer. Summer mortality rates decreased during 1976-1979 and then increased through 1981. Twenty of 91 (22%) radiocollared fawns died during summer, and predation by coyotes ($n = 18$, 90%) was the largest cause of death. They reported high mortality rates of fawns during the first few weeks of life and again at 45 to 105 days of age. In addition, 2 of 4 and 8 of 8 fawns were killed by coyotes during autumn and winter, respectively. The deer population increased after 1977 and deer density apparently had doubled by 1980 (Mackie et al. 1982:872).

Hamlin et al. (1984) also reported a correlation between vegetation production and fawn mortality. However, they indicated the relationship may not have reflected effects of increased vegetation and hiding cover on fawn survival, but rather increased microtine populations that buffered effects of coyote predation on fawn survival. Fawn mortality was lowest when microtine populations were high. Further, coyote scat analyses indicated fawns were not an important component of coyote diets during that time. They concluded coyote predation could reduce fawn survival in nutritionally healthy deer populations. However summer fawn survival increased to 96% without coyote removal, apparently in response to a natural decline in coyote numbers and because alternate prey populations had as much to do with coyote predation rates as did coyote numbers.

New Mexico. Temple (1982) summarized deer mortality research in New

Mexico conducted during 1976 through 1981. On the Fort Bayard study area, 29 of 61 (48%) (note these mortality estimates are not annual rates) radiocollared adult deer died during 1976-1981, and 55% of mortality was due to predation. Deaths were attributed to coyotes (37.5%), mountain lions (25%), dogs (12.5%), unknown predators (12.5%), felids (6.3%) and unknown canids (6.3%). Of 40 neonate fawns that were radiocollared, 72% died within an average of 25 days following birth. Predation accounted for 90% of mortalities. Causes of death were attributed to coyotes (35%), unknown canids (31%), unknown predators (23%), mountain lions (8%), and bears (4%).

Twenty-two adults and 111 newborn fawns were radiocollared in the Bosque del Apache study area during 1979-1982. Thirty-six percent of adults died and 50% of mortality was attributed to coyotes. Seventy-six percent of neonate fawns died and 51% of mortalities were attributed to predation from the following causes: coyotes (49%), bobcats (26%), unknown predators (21%), and mountain lions (2%). Sixty-seven percent of fawns died within 3 weeks of birth.

Southern New Mexico. Logan et al. (1996) studied effects of precipitation and mountain lion control on desert mule deer in the San Andres Mountains, New Mexico during 1985 through 1995. Mountain lion densities during the pre-treatment period (1987-1990) increased from 1.17 to 2.01 lions/yr/100 km^2. The lion population was reduced by 53% within a 703-km^2 treatment area during December 1990 to June 1991. During the post-control period (1991-1994) lion densities increased from 1.09 to 1.87/yr/100 km^2. Mule deer comprised 91% of the lion prey carcasses and fawns comprised 27% of the dead deer. However, these figures do not represent diet composition because many small prey carcasses (including deer and other prey species) were probably not found. Fawn:doe ratios declined during both the pre-treatment (52 to 36 fawns/100 does) and post-treatment periods (41 to 7 fawns/100 does).

Adult survival and cause-specific mortality rates for 175 radiocollared deer were compared pre- and post-lion control. Pre-control survival rates for bucks and does combined averaged 0.59 while post-control rates averaged 0.25. Buck and doe survival rates were not different during the pre-control period, but buck survival rates were lower during the post-control period. Cause-specific mortality rates from mountain lion predation averaged 0.22 and 0.59 for pre- and post-control periods, respectively. Differences were attributed to severe drought conditions during 1992-1995. The authors speculated the deer population had increased or was stable during the pre-control period because the deer population was below K. However, during the drought the deer population exceeded habitat carrying capacity, fawn production declined drastically, and deer were more vulnerable to predation by mountain lions. They concluded that during drought, mountain lion predation was a major proximate source of mortality, and that habitat quality and quantity were the ultimate limiting factors. However, neither habitat quality nor quantity was measured and such relationships were assumed because of drought.

Oregon. Trainer et al. (1981) conducted 1 of the more comprehensive fawn mortality studies in southeastern Oregon during 1968 through 1979. They reported an adult female deer pregnancy rate of 93% and an *in utero* fetal rate of 1.62 fawns per doe. However, survival of fawns through their first 9 months of life was low. They estimated mortality rates by 2 methods; they compared fawn:doe ratios among seasons and they radiocollared neonate fawns. Based upon fawn counts, most fawn mortality occurred from November through March. Fawn mortality rates during each season were estimated at 32, 39, and 43% for summer, autumn, and winter, respectively. Average annual fawn mortality rate over a 10-year period ranged from 69 to 72%. Mortality estimates based on radiocollared fawns were similar to those based on fawn counts.

A total of 163 radiocollared fawn mortalities were examined during 1971-72 through 1978-79. In decreasing order of importance, cause of death was coyote predation (49%), bobcat predation (11%), disease (7%), starvation (5%), accidents (4%), and golden eagle (*Aquila chrysaetos*) predation (1%); cause of death was undetermined for 24% of mortalities. Fawn losses due to bobcat predation were greatest during summer and autumn, whereas greatest losses due to coyotes occurred during autumn and winter. Neonatal fawn weights and weight gains indicated fawn health was normal and fawns were not predisposed to predation. The authors found no correlation between precipitation and mid-winter fawn:doe counts, nor did they find relationships between indices of weather stress and fawn losses during winter.

As a result of the above findings, Trainer et al. (1981) reduced coyote populations by helicopter gunning and compared subsequent fawn survival rates between a treated and untreated area during 1976 through 1979. During this time period, 536 coyotes were removed by helicopter gunning from the treated area (194 km^2), while an unknown number of coyotes were removed from the untreated area through public hunting and trapping. Unfortunately, there were no estimates of coyote density prior to coyote removal in either study area, but removal rates in subsequent years indicated coyote numbers were significantly reduced. Perhaps most importantly, they detected no changes in coyote age structure or reproductive rates after predator control ceased.

Fawn mortality rates were significantly reduced on the coyote treatment area after coyote removal, but no differences were detected on the untreated area. Winter fawn mortality rates in the treatment area prior to treatment averaged 51%, but fawn mortality rates decreased to 35% after coyote reductions while fawn mortality rates in the untreated area were similar before (49%) and after (48%) coyote removal. Mean fawn losses were less on the treatment area than on the untreated area, but differences were not statistically different. However, they indicated that data from all sources suggested increased fawn survival in the treated area. Causes and timing of fawn mortalities remained the same before and after coyote removal. Adult deer natural mortality remained similar at about 7% annually. There were no measurable increases in total deer numbers as a result of treatment efforts. They estimated fawn recruitment at least during the first winter was increased by 118 fawns annually within their 194 km^2 study area. Deer densities within the treated and untreated areas were estimated at 11.6 and 15.2/km^2, respectively.

Pecos County, Texas. Dickinson et al. (1980) studied causes of neonatal mule deer mortality during 1977. Deer densities had increased from 22 to 41/km^2 and were thought to be stable during the study. They indicated the deer population was at or above habitat carrying capacity during the study. *In-utero* fawn:doe (yearling and adults) ratios were estimated at 1.0/doe, but by February ratios of fawns per adult doe had declined to 0.7. Nine of 12 radiocollared fawns died, with 5 of 9 dying during the first 50 days of life. Coyotes killed 3, undetermined predators killed 2, 1 died from starvation or disease, and an unidentified factor was responsible for 3 deaths.

Utah. Austin et al. (1977) conducted 1 of the first studies that utilized a treatment and an untreated area to examine effects of coyote removal on mule deer survival on winter range. They indicated both study herds were well below habitat carrying capacity; 19 deer/km^2 on the treatment area and 6 deer/km^2 on the untreated area. Both areas actually received coyote control, but intensity of control differed; 80 coyotes were removed from the treatment area and 45 from the untreated area during winters 1973 through 1976. They concluded a significantly higher proportion of fawns entering winter survived in the treated area with heavier coyote removal than in the untreated area. Management implications were not discussed.

Washington. Steigers and Flinders (1980) studied causes of fawn mortality with radiotelemetry in south-central Washington during 1977. Coyotes were the only large predator in the area; late summer coyote density was estimated at 0.26/km^2, while deer density was estimated at 1.7/km^2. They considered the deer population to be at or above habitat carrying capacity and they believed habitat conditions were stable at low levels. Fourteen of 26 fawns (54%) died of natural causes during the first 7 months of life; coyotes killed 10, 3 drowned, and 1 died from circulatory collapse. Average age at death was 45.5 $\pm$ 43.8 days (range = 12-139 days); 7 died during the first month, 5 during the second month, and 2 during the fifth month. They speculated that, in their study area, coyote predation was a compensatory form of mortality because the deer population was at or above habitat carrying capacity. In their case, reduction of coyotes would produce no benefits for deer.

Black-tailed deer

Southeast Alaska. Klein (1995) summarized results of introducing wolves to a small island (73.3 km^2) in southeast Alaska that previously had not been occupied by wolves, but which supported a high density (5.8-7.8 deer/km^2) deer population. Prior to wolf introduction, deer forage species were over-utilized. Following release, the wolf population quickly increased, the deer population declined to very low levels, and deer forage species recovered from over-use. Wolves killed healthy deer as indicated by bone marrow fat. Wolves finally declined from starvation and the deer population recovered. Klein (1995) concluded wolves had the potential to suppress deer numbers below habitat carrying capacity in maritime areas.

Vancouver Island, British Columbia.

McNay and Voller (1995) studied survival and causes of mortality of 105 radiocollared adult female black-tailed deer among 4 study areas on Vancouver Island, British Columbia during 1982 through 1991. Wolf removal was occurring in all study areas to some degree, and all areas were open to mountain lion hunting and buck-only deer hunting. They recorded 54 deer mortalities: mountain lion (*n* = 18, 33%), wolf (*n* = 15, 28%), human-caused (*n* = 9, 17%), unknown (*n* = 6, 11%), malnutrition (*n* = 3, 6%), and accident (*n* = 3, 6%). Most (64%) mortalities occurred from April through June, and during November. Mortality rates were lowest during summer. Mountain lion predation varied by study area, but mortality from wolves was similar among study areas.

Annual survival rates for migratory deer (90%) were higher than those for resident deer (77%); apparently most migratory deer left low elevation winter ranges as soon as possible, thereby reducing risk of predation. Implications of their findings in relation to forest harvest practices suggested retention of old-growth winter habitats was vital to rebuilding deer herds.

Hatter (1988) studied timing and causes of fawn mortality during 1980-1982, and tested the hypothesis that wolf predation was the primary factor limiting fawn recruitment. Adult fetal rates were high (1.63-1.67 fetuses/doe), but by August, fawn:doe ratios declined to about 0.45, suggesting mortality rates of 61 to 79%.

Twenty-eight neonate fawns were radiocollared, of which 14 died: 8 from wolf predation, 1 from black bear predation, 2 from accidents, 1 from disease, 1 from malnutrition, and 1 from hunting. No mortalities were attributed to predation by mountain lions. Sixty-three percent of all mortalities occurred by the end of August with most mortalities occurring during June and July. Hatter (1988) concluded wolf predation was the primary factor limiting deer recruitment on northern Vancouver Island, and proposed reductions in wolf numbers to improve recruitment.

Atkinson and Janz (1994) examined effects of wolf removal on deer fawn recruitment by comparing fawns/doe in a treated area where wolf densities were reduced by an average of 59% annually with an untreated area where wolves were not purposefully reduced, but were subject to public hunting and trapping. The deer population was reportedly well below habitat carrying capacity.

Reduced wolf densities yielded increased fawn survival through the first 3 months of life, from 0.16 fawns/doe prior to removal to 0.72 fawns/doe by 1985. Recruitment increased from 3.9% in 1983 to 24.8% in 1986. Fawn:doe ratios declined by 43% following cessation of wolf control. The situation reversed in 1987 when wolf control was halted in the treatment area and initiated in the non-treatment area. They concluded that wolf removal increased fawn survival and recruitment to levels higher than those found elsewhere on Vancouver Island where wolf densities were not lowered.

White-tailed deer

Oklahoma. Stout (1982) indicated effects of coyote predation were site-specific. He reduced coyote densities and studied effects of the reduction on white-tailed deer fawn mortality during 1977-1980 based upon studies by Garner (1976), Garner et al. (1976), and Bartush (1978), which indicated 88-90% of neonate fawns died and 88-97% of mortalities were caused by coyotes.

Initial deer conception rates appeared high, ranging from 1.6 to 2.1 corpora lutea per adult doe, but fawn losses from birth to November were high. To test the hypothesis that reductions in coyote numbers could increase fawn survival, coyotes were killed by trapping and aerial shooting from helicopters in 3 areas during mid-winter to mid-spring prior to parturition by deer. Fawn:doe ratios were then compared between pre- and post-coyote removal.

Coyote densities apparently were significantly reduced, but pre- and post-removal coyote densities were not reported. Fawn recruitment from birth to mid-August through mid-September during the first year of coyote removal increased by 262, 92, and 167% on the 3 areas, respectively. Untreated study areas exhibited no increases in fawn recruitment. Fawn recruitment was significantly higher in treated areas after coyote removal than before coyote removal. Prior to coyote removal in 1976, fawn:doe ratios averaged 0.37, but after coyote removal they averaged 0.94.

Fawn mortality was greatest during the first 4-8 weeks of life and coyote removal reduced this mortality. Stout (1982) indicated coyote removal during late-winter and early-spring was effective for reducing fawn mortality. However, he indicated disease in young does may partially offset increases in fawn survival. He concluded coyote removal had markedly increased fawn survival, but effects of the increase on herd dynamics was not understood due to interactions that were difficult to identify and study.

Minnesota. Kunkel and Mech (1994) studied timing and causes of white-tailed deer fawn mortality within Superior National Forest from May through October during 1989 and 1990. Nine of 21 neonate fawns died, and 7 deaths occurred before 28 June. All deaths were due to predation: 5 from wolves and 4 from black bears. They found fawns from does which were >4 years of age were heavier and had better survival rates than fawns from younger mothers.

Nelson and Mech (1986*a*) reported survival and cause-specific mortality rates for 209 white-tailed deer from 1973 through winter 1983-84, also in Superior National Forest. Annual survival was 0.31 for fawns, 0.80 for yearling females, 0.41 for yearling males, 0.79 for adult females, and 0.47 for adult males. Of 85 deaths, 44 were attributed to wolf predation, 22 to hunting, 12 to probable wolf kills, and the remaining 7 to miscellaneous causes. Only 1 deer starved and Mech and Karns (1977) indicated this deer population was well below levels imposed by habitat and winter weather alone. Most mortality in all age cohorts occurred during January through April and was due to wolf predation. Although few fawns died of malnutrition, Mech and Karns (1977) suspected fawns were predisposed to death because they were in poorer condition at the time of capture than were surviving fawns. However, these authors indicated fate of fawns in the absence of wolf predation was debatable. Highest wolf kill rates occurred during winters of deep snow (Nelson and Mech 1986*b*). They indicated wolf predation was limiting yearling recruitment into the deer population.

Montana. Dusek et al. (1992) determined survival and cause-specific mortality rates for 154 adult female radiocollared deer in 3 habitats during 1980-1989. Hunting was the largest cause of mortality in all areas. Of 99 deaths, only 8 (8%) were attributed to natural causes. They concluded harvest regulations had little effect on natural mortality rates and therefore, hunting was an additive form of mortality in their study areas. If compensatory mortality existed in these populations, they suggested it would probably occur in juvenile age classes.

New Brunswick. Ballard et al. (1999) and Whitlaw et al. (1998) reported survival and cause-specific mortality rates of radiocollared fawn and adult white-tailed deer, respectively, during 1994-1997. Fawn survival was lowest during summer (0.47), increased during autumn (0.86) and early winter (0.95), and then declined during late winter (0.76) and spring (0.81). Predation by coyotes was the largest source of annual cause-specific mortality (0.37), followed by black bear predation (0.14), predation by domestic dogs (0.08), unknown causes (0.07), predation by bobcats (0.06), and other causes (0.04).

Predation by coyotes was also the largest natural mortality factor among adult deer, with most mortality occurring during winter (Whitlaw et al. 1998). These authors indicated eastern coyotes appeared to have replaced wolves as major predators of deer in northeast North America where wolves were extirpated. They suggested predator management along with continued provision of adequate winter habitats, and mild winters, would be necessary to maintain and increase that deer population.

King Ranch, Texas. Beasom (1974*a*) conducted 1 of the first predator removal experiments on white-tailed deer by contrasting fawn:doe ratios and deer densities between a 2,186-ha treated and a 2,186-ha untreated area. Deer densities within the area were estimated at 7.4 to 14.7/km^2 and apparently the deer population was below habitat carrying capacity because deer appeared to be almost unanimously in good condition (Beasom 1974*a*). Autumn coyote densities were estimated at 1.5 to 2.3/km^2 (Knowlton 1972) and bobcats were thought to be common (Beasom 1974*a*).

Predator numbers were reduced in the treated area from February through June in 1971 and 1972 with the use of steel traps, M-44s, strychnine-treated meat and egg baits, and shooting (Beasom 1974*a*). A total of 129 coyotes and 66 bobcats were removed during 1971 and 59 coyotes and 54 bobcats were removed during 1972. Predator track counts indicated predator densities were similar between treated and untreated areas prior to predator reductions, but after predator removal, track counts suggested near elimination of predators in the treatment area. When the experiment ended, predator numbers rebounded to pre-removal levels within 6 months.

August deer fawn:doe ratios in the treatment area were 0.47 and 0.82 in 1971 and 1972, respectively, while in the untreated area, fawn:doe ratios averaged 0.12 and 0.32 in 1971 and 1972, respectively. Fawn mortality was 74 and 61% higher in the untreated area during 1971 and 1972, respectively. Deer density within the treatment area increased from 15.6 to 19.6/km^2 while those in the untreated area declined from 8.0 to 7.8/km^2 between 1971 and 1972, respectively.

Beasom (1974*a*) indicated fawn:doe ratio data suggested there may have been an influence of predator removal out to 23 km, but data were highly variable. There were clearly higher ratios out to 3.2 km from the treatment area. It should also be noted that poisons were used. Beasom (1974*a*) concluded there was potential for producing many more deer on a sustained yield basis through use of predator removal, but there would have to be adequate hunter harvests to prevent overabundance. Another experimental removal of predators was conducted in south Texas with similar results (Guthery and Beasom 1977). Beasom (1974*b*) and Guthery and Beasom (1977) also monitored effects of predator removal on small mammal and lagomorph populations and found no effect.

South Texas. Heffelfinger et al. (1990) tested the hypothesis that adult male (>4 year of age) mortality would be lower following coyote treatment than without coyote treatment. The hypothesis was based on the observation that adult male white-tailed deer suffered high rates of natural mortality (20-23%; DeYoung 1989) during the post-rut period. During January 1987 through June 1989, 97 radiocollared male deer were monitored. During this time period, only 8 males died; all were either killed or scavenged by coyotes. Natural mortality rates between coyote removal areas (9.3%) and non-removal areas (11.9%) were not different. Neither coyote nor deer densities before or after coyote treatment were reported, but scent-station surveys indicated coyote populations were reduced by 81% (Heffelfinger 1989). He indicated the coyote treatment did not increase numbers of bucks available for harvest. More intensive coyote treatment may have produced a different result, but such treatment would be impractical given methods they had available at that time (e.g., traps, M-44s, hunting, incidental shooting, and aerial gunning). A total of $28,000 was spent controlling coyotes, yet no positive results were documented in terms of increased bucks available for harvest, total numbers of deer, or numbers of mature bucks (Heffelfinger 1989:85).

South-central Texas. Carroll and Brown (1977) studied causes and timing of neonate fawn mortality in 2 counties of south-central Texas for 2-month periods during 1971 through 1973. Deer densities were 41.1/km^2 and 9.9/km^2 in the Lavaca and Gonzales county study areas, respectively. Natality rates were estimated to be 1.50/doe. Sixty fawns were radiocollared in each study area over the 3-year period. In the Lavaca study area, 37% of fawns died, and 45% of mortalities were attributed to coyote predation. In the Gonzales study area, 45% of fawns died, with coyotes and bobcats being responsible for 55 and 11% of mortalities, respectively. They indicated there were substantial differences between study areas. In the Gonzales area, 50% of adult deer died in 1970 due to starvation from drought conditions. Consequently, they attributed the 90% loss of fawns in 1971 to lack of ground cover and poor nutrition (presumably deer were above K at that point). They indicated wetter conditions in 1972 and 1973 resulted in improved fawn survival (65 and 90%, respectively). Fawn-at-heel counts indicated there were few fawn mortalities after August. They concluded these high density deer populations seemed to sustain moderate fawn mortality.

Welder Wildlife Refuge, Texas. Teer

et al. (1991) summarized studies of white-tailed deer on Welder Wildlife Refuge (WWR) from 1954 through 1990. First, Knowlton (1976) found fawn survival to weaning appeared related to precipitation during gestation. Kie and White (1985) found no relationship between conception rates and deer densities of 20 to 60 per km^2, but they did find lower conception rates when deer densities peaked at $84/km^2$. Teer et al. (1991) indicated deer densities appeared to stabilize at about 34.2 ± 10 deer per km^2 from 1962 through 1990.

Coyote densities in and near WWR have varied over the years from 0.2 to a high of $2.3/km^2$ in favorable habitat. Coyote diets varied by year, with a pronounced shift to deer fawns during fawning season. As fruits became abundant, coyote diets shifted to fruit. Deer also became an important coyote food item during late winter and early spring.

Cook et al. (1971) were the first biologists to study causes of fawn mortality with the aid of radiotelemetry. Seventy-two percent (58 of 81) of radiocollared fawns died within 60 days of birth; 93% of those died during the first month of life. Predation accounted for 83% of losses. Seventeen percent died as a result of starvation, disease, or accidents.

Following the studies of Cook et al. (1971), a predator-proof exclosure encompassing 391 ha was constructed. Coyote populations were reduced and fawn survival immediately increased by 30% over areas outside the enclosure (Teer et al. 1991). Deer increased until food became the limiting factor, and then deer densities declined. Increased deer densities were accompanied by increased parasite loads.

Teer et al. (1991) indicated the largest changes in deer numbers on WWR occurred during drought years. They speculated increased ground cover during wet years was responsible for reduced fawn mortality. They indicated their studies fell short of demonstrating that coyotes had controlled deer numbers since 1954, but that coyote control could be used to manage deer numbers. Teer et al. (1991:559) concluded: Control of coyotes need not be a management strategy when numbers are not cropped by hunting or natural means. Conversely, control of coyotes can be a management strategy when there is adequate habitat and deer numbers need to be increased for greater productivity.

Midwest United States. Several studies of neonatal white-tailed deer have been conducted in mixed agricultural and forested habitats in the East and Midwest. Huegel et al. (1985) indicated fawn mortality in these areas was relatively low in comparison to semiarid areas of the Southwest. For example, McGinnes and Downing (1969) indicated 8% fawn mortality in a Virginia enclosure, while Ozoga et al. (1982) reported mortality rates of 2 to 23% in a Michigan enclosure. Schultz (1982) reported 15% fawn mortality rate in Minnesota and Huegel et al. (1985) reported a 27% mortality rate in Iowa. Huegel et al. (1985) suggested better growing conditions in the Midwest provided better fawning habitat, which made fawns less susceptible to predation.

CONCLUSIONS

Ballard et al. (2001) indicated that study results were confounded by a number of factors. A deer population′s relationship to forage carrying capacity was crucial to the impacts of predation. Deer populations at or near carrying capacity did not respond to predator removal experiments. When deer populations appeared limited by predation and such populations were well below forage carrying capacity, deer mortality was significantly reduced when predator populations were reduced. Only 1 case, however, demonstrated that deer population increases resulted in larger harvests although there were considerable data that indicated that wolf control resulted in larger harvests of moose (*Alces alces*) and caribou (*Rangifer tarandus*). The most convincing evidence for deer population increases occurs when relatively small enclosures (2-39 km^2) were used as part of the experiment (Ballard et al. 2001).

Available studies suggest predation by coyotes, mountain lions, or wolves may be a significant mortality factor in some areas under certain conditions (Ballard et al. 2001). Relation to forage carrying capacity, weather, human-use patterns, number and type of predator species, and habitat alterations all affect predator:prey relationships. Only through intensive radiotelemetry and manipulative studies can predation be identified as a major limiting factor. When identified, deer managers face crucial decisions.

Reductions in predator densities have only occurred on relatively small study areas (2-180 km^2) where predators were identified as a major limiting factor and deer populations were well below forage carrying capacity (an important criterion). Thus a problem of scale, methods used to kill predators, and benefit:cost ratios in terms of dollars spent, results to hunters, and public acceptance are primary considerations (Ballard et al. 2001). Methods of predator control available to deer managers have been severely restricted and current methods may not be feasible over large areas when and if predation becomes a problem. Public acceptance of predator reduction programs is essential for predator:prey management, but may not be achievable given current public attitudes towards predators. Ballard et al. (2001) identified several recommendations and research needs based on their review of the literature given current social and political limitations.

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