Survivorship and cause-specific mortality in five populations of mule deer

Vernon C. Bleich
California Department of Fish and Game and University of Alaska, Fairbanks

Timothy J. Taylor
June Lake, California

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SURVIVORSHIP AND CAUSE-SPECIFIC MORTALITY IN FIVE POPULATIONS OF MULE DEER

Vernon C. Bleich and Timothy J. Taylor

ABSTRACT.—We used retrospective analyses to investigate cause-specific mortality and survivorship among 5 populations of mule deer (N = 168 telemetered animals) wintering in the western Great Basin during 1986–1994. These populations existed under similar environmental conditions, but survivorship functions differed among them. Monthly survival ranged from 0.964 to 0.990, and annual survival ranged from 0.643 to 0.884. The proportion of deaths attributed to predation and malnutrition or anthropogenic causes did not differ among the 5 populations. Predation was the leading cause of mortality; mountain lions were responsible for approximately 90% of the deer killed by predators. No difference existed among these populations in the proportion of telemetered deer that were killed by mountain lions, but proportionally more females than males were killed by these large felids. Predation by mountain lions is the primary source of mortality and a widespread phenomenon among the populations of mule deer we investigated.

Key words: California, Felis concolor, Odocoileus hemionus, mule deer, mortality, mountain lion, predation, survivorship.

Populations of mule deer (Odocoileus hemionus) have been declining in western North America for many years (Workman and Low 1976), and effects of nutrients, competition, predation, and climate on these populations have been debated among numerous investigators. Mule deer are thought to be density dependent in their response to resource availability (McCullough 1990). In unpredictable environments (typical of much of the Great Basin), however, it may be difficult to base management recommendations on density-dependent responses anticipated to follow population declines (Mackie et al. 1990). Whatever factors, singularly or in combination, regulate mule deer populations remain open to discussion. Indeed, there is general agreement that no single cause can be invoked. Detailed and specific investigations are necessary to evaluate factors that may regulate populations of these important game animals (Hornocker 1976, Knowlton 1976, Connolly 1981).

Recently, Wertz (1996) expressed concern about the dynamics of several mule deer populations wintering in the western Great Basin. Highway mortality has been a basis for this concern, as have the effects of predation and disease. Persistent drought has lowered the carrying capacity of deer winter ranges in this general area, with resultant negative influences on the physical condition of these large herbivores (Kucera 1988, Taylor 1996). Moreover, the harsh winter of 1992–93 killed many deer, particularly in northeastern California and northwestern Nevada (Wertz 1996).

To better understand factors affecting deer populations in the western Great Basin, we investigated seasonal distribution, habitat selection, cause-specific mortality, and survivorship in 5 populations of mule deer wintering in eastern California and western Nevada. In this paper we use retrospective analyses based on telemetered animals (White and Garrot 1990) to compare cause-specific mortality among 5 mule deer populations that winter in the western Great Basin. Additionally, we describe and compare survivorship functions for female deer in these populations.

DESCRIPTION OF THE STUDY AREA

Our study area is located in Mono and Inyo counties, California, and Douglas County, Nevada (Fig. 1). Deer from the West Walker, East Walker, Mono Lake, and Casa Diablo winter ranges are migratory and display annual patterns of movement and range use. In spring they make long-distance movements, sometimes >60 km, and spend summers on both the east and west slopes of the Sierra Nevada.
Fig. 1. Location of 5 winter ranges in northeastern California and western Nevada. Mule deer concentrate on these areas from approximately 1 November to 15 May each year.

(Taylor 1988, 1991). During autumn deer from these populations return to discrete winter ranges on the western edge of the Great Basin, where they remain from about 1 November to 15 May (Taylor 1988, 1991). Deer inhabiting the Inyo Mountains undergo altitudinal migrations similar to those described by Nicholson et al. (1997), but generally do not exhibit the extensive movements made by deer from the other 4 populations. Currently, 4 of the populations (West Walker, East Walker, Mono Lake, Casa Diablo) are classified as Rocky Mountain mule deer (O. h. hemionus); deer occupying the Inyo Mountains are classified as Inyo mule deer (O. h. inyoensis), a taxon of questionable validity (Wallmo 1981, Cronin and Bleich 1995).

During winter all 5 populations of deer occur largely in sagebrush (Artemisia tridentata) steppe or pinyon pine (Pinus monophylla) habitat, ranging in elevation from 1500 m to 2300 m (Taylor 1988, 1991, V.C. Bleich and D. Racine unpublished data). The primary winter forage for the 4 northern populations is bitterbrush (Purshia spp.; Taylor 1988, 1991). Although bitterbrush occurs in the Inyo Mountains (DeDecker 1991), specific data on deer diets in that range are lacking.

The Sierra Nevada creates a formidable rain shadow, and during winter these deer occupy an arid region with low and unpredictable precipitation (Fig. 2), similar to that described by Kucera (1988). Since 1986, the Great Basin immediately east of the Sierra Nevada has experienced repeated annual droughts; as a result, ecological carrying capacity of many winter ranges has declined (Taylor 1991). Migratory populations of mule deer can be substantially affected by drought conditions on winter ranges despite adequate forage during summer (Kucera 1988). During years of low precipitation, bitterbrush production is poor and deer subsist on suboptimal diets consisting largely of conifers, sagebrush, and blackbrush (Coleogyne ramosissima; Kucera 1988, Taylor 1991).

METHODS

During 1986–1991, we used Clover (1956) traps, a helicopter and linear drive nets (Thomas and Novak 1991), and a hand-held net gun fired from a helicopter (Krausman et al. 1985) to capture mule deer. We fitted adult (>1-yr-old) animals with color-coded ear tags and telemetry collars (Model 500, Telonics, Inc., Mesa, AZ) that incorporated a mortality sensor with a 6-h delay. We collared each animal at its capture site and released it when processing was completed. By distributing our
capture efforts throughout all winter ranges, we minimized potential biases associated with heterogeneous use of those areas by deer. We collared male and female deer in the approximate proportion of their occurrence in each population. Each winter, we used ground-based chemical immobilization or a helicopter and net gun to capture and radio-collar additional deer in each population.

In the 4 northern populations, we used aerial and ground telemetry to monitor the status of deer at intervals \( \leq 1 \) wk; thus, date of death could be closely estimated. Using only aerial telemetry in the Inyo Mountains, we monitored those deer at approximately 2-wk intervals. For animals for which we could not ascertain the date of death, we assumed death occurred midway between the last known live observation and the date on which a mortality signal was first received.

We attempted to determine the cause of mortality for every deer that died. For animals killed by predators, we used the criteria of Shaw (1983) and Woolsey (1985) to identify the species of predator in all but one instance. Nutritional status was indexed by condition of marrow in long bones (Cheatum 1949). When we could not ascertain the source of mortality, we listed the cause of death as undetermined. C-tests were used for categorical analyses, and a binomial test compared the proportion of deer killed by mountain lions during different years (Zar 1984).

We used the Kaplan-Meier (1958) estimator, as modified by Pollock et al. (1989), for staggered entry of telemetered females into each population, and determined survivorship on a monthly basis. To compare survivorship functions, we used the log-rank test (Cox and Oakes 1984) as modified by Pollock et al. (1989). We calculated the most conservative chi-square statistic presented by Pollock et al. (1989) to enhance the probability that any differences detected between survivorship functions were real.

Survivorship was not evaluated on all winter ranges concurrently, and deer were not initially collared at the same time of year. To minimize seasonal effects on mortality in this retrospective analysis, we compared survivorship of females from paired populations from the beginning of the 1st April during which collared deer from each population pair were available to the end of the period for which paired monthly data were available for those particular populations. For example, we studied cause-specific mortality in the West Walker population during April 1992-January 1995, and in the Inyo Mountains population during October 1991-December 1994; for this pair, comparisons of survivorship curves spanned a period of 2 yr and 9 mon, from 1 April in year 1 to 31 December in year 3. Using this method, we compared survivorship over periods of 21 mon for 4 pairs of populations, and over 27 mon for 5 other pairs. To facilitate comparisons, we also calculated finite, annual, and monthly survivorship for females in each population. We restricted our analyses to females because the genders of sexually dimorphic ungulates may occupy different habitats, experience different risks of natural mortality (Bleich et al. 1997), and respond differently to the threat of predation (Bleich in press).

We collected data for a minimum of 24 mon in the Casa Diablo population and a maximum of 39 mon in the Inyo Mountains. Although the investigations did not all run concurrently, these 5 populations occupy similar habitats in close proximity to each other, they were exposed to similar climatic regimes (Table 1),
Table 1. Correlation matrices for climatological data obtained 1961–1990 from the Western Regional Climate Center for Bishop, Bridgeport, Bodie, and Independence, California. These stations are all located on or near the winter ranges investigated herein.

<table>
<thead>
<tr>
<th></th>
<th>Average monthly maximum temperature</th>
<th>Average monthly minimum temperature</th>
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<td>Bishop</td>
<td>Bodie</td>
<td>Bridgeport</td>
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<td>Independence</td>
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and several of the investigations were ongoing simultaneously. Thus, we assumed that qualitative differences among these winter ranges were minimal.

RESULTS

We radio-collared 168 adult mule deer (27 males, 141 females) and monitored them for 21–39 mon (2829 telemetry-months; Table 2). We determined the proximate source of mortality for 76% of the females (41 of 54) and 85% of males (11 of 13) that died. Among females, confirmed causes of death ranged from 57% in the Inyo Mountains to 100% in the East Walker population. Among the 41 mortalities of females for which the cause of death is known, 83% were attributed to predation, 4.8% were human-induced, and 12.2% were due to malnutrition. In the northernmost population (West Walker), 3 of 10 mortalities resulting from predation occurred during or immediately after the severe winter of 1992–93, and 7 of 10 occurred during or following the mild winter of 1993–94 (P > 0.10). Among males that died, predation by mountain lions accounted for 36% and hunting for 64% of the 11 mortalities for which the cause of death was determined; the source of mortality for 2 males could not be ascertained. We detected no evidence of malnutrition among animals killed by predators or among those dying of anthropogenic causes.

Predation accounted for >70% of the known causes of death for females on each winter range (Fig. 3). The proportion of deaths attributed to predation did not differ among these populations (G = 5.987, df = 4, P = 0.200) when human-induced mortality and malnutrition were pooled. For males, sample sizes were too small to allow a comparison among populations.

Of 34 female mule deer killed by predators, mountain lions accounted for 91% of the deaths (Fig. 4). No difference existed among the 5 populations in the proportion of females killed by mountain lions (G = 2.979, df = 4, P = 0.561). Overall, the proportion of female deer whose deaths were attributable to predation by mountain lions (31 of 41) was significantly greater than the proportion of males killed by these large felids (4 of 11; G = 5.751, df = 1, P = 0.016).

Survivorship functions of female deer differed significantly for 3 of 10 pairwise comparisons (Table 3). Survivorship for the West Walker population differed from the Mono Lake, Inyo Mountains, and East Walker populations, and was marginally nonsignificant for the Casa Diablo population. The finite survival
rate among these populations ranged from about 0.75 in the East Walker population to about 0.30 in the West Walker population, which had the highest proportion of mortality caused by malnutrition. Among these populations, monthly survival estimates ranged from 0.964 to 0.990, and annual survival estimates ranged from 0.643 to 0.884 (Table 2). Too few males were marked to allow a meaningful estimate of survivorship for males occurring in these populations.

## Discussion

Predation was the most common cause of mortality among 5 mule deer populations that winter east of the Sierra Nevada (Fig. 3). Human-induced mortality and malnutrition varied among these populations. Based on our analyses, we conclude that sources of mortality were similar among these winter ranges for the periods we studied. Deaths of female deer resulting from human activities were recorded only in the West Walker and Casa Diablo populations. Death resulting from malnutrition was restricted to the West Walker and Mono Lake populations and accounted for 25% and 21% of the mortality in those populations, respectively. Malnutrition overall (9.8%) was, however, not an important cause of death.

Among deer killed by carnivores, mountain lions were the most common predator; and no differences existed in the proportion of female deer killed by mountain lions among the 5 populations we investigated (Fig. 4). Our findings are consistent with previous ones that mule deer are important prey of mountain lions throughout western North America (Hornocker 1976, Russell 1978). Proportionally more telemetered females than males were killed, suggesting that females may be more vulnerable to predation by mountain lions.

There was a difference in survivorship functions between 3 of 10 pairs of populations that we compared (Table 3), and the results were but marginally nonsignificant for a 4th pair. Small samples possibly influenced our ability to detect differences (Pollock et al. 1989) between other population pairs, but the magnitude of differences between 6 pairs, when compared to the remaining 4, suggests sample size was not problematic (Table 3). These findings were somewhat unexpected given the physical, climatological, vegetational, and faunal similarities among the winter ranges we examined, and may be attributable to the high proportion of mortality from malnutrition in the West Walker population during the winter of 1992–93; that winter was especially severe in northeastern California (Wertz 1996).

In none of our study populations are historical demography and habitat quality adequately known to begin to factor out the relative roles of nutrition, predation, and climate as factors influencing the dynamics of these populations. Additionally, the effects of these factors on survival of young <1 yr old were not investigated. With the exception of the Mono Lake and West Walker populations, the absence of animals dying of malnutrition suggests that mortality from predation generally was not compensatory. Many female deer collected from the West Walker winter range were in poor physical condition following the winter of 1992–93 (Taylor 1996), and some animals in that population may have been predisposed to death by predation during our investigation. Nevertheless, only 3 of 10 animals killed by predators in the West Walker population died that winter, but 7 of 10 were killed during the mild winter of 1993–94. Despite the deaths of 2 females from malnutrition in the Mono Lake population, individuals there were in much better condition than were West Walker females.
During 1992–93 (Taylor 1991). Body condition of Mono Lake females during the period they were under study approached that of the West Walker population during 1994, a year when no animals died of malnutrition. None of the animals killed by predators exhibited evidence of depleted fat reserves upon examination of femur marrow. If malnutrition was an important factor predisposing individuals to death by other causes, we would have expected to find evidence of such among victims of predation or human-induced mortality; this was not the case.

The role of predation in regulating populations of large mammals remains open to debate (Skogland 1991), and predation as a factor potentially regulating deer populations has not been widely accepted (Connolly 1981). For example, the effects of mountain lion predation have been described as unimportant (Janz and Hatter 1986) and conversely as having strong local effects (McNay and Voller 1995) on deer occurring in the same geographic area. These large felids were responsible for most mortality of adult female deer in each of the populations we investigated. Although we noted few adults killed by coyotes (Canis latrans), these canids can have important effects on deer population dynamics, especially through their influence on fawn survival (Knowlton 1976, Bowyer 1987).

Predation may warrant special consideration as a factor in the dynamics of mule deer occupying unpredictable environments. Indeed, investigations in boreal systems have suggested that predation by wolves (Canis lupus) and bears (Ursus spp.) can preclude recovery of large mammal populations that have become depressed by a single source, or a combination of several sources, of mortality (Gasaway et al. 1983, 1992, Van Ballenberghe 1987). Based on observations in the Sierra Nevada, Wehausen (1996) suggested that predation by mountain lions has substantially influenced the population dynamics of mountain sheep in part of the western Great Basin. Removal of several mountain lions was necessary to preclude the extirpation of one population of these specialized ungulates (Bleich et al. 1991), and that population of mountain sheep is sympatric with the Casa Diablo deer population for part of the year (Taylor 1991).

Given the similarities in cause-specific mortality and the importance of predation as a cause of death among the populations we studied, the potential for predation to regulate deer populations might be reconsidered and further investigated, particularly for migratory deer inhabiting the arid, unpredictable ecosystems typical of the western Great Basin. In such systems predation clearly is an important source of mortality and may assume greater importance.
in population limitation than in more mesic environments where the effects of climate are more tempered and more predictable.

In highly variable systems, density-independent events (i.e., droughts and harsh winters) occur unpredictably (Mackie et al. 1990) and can result in unanticipated population declines that confound conservation strategies. Nonetheless, density dependence would continue to operate (McCullough 1990) in such systems and could indirectly affect predation rates (McCullough 1979). Only through carefully designed, long-term investigations, however, will it be possible to reach meaningful conclusions regarding effects of predation and other sources of mortality on populations of migratory deer occupying Great Basin ecosystems.

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**LITERATURE CITED**


