

## NOTES

# MASS MORTALITIES OF MIGRATORY MULE DEER (*ODOCOILEUS HEMIONUS*): IMPLICATIONS FOR ECOSYSTEM FUNCTION, CONSERVATION, OR MANAGEMENT?

VERNON C. BLEICH

*Department of Natural Resources and Environmental Science, University of Nevada Reno, Reno, Nevada 89557, and  
Eastern Sierra Center for Applied Population Ecology, Bismarck, North Dakota 58504, vbleich@gmail.com*

**Abstract.**—Mass mortality events involving migratory Mule Deer (*Odocoileus hemionus*) in natural settings rarely have been reported. I describe two such events that occurred in the Sierra Nevada, California, during the fall migration in 2017. In both cases, large numbers of Mule Deer fell to their deaths while attempting to cross patches of ice-covered rocky terrain, a result of heavy snowfall the previous winter that persisted through summer. Heavy snowfall appears to be a precursor to mass mortality events and, if that is the case, snowpack records indicate such losses could occur more often than previously recognized. I discuss mass mortality events among Mule Deer in the context of ecosystem function and their potential relationship to life histories of two scavenging carnivores (*Gulo gulo* and *Vulpes vulpes*), and the hypothetical implications of those events for management and composition of populations of migratory Mule Deer.

**Key Words.**—accident; *Gulo gulo*; Red Fox; Sierra Nevada; snowpack; *Vulpes vulpes*; Wolverine

---

Migration is a widespread, and in some cases a threatened, phenomenon throughout the animal kingdom (Berger 2004; Wilcove 2008; Dingle 2014). In general, migratory behavior can be viewed as a basic response to adversity (Taylor and Taylor 1977), and likely evolved as an adaptation to variability in the environment (Baker 1978). Moreover, migratory behavior will be adaptive if individuals occupying specific ranges at certain times of the year achieve fitness gains greater than those incurred by resident (i.e., nonmigratory) individuals (Avgar et al. 2014).

Explanations for prehistoric mass mortality events have been varied and diverse (Keim 1969; Guthrie 1990), but often are attributed to natural deaths in a rigorous environment (Pewe 1975). Descriptions of contemporary mass mortality events are encountered infrequently (Berger 1983), but recently have been reported for several migratory artiodactyls, among which are Saiga Antelope (*Saiga tatarica*; Kock et al. 2018), Wildebeest (*Connochaetes taurinus*; Subalusky et al. 2017), Reindeer (*Rangifer tarandus*; Henrik Libell, unpubl. report), and Mule Deer (*Odocoileus hemionus*; Jones 1954; Bleich and Pierce 2001). As a result, the potential role of mass mortality events in ecosystem function is receiving increased attention (Pennisi 2017). In this note, I add to the literature on mass mortality events, and consider their potential role in ecosystem function and in the conservation and management of migratory Mule Deer in the Sierra Nevada of California.

The importance of unimpaired migration to Mule Deer occupying the Sierra Nevada is well established (Longhurst et al. 1952; Kucera and McCarthy 1988; Loft and Bleich 2014). Migration typically occurs along

traditional routes (Sawyer et al. 2009), and Mule Deer inhabiting those mountains move to and from seasonal ranges each year (Longhurst et al. 1952). During spring, they travel through high-elevation passes to summer ranges west of the Sierra crest and return eastward through those passes to winter ranges during autumn (Kucera 1992; Bleich et al. 2006; Monteith et al. 2011, 2014). Although migration is a widespread phenomenon, there are benefits and tradeoffs associated with that behavior (Nicholson et al. 1997). For example, Mule Deer remaining longer on summer ranges incurred significant nutritional advantages, but likely faced greater threats to survival than did those that migrated earlier (Monteith et al. 2011).

Accidental deaths of individual Mule Deer are not uncommon (Heffelfinger 2006), but at least two mass mortality events previously have occurred in the Sierra Nevada at Bishop Pass (3,680 m; 37°06'54"N, 118°32'41"W) when dozens of deer slipped and fell while traversing steep, ice-covered slopes during autumn migrations in 1952 and 1995 (Jones 1954; Bleich and Pierce 2001). In late October and early November 2017, at least 76 additional Mule Deer fell to their deaths near Bishop Pass, and at least 44 others died in a separate event near Shepherd Pass (3,672 m; 36°40'21"N, 118°20'44"W) about 50 km SSE of Bishop Pass (Paula Brown-Williams, unpubl. report). In both of those cases, deer slipped on ice that had persisted through summer and, unable to regain their footing, plunged to their deaths as described previously (Jones 1954; Bleich and Pierce 2001). Among the dead at both locations were adult males and females, as well as young-of-the-year (Fig. 1). Blood trails likely associated with crippled deer



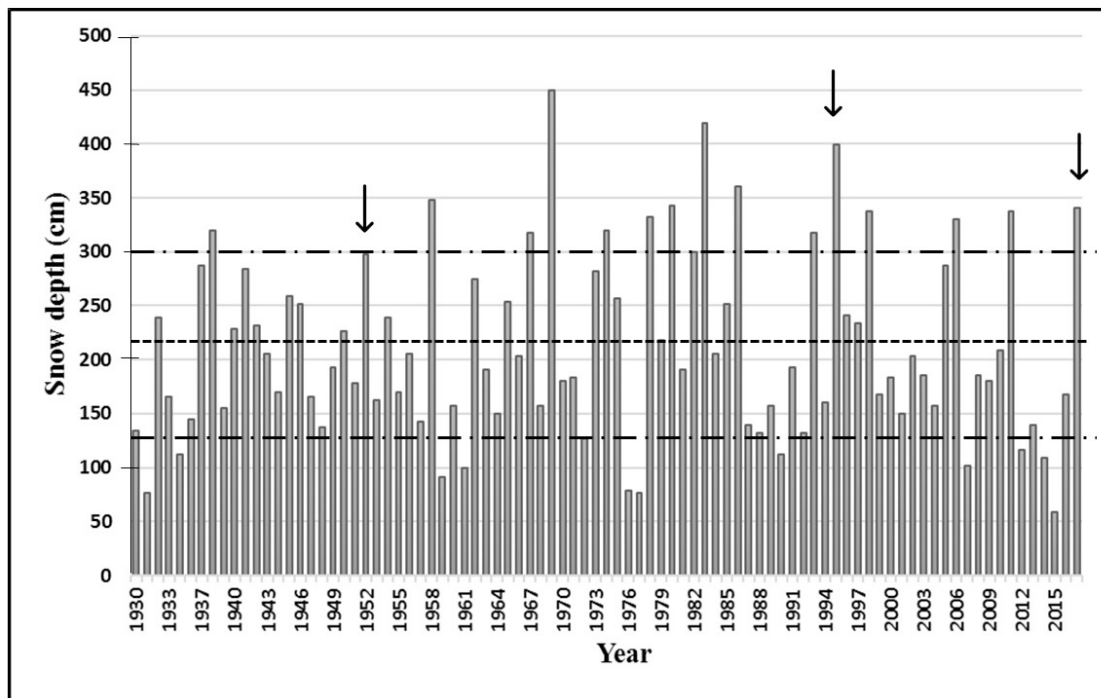
**FIGURE 1.** At least 76 Mule Deer (*Odocoileus hemionus*) representing all age classes and both sexes were killed in a mass mortality event in the Sierra Nevada near Bishop Pass, which separates Inyo and Fresno counties, California, in Fall 2017. (Photograph courtesy of California Department of Fish and Wildlife).

indicated others were injured at each location, but their fate is unknown. The 2017 incident at Bishop Pass was the third such loss documented there, and the event at Shepherd Pass is the fourth such incident in the Sierra Nevada of which I am aware. Those four events all followed winters of exceptionally high snowfall that resulted in ice-covered terrain persisting near those passes. Based on preliminary information, Bleich and Pierce (2001) hypothesized that mass mortality events have occurred at Bishop Pass more frequently than previously reported.

The Sierra Nevada is a massive mountain range, reaching elevations > 4,400 m above sea level (ASL) and extending 640 km in a north-south direction while separating the Great Basin from the San Joaquin and Sacramento valleys (Storer and Usinger 1968). Vegetation on winter ranges ( $\bar{x} \approx 1,600$  m ASL) east of the Sierra crest is representative of the Great Basin and conforms to the Sagebrush (*Artemisia* sp.) belt of Storer

and Usinger (1968). Summer ranges west of the crest range in elevation from 2,200 to 3,600 m ASL (Kucera 1988). Vegetation zones on summer ranges include the Lodgepole Pine-Red Fir, Subalpine, and Alpine belts (Storer and Usinger 1968; Kucera 1992). High-elevation passes used during migration are in the Alpine belt, which is characterized by vast, rocky areas that are nearly devoid of vegetation (Wehausen 1980).

Summer ranges are more mesic than winter ranges, and average annual rainfall is substantially less on the east side of the mountains because of the rain shadow cast by the Sierra Nevada (Mulch et al. 2008). On typical summer range near Huntington Lake, Fresno County (2,260 m ASL; 37°22'N, 119°13'W), mean annual precipitation is 101 cm, whereas mean annual precipitation is 13 cm at Bishop, Inyo County (1,260 m ASL; 37°22'N, 118°24'W), and is representative of winter ranges east of the Sierra crest (Bleich and Taylor 1998).



**FIGURE 2.** Depth of April snowpack at the Bishop Pass Snow Survey Station (BSH), Fresno County, California, 1930–2017. For reference the long-term mean (-----) and  $\pm 1$  standard deviation (--- · ---) are shown. Snowpack during April was  $\geq 297$  cm, the minimum known to have been followed by a mass mortality event at Bishop Pass in 17 y from 1930 to 2017; no information was available for 1936. Years in which mass mortality events were documented are indicated by downward arrows.

Mean annual snowfall is 465 cm and 15 cm at Huntington Lake and Bishop, respectively. Mean annual temperature at Huntington Lake ( $7.1^{\circ}\text{C}$ ) is substantially less than at Bishop ( $13.3^{\circ}\text{C}$ ). Weather conditions at high elevations are quite variable and can be extreme during winter. Years of heavy snowfall result in icy conditions on bare talus slopes near some of those passes, and ice persisting on steep hillsides through summer presents a danger to migrating deer (Jones 1954; Bleich and Pierce 2001).

Among carnivores capable of preying on Mule Deer, Grizzly Bear (*Ursus arctos*) and Wolverine (*Gulo gulo*) have been extirpated from the Sierra Nevada (Storer and Tevis 1955; Aubrey et al. 2007; Schwartz et al. 2007); historical presence of Gray Wolf (*Canis lupus*) remains uncertain (Schmidt 1991; Shelton and Weckerly 2007). Mountain Lion (*Puma concolor*) and Coyote (*Canis latrans*), however, are important predators of Mule Deer (Pierce et al. 2000) and occur throughout the range (Storer and Usinger 1968). Black Bears (*Ursus americanus*) prey extensively on neonatal Mule Deer on summer range, but prey on fawns infrequently east of the Sierra crest (Monteith et al. 2014). Sierra Nevada Red Fox (*Vulpes vulpes nescator*) remain extant but are a threatened taxon (Barrett and Golightly 1994), and feed on Mule Deer as carrion when it is available (Perrine 2005). The deer population occupying the Round Valley winter range ( $37^{\circ}25'\text{N}$ ,  $118^{\circ}36'\text{W}$ ), 33 km north of Bishop Pass, declined rapidly from  $\geq 6,000$  in 1985 to

about 1,000 in 1991, where it remained until 1992 when it began to increase slowly (Pierce et al. 2012).

April snowpack is a reliable measure of maximum winter snow depth (Mote et al. 2005) and, apart from 1936, has been recorded annually at the Bishop Pass Snow Survey Station, Fresno County ( $3,414\text{ m}$ ;  $37^{\circ}06'00''\text{N}$ ,  $118^{\circ}33'25''\text{W}$ ) since 1930 (California Department of Water Resources. 2017. Bishop Pass [BSH]. Available from <http://cdec.water.ca.gov> [Accessed 26 November 2017]). I reviewed those records and explored snowpack conditions over the previous 87 y. April snowpack ( $\bar{x} = 211 \pm 84.7$  [SD] cm) ranged from a low of 58 cm in 2015 to a high of 419 cm in 1969 (Fig. 2). In 1952, when ice persisted at Bishop Pass and a mass mortality event occurred there during fall migration (Jones 1954), April snowpack was 297 cm. Additional mass mortality events are known to have occurred during Fall of 1995 and 2017, when April snowpack was 399 cm and 340 cm, respectively (Bleich and Pierce 2001; this paper). Thus, I considered any year with April snowpack  $\geq 297$  cm to be a precursor for a mass mortality event at this location during the subsequent fall migration, but interannual variation in local conditions affects persistence of snowpack (Mote et al. 2005), and the threshold for such could be less. During 17 of the 86 y (20%) for which data are available, April snowpack was  $\geq 297$  cm. On average, April snowpack  $\geq 297$  cm has occurred about once every 5 y (Fig. 2).

Historical distributions of Sierra Nevada Red Fox and now extirpated Wolverine coincided closely with that of Mule Deer in the Sierra Nevada, and both occurred at high elevations (Schempf and White 1977; Barrett and Golightly 1994; Statham et al. 2012) used by Mule Deer during migration. Red Fox and Wolverine are opportunistic feeders and large mammals in their respective diets likely originate as carrion (Wilson 1982; Pasitschniak-Arts and Lariviere 1995; Copeland and Whitman 2003; Cypher 2003; Perrine 2005). Thus, carrion resulting from mass mortality events might have been an important food source for Wolverine prior to extirpation and may yet play a role in the foraging ecology of Red Fox on a seasonal, even if irregular, basis. To the best of my knowledge, this note is the first to posit a potential role of mass mortality events in the ecology of those secretive carnivores.

Density independent events occur unpredictably and complicate management in highly variable ecosystems (Mackie et al. 1990; Bleich and Taylor 1998). Hypothetically, April snowpack of a depth adequate to persist into the period of fall migration could play a role in the demographics of some migratory deer populations following winters of heavy snowfall. For example, deep April snowpack (as precursors to potential mass mortality events) occurred in 1985 and 1986 (Fig. 2) during the precipitous crash of deer occupying the Round Valley winter range, a decline attributed largely to drought (Pierce et al. 2012). Thus, the rate of decline may have been exacerbated by undocumented mass mortality events during autumn migrations in 1985 and 1986, when April snowpack was 250 cm and 360 cm, respectively. Rate of recovery of that population might also have been slowed by similar events. Since 1992, when the population began to recover, April snowpack > 297 cm has been recorded six times, and was 287 cm in a seventh year. Neither of these possibilities had been considered previously (Kucera 1988; Pierce et al. 2012). Clearly, better understanding of the relationship between annual snowfall and mass mortality events, as well as quantification of the population-level impacts of such events, is necessary to interpret their demographic consequences.

Heavy snowfall during winters of 1968–1969, 1982–1983, 1984–1985, and 1985–1986 (Fig. 2) promulgated regulatory changes to reduce harvest of deer throughout the eastern Sierra Nevada. Those changes were based on the deaths of several hundred deer during the winter of 1968–1969, and early fall storms in 1983, 1985, and 1986 that resulted in extremely high harvests (Blankinship 1987). That accidental deaths of the type described here played a role in the dynamics of some migratory populations in the Sierra Nevada remains hypothetical but, given the relative probability (20% in any given year) of April snowpack  $\geq 297$  cm as a precursor to such a mass mortality event, I suggest that metric be a consideration when formulating harvest regulations during population

declines of the magnitude described previously (Kucera 1988; Pierce et al. 2012).

The composition of deer populations exhibiting partial migration (Chapman et al. 2011) may also be affected by mass mortality events, a factor not considered by previous investigators (Kucera 1992; Monteith et al. 2011). In the Sierra Nevada, timing of deer migration from summer to winter ranges is mediated by phenological changes in forage and by body condition of migrants (Monteith et al. 2011). At the onset of migration, however, deer cannot be aware of risks associated with ice conditions at isolated high-elevation locations on steep, north-facing slopes described herein. The proportion of Mule Deer occupying the Round Valley winter range but that migrates across the Sierra crest each year declined from 87% in 1987 to 58% in 1998 and was  $\leq 50\%$  in 2009 (Kucera 1988; Monteith et al. 2014). Much of that change has been a demographic consequence of predation on neonatal deer by Black Bears west of the Sierra crest and the near absence of bear predation on offspring of deer that do not cross the range (Monteith et al. 2014). Mass mortality events would exacerbate selection against the migratory component of a deer population (i.e., migration thus becomes maladaptive; Avgar et al. 2014) and, thereby, contribute to an increase in the relative abundance of deer that remain east of the Sierra Crest during winter but co-occur with migrants on winter range. Such mortality would be additive (Bowyer et al. 2014) to that attributed to predation and compound the already severe shift in population structure described by Monteith et al. (2014).

It is often through observations of unanticipated or unusual events that questions arise and our understanding of nature ultimately is enhanced (Estes 2016). Mass mortality events involving Mule Deer in the Sierra Nevada have been reported only infrequently and observations of those events may have been serendipitous. The rarity of such reports, however, begs questions about whether mass mortality events truly are rare, or have simply gone undetected or not been reported when they do occur, and where in the Sierra Nevada they might occur. That those events take place at high elevations in remote, rugged, and isolated terrain immediately prior to winter is consistent with the notion that they may well go unnoticed. Historical snowpack records indicate that climatic conditions as possible precursors to such losses occur at Bishop Pass, on average, about every 5 y; hence, mass mortality events may be more frequent than recognized. If so, those accidental deaths have greater implications, both for ecosystem function and for management of migratory Mule Deer than considered previously and warrant further investigation.

*Acknowledgments.*—I thank Steve Hill and Steve Yeager for in-depth discussions regarding the recent mass mortality events described herein, and Philip (Pep) Partridge for detailed descriptions of the winter of 1968–

1969 and its impacts to Mule Deer. Pep Partridge and, the late, Earl Brown and Dick Noles provided many hours of animated conversation regarding the management of Mule Deer and never hesitated to share advice; I learned a great deal from them. I thank Kevin Monteith and Jim Heffelfinger for many helpful suggestions that improved the manuscript. This is Professional Paper 124 from the Eastern Sierra Center for Applied Population Ecology.

#### LITERATURE CITED

- Aubrey, K.B., K.S. McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the Wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147–2158.
- Avgar, T., G. Street, and J.M. Fryxell. 2014. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 92:481–490.
- Baker, R.R. 1978. *The evolutionary ecology of animal migration*. Homes and Meier Publishers, New York, New York.
- Barrett, R., and R. Golightly. 1994. Sierra Nevada Red Fox. Pp. 84–85 in *Life on the Edge: A Guide to California's Endangered Natural Resources*. Thelander, C. (Ed.). BioSystems Books, Santa Cruz, California.
- Berger, J. 1983. Ecology and catastrophic mortality in wild horses: implications for sociality in fossil assemblages. *Science* 220:1403–1404.
- Berger, J. 2004. The last mile: how to sustain long distance migration in mammals. *Conservation Biology* 18:320–331.
- Blankinship, T.E. 1987. *Buttermilk Deer Herd Management Plan*. California Department of Fish and Game, Bishop, California.
- Bleich, V.C., and B.M. Pierce. 2001. Accidental mass mortality of migrating Mule Deer. *Western North American Naturalist* 61:124–125.
- Bleich, V.C., and T.J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of Mule Deer. *Great Basin Naturalist* 58:265–272.
- Bleich, V.C., B.M. Pierce, J. Jones, and R.T. Bowyer. 2006. Variance in survival rates among young Mule Deer in the Sierra Nevada, California. *California Fish and Game* 92:24–38.
- Bowyer, R.T., V.C. Bleich, K.M. Stewart, J.T. Whiting, and K.L. Monteith. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. *California Fish and Game* 100:550–572.
- Chapman, B.B., C. Bronmark, J.A. Nilsson, and L.A. Hansson. 2011. The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- Copeland, J.P., and J.S. Whitman. 2003. Wolverine (*Gulo gulo*). Pp. 672–682 in *Wild Mammals of North America: Biology, Management, and Conservation*. 2nd Edition. Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.
- Cypher, B.L. 2003. Foxes (*Vulpes* species, *Urocyon* species, and *Alopex lagopus*). Pp. 511–546 in *Wild Mammals of North America: Biology, Management, and Conservation*. 2nd Edition. Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.
- Dingle, H. 2014. *Migration: The Biology of Life on the Move*. 2nd Edition. Oxford University Press, Oxford, UK.
- Estes, J.A. 2016. *Serendipity: An Ecologist's Quest to Understand Nature*. University of California Press, Oakland, California.
- Guthrie, R.D. 1990. *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. University of Chicago Press, Chicago, Illinois.
- Heffelfinger, J.R. 2006. *Deer of the Southwest*. Texas A&M University Press, College Station, Texas.
- Jones, F.L. 1954. An unusual cause of deer mortality. *Journal of Wildlife Management* 18:142.
- Keim, C.J. 1969. *Aghvook, White Eskimo: Otto Geist and Alaskan Archaeology*. University of Alaska Press, Fairbanks, Alaska.
- Kock, R.A., M. Orynbayev, S. Robinson, S. Zuther, N.J. Singh, W. Beauvais, E.R. Morgan, A. Kerimbayev, S. Khomenko, H.M. Martineau, et al. 2018. Saigas on the brink: multidisciplinary analysis of the factors influencing mass mortality events. *Science Advances* 4(1):eaao2314. doi:10.1126/sciadv.aao2314.
- Kucera, T.E. 1988. *Ecology and Population Dynamics of Mule Deer in the Eastern Sierra Nevada, California*. Ph.D. Dissertation, University of California, Berkeley, California. 207 p.
- Kucera, T.E. 1992. Influences of sex and weather on migration of Mule Deer in California. *Great Basin Naturalist* 52:122–130.
- Kucera, T.E., and C.W. McCarthy. 1988. Habitat fragmentation and Mule Deer migration corridors: a need for evaluation. *Transactions of the Western Section of The Wildlife Society* 24:61–67.
- Loft, E.R., and V.C. Bleich. 2014. An historical perspective on deer ranges in California: terminology and its relevance to wildlife conservation. *California Fish and Game* 100:451–472.
- Longhurst, W.M., A.S. Leopold, and R.F. Dasmann. 1952. A survey of California deer herds: their ranges and management problems. *Game Bulletin* 6:1–136.
- Mackie, R.J., K.L. Hamlin, D.F. Pac, G.L. Dusek, and A.K. Wood. 1990. Compensation in free-ranging deer populations. *Transactions of the North American Wildlife and Natural Resources Conference* 55:518–526.
- Monteith, K.M., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in Mule Deer: effects of climate, plant phenology, and life-history

- characteristics. *Ecosphere* 2(4):art47. doi:10.1890/es10-00096.1.
- Monteith, K.M., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, J.G. Kie, and R.T. Bowyer. 2014. Life history characteristics of Mule Deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–63.
- Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society* 86:39–49.
- Mulch, A., A.M. Sarna-Wojcicki, M.E. Perkins, and C.P. Chamberlin. 2008. A Miocene to Pleistocene climate and elevation record of the Sierra Nevada (California). *Proceedings of the National Academy of Sciences* 105:6819–6824.
- Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of Mule Deer: tradeoffs associated with migration. *Journal of Mammalogy* 78:483–504.
- Paitschniak-Arts, M., and S. Lariviere. 1995. *Gulo gulo*. *Mammalian Species* 499:1–10.
- Pennisi, E. 2017. Drowned Wildebeest provide ecological feast. *Science* 356:1217–1218.
- Perrine, J.D. 2005. Ecology of Red Fox (*Vulpes vulpes*) in the Lassen Park Region of California, USA. Ph.D. Dissertation, University of California, Berkeley, California. 236 p.
- Pewe, T.L. 1975. Quaternary geology of Alaska. U.S. Geological Survey Professional Paper 835:1–145.
- Pierce, B.M., V.C. Bleich, and R.T. Bowyer. 2000. Prey selection by Mountain Lions and Coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* 81:462–472.
- Pierce, B.M., V.C. Bleich, K.L. Monteith, and R.T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from Mountain Lions and Mule Deer. *Journal of Mammalogy* 93:977–988.
- Sawyer, H., M.J. Kauffman, R.M. Nielson, and J.S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.
- Schempf, P.M., and M. White. 1977. Status of six furbearer populations in the mountains of northern California. U.S. Department of Agriculture, Forest Service, Region 5. San Francisco, California.
- Schmidt, R.H. 1991. Gray wolves in California: their presence and absence. *California Fish and Game* 77:79–85.
- Schwartz, M.K., K.B. Aubrey, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation of Wolverines in California using historical DNA. *Journal of Wildlife Management* 71:2170–2179.
- Shelton, S.L., and F.W. Weckerly. 2007. Inconsistencies in historical geographic range maps: the Gray Wolf as an example. *California Fish and Game* 93:224–227.
- Statham, M.J., A.C. Rich, S.K. Lisius, and B.N. Sacks. 2012. Discovery of a remnant population of Sierra Nevada Red Fox (*Vulpes vulpes necator*). *Northwest Science* 86:122–132.
- Storer, T.I., and L.P. Tevis, Jr. 1955. *The California Grizzly*. University of California Press, Berkeley, California.
- Storer, T.I., and R.L. Usinger. 1968. *Sierra Nevada Natural History*. University of California Press, Berkeley, California.
- Subalusky, A.L., C.L. Dutton, E.J. Rosi, and D.M. Post. 2017. Annual mass drownings of the Serengeti Wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences* 114:7647–7652.
- Taylor, L.R., and R.A.J. Taylor. 1977. Aggregation, migration, and population mechanics. *Nature* 265:415–421.
- Wehausen, J.D. 1980. *Sierra Nevada Bighorn Sheep: History and Population Ecology*. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan. 240 p.
- Wilcove, D.S. 2008. *No Way Home: The Decline of the World's Great Animal Migrations*. Island Press, Washington, D.C.
- Wilson, D.E. 1982. Wolverine. Pp. 644–652 in *Wild Mammals of North America: Biology, Management, and Conservation*. 2<sup>nd</sup> Edition. Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.



**VERN BLEICH** was a Wildlife Biologist with the California Department of Fish and Game for 34 y, where his responsibilities centered largely on the conservation and management of large mammals occupying the eastern Sierra Nevada and the Great Basin, Mojave, and Sonoran deserts. Currently, he is Research Professor in the Department of Natural Resources and Environmental Science at the University of Nevada Reno. Although he has emigrated from California to North Dakota, he continues to contribute to the conservation and management of large mammals inhabiting arid landscapes throughout the western United States. He serves as an advisor to the Society for the Conservation of Bighorn Sheep, the Texas Bighorn Society, the Wild Sheep Foundation, and the California Chapter of the Wildlife Sheep Foundation, and is midway through his second term on the Montana-Dakotas Resource Advisory Council of the Bureau of Land Management. (Photographed by Riley Heater).