Wildlife Society Bulletin 35(3):252–260; 2011; DOI: 10.1002/wsb.41

Original Article

Biological Consequences of Winter-Feeding of Mule Deer in Developed Landscapes in Northern Utah

CHRIS PETERSON,[1] *Department of Wildland Resources, Jack H. Berryman Institute, Utah State University, Logan, UT 84322-5230, USA*
TERRY A. MESSMER, *Department of Wildland Resources, Jack H. Berryman Institute, Utah State University, Logan, UT 84322-5230, USA*

ABSTRACT Winter-feeding of mule deer (*Odocoileus hemionus*) in developed landscapes is often advocated by stakeholders to compensate for lost or fragmented winter range. However the reported benefits of winter-feeding mule deer to increase survival and productivity in altered landscapes are mixed. Few studies have examined the long-term effects of winter-feeding on mule deer productivity. We studied the effects of a winter-feeding program conducted in a developed landscape in northern Utah, USA from 2001 to 2006 on the productivity, survival, and mortality of 92 adult female deer (does) that were captured and radiocollared on 4 feed and 4 nonfeed sites. We also evaluated the potential for feeding programs to impact winter-range habitat quality through increased browse utilization. Fawn production ($P = 0.36$), and survival ($P = 0.12$) did not differ for fed and nonfed does. Deer–vehicle collisions were the primary cause of mortality for radiocollared deer in both populations ($P = 0.97$). Utilization of desired browse species was higher on sites where deer were fed ($P \leq 0.001$), although deer numbers were similar at feed and nonfeed sites. When developing big game winter-feeding policies for developed landscapes, managers must consider the full range of long-term potential population and habitat impacts to include increased anthropogenic-related mortality and increased potential for habitat degradation prior to policy implementation. © 2011 The Wildlife Society.

KEY WORDS browse utilization, developed landscapes, mortality, mule deer, *Odocoileus hemionus*, productivity, survival, Utah, winter-feeding.

Feeding programs have been advocated by sportsmen to mitigate mule deer (*Odocoileus hemionus*) mortality in developed landscapes where winter range has been lost, fragmented, or is in poor condition and subjected to reduced browse accessibility because of seasonal deep snow (Urness 1980). However, the reported results regarding the benefits of winter-feeding programs on overall herd survival and production are mixed, possibly because of the limited duration of previous evaluations (Peterson and Messmer 2007). Ozoga and Verme (1982) and Peterson and Messmer (2007) reported improved individual body condition in fed deer. Robinette et al. (1973), Ozoga and Verme (1982), Baker and Hobbs (1985), and Peterson and Messmer (2007) documented short-term (<3 yr) increased survival and productivity in fed deer. Baker and Hobbs (1985) also reported that although feeding of deer may increase adult survival, it did not eliminate winter losses during prolonged severe weather conditions. Other published consequences of feeding programs included range degradation (white-tailed deer [*O. virginianus*]; Cooper et al. 2006), increased intraspecific competition (Schmitz 1990), redistribution of animals on the landscape resulting in changes in habitat use (Murden and Risenhoover 1993), and altered seasonal migration patterns (Peterson and Messmer 2007).

The differing effects of feeding programs on mule deer appear to be an artifact of site-specific conditions (Doenier et al. 1997, Smith 2001, Tarr and Pekins 2002, Peterson and Messmer 2007). Site-specific factors may include placement, type, and number of feed stations used (Schmitz 1990), nutritional content of supplements (Doman and Rasmussen 1944, Schoonveld et al. 1974, DelGiudice et al. 2000, Ouellet et al. 2001), and timely implementation of feeding (deCalesta et al. 1975). Given these site-specific variables, the long-term effects of feeding programs on deer populations may be determined only through site-specific monitoring over time (Doenier et al. 1997).

In 2001, the Utah Division of Wildlife Resources (UDWR), in response to sportsmen concerns, implemented their emergency winter-feeding policy for mule deer in northern Utah, USA. Winter-feeding continued through winter 2006–2007, excluding winter 2005–2006. This area is characterized by rapid urban development that has gradually encroached on historic mule deer winter range (Peterson and Messmer 2010).

This management decision afforded the UDWR an opportunity to evaluate the long-term effects of winter-feeding on mule deer populations in northern Utah. The primary objectives of this study were to determine whether survival,

Received: 16 December 2010; Accepted: 7 May 2011

[1] *E-mail: christine_peterson@fws.gov*

productivity, and mortality factors differed for cohorts of fed and nonfed mule deer over multiple, consecutive years under variable environmental conditions. In addition we were interested in learning whether winter-feeding would also contribute to winter-range habitat degradation through increased utilization of preferred winter browse. The mule deer population that we studied shared summer and transitional ranges but occupied different winter ranges.

STUDY AREA

We conducted this study in the Cache–Wasatch Mountains of northern Utah. Our study area was bisected by U.S. Highway 89, which extended from Logan, Utah, northeast to the west shore of Bear Lake at Garden City, Utah, and by U.S. Highway 91 on the west face of the Cache–Wasatch Mountains. Elevations ranged from 1,350 m to 2,997 m. The higher elevations in the unit constituted mule deer fawning and summer range, while lower elevations constituted winter range.

Range vegetation of the area was typical of the Intermountain West (West 1983). Mule deer summer range consisted largely of Douglas fir (*Pseudotsuga menziesii*) and quaking aspen (*Populus tremuloides*) forest interspersed with alpine meadows and shrublands. Lower elevation winter range consisted of sagebrush–steppe with sagebrush (*Artemisia* spp.) and bitterbrush (*Purshia tridentata*) interspersed with stands of bigtooth maple (*Acer grandidentatum*) and Utah juniper (*Juniperus osteosperma*). Cheatgrass (*Bromus tectorum*), broom snakeweed (*Gutierrezia sarothrae*), bulbous bluegrass (*Poa bulbosa*), balsamroot (*Balsamorhiza sagittata*), and mulesear (*Wyethia amplexicaulis*) were also common on lower elevations (Welsh and Moore 1973). Multiple farms were intermixed within the native ranges. This winter range was also highly fragmented due to increasing urbanization (UDWR 2003, Peterson and Messmer 2010).

The study area encompassed UDWR mule deer herd management-unit number 2. The population goal for this herd unit is 25,000 mule deer with a postseason ratio of 10–15 males:100 females. The unit averaged 66.5 fawns:100 adults and 12 males:100 females from 1992 to 2001. Total estimated postseason herd population for this herd unit as of December 2001 was 13,000 deer (D. Austin, retired, UDWR, unpublished data).

This area typically had warm, dry summers, and cold, snowy winters. Average annual temperatures ranged from -34° C to 38° C. Annual average precipitation (42 cm) in the area ranged from 16 cm to 83 cm, with most of this as snowfall in winter months, and rain–snow mix in April and May. During this study, weather extremes were recorded for snow accumulation, high and low temperatures, and severe drought. All study sites experienced greater snow accumulation and lower temperatures than were recorded at the local climate center.

Study Sites

We identified 19 potential study sites based on the historical presence of winter deer concentrations. From these we randomly selected 8 sites and assigned 4 as treatment and 4 as control sites. All sites had similar vegetation types, slope, aspect, elevation, and climate, and were located in the mouths of canyons within critical winter range. The actual feeding sites were placed in locations that facilitated access for feed distribution.

McClure (2001) reported maximum winter home ranges of about 469 ha for mule deer that wintered in our study area. In general, distance from bedding to feeding site for deer in winter in northern Utah does not exceed 1,500 m (D. Austin, personal communication). To minimize the chance of overlapping use of treatment and control sites by individual deer, we used this information to define the radius of each circular experimental site as 1,500 m, inclusive of 706 ha, then located the center of treatment sites >3 km from the center of control sites.

METHODS

Feeding Operations

Daily ad libitum feeding was initiated by local sportsmen under the supervision of the UDWR in late December of winter 2001–2002, and in early January in winter 2002–2003, 2003–2004, and 2004–2005. All winter-feeding programs were terminated concurrent with spring green-up in mid- to late March. No feeding was conducted in winter 2005–2006.

Feed rations consisted of whole corn (*Zea mays*), high-quality alfalfa hay (*Medicago sativa*), and commercially formulated 14% protein pellets. Formulated pellets consisted of alfalfa (23.0%), barley (11.0%), beet pulp (13.5%), calcite (1.0%), corn (20.0%), molasses (7.0%), monocal (1%), salt (1.0%), soy meal (8.5%), and wheat (14%). Feed rations were distributed in poly-resin half-barrels separated by 5–10 m. Rations were provided at a recommended rate of 0.9 kg/deer/day and based on daily population estimates (D. Austin, unpublished report). The same rations were offered each year on all feed sites. Access to the rations was closely monitored. Although there were Rocky Mountain elk (*Cervus elaphus*) in the area of several study sites, seasonal hunting pressure drove them from study sites as feeding was implemented, eliminating the need to control access to rations.

Radiotelemetry

From January through early March of 2001–2005, we captured 92 adult female mule deer in Clover traps (fed $n = 53$, nonfed $n = 39$; Rongstad and McCabe 1984). To reduce stress, captured animals were hobbled, fitted with blinders, and immediately processed on site (DelGiudice et al. 1990, Millspaugh et al. 2000). We fitted each adult doe with a radiocollar with mortality sensor (AVM Instrument Co., Ltd., Colfax, CA). We monitored these deer from May of 2002 through January of 2006. The study protocol was approved by the Utah State Institutional Animal Care and Use Committee (Permit no. 1084).

Annual Survival, Mortality Factors, and Productivity

We monitored radiocollared does 2–3 times/week to determine their status. To analyze annual survival for radiocollared deer, we pooled data by season: 1) winter and feeding season (25 Dec–30 Apr), 2) fawning season and summer (1 May–31 Aug), and 3) autumn and hunting season

(1 Sep–24 Dec). We calculated survival probabilities for 3 seasons and estimated survival, using the known-fate model in Program Mark (White and Burnham 1999). The sampling periods for determining survival were of different length each year; therefore, we standardized all estimates to annual survival probabilities using unequal time intervals in Program MARK ($\alpha = 0.05$).

When a mortality signal was detected, carcasses were located and examined within 48 hr (Harris 1945, Gill and O'Meara 1965, Ransom 1965, Trainer et al. 1981). When mortality occurred within 14 days of capture, we removed the individual from evaluation to reduce bias from possible capture myopathy (Williams and Thorne 1996). We assigned mortalities to 1 of 7 categories: 1) deer–vehicle collision (DVC), 2) predation, 3) malnourishment, 4) complications incidental to parturition, 5) poaching, 6) causes incidental to age, 7) unknown or other (Carrel et al. 1999, Mayer et al. 2002). When there was no apparent cause of death, we took the carcass to the U.S. Department of Agriculture Veterinary Diagnostic Lab in Logan, Utah for a detailed necropsy. To test for differences in cause of annual mortality for fed and nonfed does, we evaluated these data using a Pearson's chi-square test of homogeneity of proportions. Because of small cell counts, we based the *P*-value on all possible permutations, rather than on an asymptotic assessment (SAS 2001). Inferential tests with $\alpha = 0.05$ were considered significant.

During each fawning period, mid-May through mid-July, we monitored radiocollared does to determine reproductive status and identify specific fawning grounds. When fawning was imminent, we visually monitored each doe to determine the number of fawns produced. Feeding was not implemented in 2006; therefore, fawn:doe ratios for this year were dropped from analysis. We weighted fawn:doe data of radiocollared does according to the percentage seen relative to availability, that is, number present, on each site. We tested weighted fawn:doe ratios for effects of feeding, year, and site with a repeated-measures mixed model, repeated over 4 yr (SAS 2001). We included site in the model as a random factor nested within treatment. We considered it significant at $\alpha = 0.05$.

Browse Production and Utilization

We randomly established from 3 to 9, 13-m^2 circular plots, in areas of sagebrush–bitterbrush cover, and constructed 2 9-m^2 utilization exclosures on each site. We used double-sampling ocular estimation with reference units (Pechanec 1937, Austin and Urness 1983) to estimate current annual growth (CAG) as a measure of browse production (Lyon 1968, Anderson et al. 1972). We clipped and weighed check units at least once per sampling period. Immediately following spring migration, we used reference units from within the exclosures to estimate utilization on all plots from October 2002 to September 2006. We air-dried 50–100-g samples of check units in paper bags and calculated the percent air-dry weights for all CAG and utilization estimates. Current annual growth was estimated for sagebrush and bitterbrush on 90 random plots on feed sites in October and early November of 2002, 2003, and 2005, but early, deep snows precluded access to browse and prevented CAG measurements in October 2004. Current annual growth was also estimated for sagebrush and bitterbrush on 62 plots on nonfeed sites in 2002, but in autumn 2003 and 2005 deep snows and inaccessibility reduced CAG measurements to 24 plots on one site. We estimated utilization of browse for sagebrush and bitterbrush on 90 plots on feed sites in April of 2003, 2004, 2005, and 2006. We also estimated browse utilization for sagebrush and bitterbrush on 62 plots on nonfeed sites in 2002, but logistic constraints reduced utilization measurements to 24 plots on one site from 2004 to 2006.

We analyzed air-dry browse production and utilization data on feed versus nonfeed sites through generalized linear mixed models (GLMMIX) with SAS software. We tested for main effects and interactions due to treatment, zone, and year. For utilization we used a β distribution with a logit function and Kenward–Rogers degrees of freedom (SAS 2000). The β distribution resulted in utilization values of zero being interpreted as missing data, so we recoded zero values as 0.0001. For production, we used a γ distribution with a log function, and Kenward–Rogers degrees of freedom (SAS 2000). Given the modest degree of replication among sites ($n = 8$), and the influence of several factors such as weather, sample size, snow frozen to foliage, and wildfire, we considered $\alpha = 0.10$ significant.

We surveyed the number of deer utilizing feed and nonfeed sites during the feeding period in 2002–2006. Surveys consisted of counting all deer visible from a 1.6-km observational track emanating from the site center-point, over a 1–2-hr period. With this information we calculated the mean number of deer per day using the site, and percent annual change in numbers.

RESULTS

Annual Survival, Mortality, and Productivity

We included 90 does in the analysis of survival, 52 in the feed and 38 in the nonfeed groups. On the basis of minimum Akaike's Information Criterion (AIC_c) the best model was *S*(.), in which survival is constant between fed and nonfed groups, as well as being constant through time and across sites (Table 1; Burnham and Anderson 2002). The second-best model, which was 0.6 ΔAIC_c units from the top model, was *S*(group), in which survival differed between the fed and nonfed groups, but was constant through time and across sites. Because this was the best model with fed and nonfed groups, and because it is similar to the top model, we used this model to estimate survival in the known-fate model. In this study, vital rates for both fed and nonfed groups were declining (Table 2). Although survival for fed deer ($S = 0.80$, $SE = 0.03$) was slightly higher than for nonfed deer ($S = 0.73$, $SE = 0.05$), this difference was not significant ($P = 0.121$, 1-tailed test).

Fourteen radiocollars (15%) were found without a carcass present. Thus, we were unable to determine the fate of these animals. At the conclusion of this study, 53 of the 92 radio-

Table 1. Model selection results from analysis of doe survival for fed and nonfed mule deer, northern Utah, USA, 2001–2007.

Model[a]	No. of parameters	AIC$_c$	ΔAIC$_c$	Akaike wt	Model likelihood	Deviance
{*S*(.)}	1	340.87	0.00	0.31	1.00	338.86
{*S*group)}	2	341.46	0.60	0.23	0.74	337.44
{*S*(group × site)}	4	342.51	1.65	0.13	0.44	334.45
{*S*(group + site)}	3	343.35	2.48	0.09	0.29	337.31
{*S*(group + season)}	4	344.36	3.50	0.05	0.17	336.29
{*S*(group + yr)}	7	345.06	4.19	0.04	0.12	330.87
{*S*(group × yr)}	11	345.48	4.61	0.03	0.10	323.02
{*S*(group × season)}	6	347.55	6.68	0.01	0.04	335.41
{*S*(group + yr + season)}	9	347.94	7.07	0.01	0.03	329.63
{*S*(group + *t*)}	18	348.81	7.94	0.01	0.02	311.62
{*S*(group × *t*)}	34	367.12	26.25	0.00	0.00	294.88

[a] Group, fed or nonfed deer; site, feeding-site quality; season, winter, summer, or autumn; *t*, season and yr; that is, survival is different for each time period, or in this case, different for each season of each yr.

Table 2. Production estimates used in the population model for mule deer, northern Utah, USA, 2001–2006.

Group	Parameter[a]	Data time frame	Estimate	Variance[b]
Feed	Survival	2001–2006	0.799	0.004
	Recruitment	2003–2006	0.584	0.016
	Initial proportion fawns	2003–2006	0.318	
	Initial proportion does	2003–2006	0.469	
Nonfeed	Survival	2001–2006	0.715	0.006
	Recruitment	2003–2006	0.569	0.024
	Initial proportion fawns	2003–2006	0.381	
	Initial proportion does	2003–2006	0.533	

[a] Survival and recruitment were based on averages of annual estimates, while estimates of initial proportion fawns and does were based on average proportion for all yr.

[b] No variance was included in the model for the initial proportion of fawns and does.

collared does had died (58%), including 28 of 53 fed deer (53%), and 25 of 39 nonfed deer (64%). The cause of mortality was determined for 43 of the 53 (81%) radiocollared does (Table 3) and did not differ for fed and nonfed does ($\chi^2_6 = 1.85$, $P = 0.97$). Deer–vehicle collisions and malnourishment were the primary causes of mortality (DVC: fed $n = 8$, 29%; nonfed $n = 10$, 40%; and malnourishment: fed $n = 9$, 32%; nonfed $n = 8$, 32%). Deer–vehicle collision mortalities occurred predominantly, though not exclusively, from February to April and August to November. Malnourishment mortalities occurred mainly from February to April. The increased number of DVCs we recorded appeared to negate any production gains attributed to feeding. When we removed DVCs from the model, survival of fed (0.84, SE $= 0.033$, $P = 0.19$), and nonfed deer (0.79, SE $= 0.05$, $P = 0.19$) increased.

Productivity for fed and nonfed does was also similar. Summer fawn:doe ratios of radiocollared fed and nonfed deer did not differ (treatment × yr: $F_{3,13.6} = 1.17$, $P = 0.36$; treatment: $F_{1,9.08} = 0.01$, $P = 0.91$; yr: $F_{3,13.6} = 2.76$, $P = 0.08$).

Browse Production and Utilization

Mean production of sagebrush showed no effect from feeding ($F_{1,6} = 0.08$, $P = 0.79$), but increased 4% (26 kg/ha) from autumn 2002 (695 kg/ha) to autumn 2003 (721 kg/ha), and 25% (177 kg/ha) from autumn 2003 to autumn 2005 (898 kg/ha; yr: $F_{2,188} = 3.57$, $P = 0.03$). Production

Table 3. Causes of mortality for 53 monitored fed and nonfed mule deer, northern Utah, USA, 2001–2007.

			Treatment			
Mortality cause ($n = 53$)	Total no.	Total %	Fed no. ($n = 28$)	Fed %	Nonfed no. ($n = 25$)	Nonfed %
DVC[a]	18	34	8	29	10	40
Predation	2	4	1	4	1	4
Malnourishment	17	32	9	32	8	32
Parturition-related	2	4	1	4	1	4
Poaching	1	2	1	4	0	0
Age-related	3	5	2	7	1	4
Unknown[b] or other	10	19	6	21	4	16

[a] DVC = deer–vehicle collision.

[b] Unknown does not include any possibility of DVC.

of bitterbrush was greater on feed sites compared with nonfeed sites by 171% in autumn 2002 (539 kg/ha), 75% in autumn 2003 (515 kg/ha), and 55% in autumn 2005 (630 kg/ha; treatment × yr: $F_{2,19.5} = 3.26$, $P = 0.06$). Mean production of bitterbrush on all sites increased 19% (62 kg/ha) from autumn 2002 (327 kg/ha) to autumn 2003 (389 kg/ha), and 30% (116 kg/ha) from autumn 2003 to autumn 2005 (505 kg/ha; yr: $F_{2,19.5} = 6.37$, $P = 0.01$).

There was no effect of feeding on utilization of sagebrush (0.02 kg/ha; treatment: $F_{1,7} = 0.06$, $P = 0.81$), but utilization varied from 0.04 kg/ha in spring 2004 to 0.05 kg/ha in spring 2006 (yr: $F_{3,57} = 8.45$, $P = 0.001$). Feeding interacted with year to affect utilization of bitterbrush ($F_{3,28} = 11.22$, $P = 0.001$). Although utilization of bitterbrush was 65% higher on nonfeed sites (nonfed = 0.18 kg/ha, fed = 0.11 kg/ha) in spring 2003, utilization on feed sites was 300% higher (0.24 kg/ha) in spring 2004, 854% higher in spring 2005 (0.30 kg/ha), and 302% higher in spring 2006 (0.17 kg/ha) than on nonfeed sites.

On feed sites, mean numbers of deer increased 71% from winter 2002–2003 to winter 2003–2004, and 26% from this winter to winter 2004–2005. In winter 2005–2006, when feeding was not conducted, numbers on feed sites decreased by 23%. On nonfeed sites, mean numbers of deer increased by 46% from winter 2002–2003 to winter 2003–2004, 17% from this winter to the next, and by 1.5% to winter 2005–2006 when feeding was not conducted. Mean numbers of deer at each feed and nonfeed site increased annually from winter 2002–2003 to winter 2004–2005 (Table 4).

DISCUSSION

Growth of mule deer populations is linked to survival of does (Carpenter 1998, White and Bartmann 1998, Unsworth et al. 1999). Reported average doe survival for mule deer in the Intermountain West is 5–12% higher (mean = 0.85, SE = 0.011; Unsworth et al. 1999) than for the population we studied. Although our model suggested that even small increases in doe survival attributed to winter-feeding can affect production and population trends (Peterson and Messmer 2007), these short-term (<3 yr) benefits may not be enough to sustain these herds without major investments to protect and restore the remaining winter range (Austin 2010).

The 2 most frequent causes of mortality for our study populations were DVCs and malnourishment. The number of DVCs we recorded was 3 times higher than reported for other mule deer herds (Sawyer and Lindzey 2001). The effect of the high number of DVCs on doe survival was similar to that reported for a mule deer herd inhabiting range near Estes Park, Colorado, USA (Conner 2004). Overall, the decrease in survival via DVC was offset by the survival increase incurred during the feeding program.

More mortality attributed to malnourishment occurred in winters with the most severe conditions when feeding was conducted. However, feeding did not decrease the percent of total mortalities attributed to malnourishment. Generally the average duration of winter malnourishment (30–60 days) depends on not only the severity and duration of the conditions, but also on the initial condition of the deer and of the winter habitat (deCalesta et al. 1975, Wallmo et al. 1977, Anderson 1981, DelGiudice et al. 1990, Olson and Lewis 1994). This strongly suggests that there may be other factors involved in the malnourishment, such as timing of severe conditions and seasonal micronutrient deficiencies.

Although feeding programs may increase body condition and short-term survival (Ullrey et al. 1975, Peterson and Messmer 2007), the onset of severe storms coupled with normal winter malnourishment may increase metabolic costs beyond survivable levels (Kistner et al. 1980, Baker and Hobbs 1985, Smith 2001). This effect may be greater in fawns because of their higher relative metabolic rates (Moen 1968, Verme and Ozoga 1980, Parker et al. 1984, Hobbs 1989, DelGiudice et al. 2002). In addition, it may not be possible to prevent fawn mortality on feed sites due to increased competition and indigestibility of feed rations (Doman and Rasmussen 1944, Langenau 1996).

During our regular visits to the feed sites, we routinely observed adult deer chasing fawns from feed rations, even when feed stations were well-dispersed and filled. Severe winter conditions did not occur equally on all sites and may have contributed to the high variability. The inference from these data is that feeding programs do not meet the needs of all fawns under most conditions, and benefits are more likely to occur during the most severe conditions (Baker and Hobbs 1985).

Table 4. Average daily number of mule deer recorded using feed (F) and nonfeed (C) sites, Utah, USA, 2002–2006.

	Winter 2001–2002		Winter 2002–2003		Winter 2003–2004		Winter 2004–2005		Winter[a] 2005–2006	
Site	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
Feed										
F1	No data		52	25–81	49	11–83	No data		59	20–113
F2	109	32–166	46	5–160	126	57–183	137	58–210	72	21–216
F3	No data		25	7–33	34	13–52	38	14–61	72	28–128
Nonfeed										
C2	No data		11	3–32	46	27–76	24	15–33	42	10–85
C3	No data		38	13–73	61	23–156	45	32–56	83	27–206
C4	107	91–125	61	34–77	56	34–75	119	67–170	67	26–120
Feed site	Mean	SE	41	14.2	70	49.4	88	70.0	68	7.5
Nonfeed sites	Mean	SE	37	25.0	54	7.6	63	50.0	64	20.7

[a] No feeding was conducted in Winter 2005–2006.

In addition, distribution of corn, hay, and formulated pellets, although high in energy and protein, does not address the possibility of other nutrient deficiencies. Seldom addressed, but common, chronic or low-level mineral deficiencies reduce survival (Robbins 1983, McDowell 1992), and productivity (Underwood 1977, Robbins 1983, Flueck 1994). Furthermore, mineral deficiencies may increase seasonally with food shortages, with typical winter low-protein high-lignin diets, or with the increased requirements of gestation (Robbins 1983, McDowell 1992).

Fawn production in our radiocollared does was highly variable. Extremes in winter weather coupled with differential quality of winter range habitat may again have played a role in this variability. Alternatively, the variability may have been due to the small sample sizes and few years of the study. Still, our fawn:doe ratios compare favorably with some high ratios reported for this herd from 1930 to 1950 (Robinette 1976).

Winter-feeding programs implemented only occasionally may result in little short-term damage to habitat (Gill and Carpenter 1985, Sonant and Maestro 2006). However, small effects on browse species, particularly in arid climates, can have long-term impacts through altering plant community structure and species composition (Wandera et al. 1992, Jeffries et al. 1994, Manier and Hobbs 2006, Ward 2006). Previous research suggests that changes in nutrient availability may modify animal nutritional status, as well as food and habitat selection behaviors (Moen 1968, Kautz et al. 1982, Parker et al. 1996), migratory behavior (Augustine and McNaughton 1998), and may also alter vegetation (Murden and Risenhoover 1993). This winter-feeding program may have altered mule deer migratory behavior and habitat use, and ultimately contributed to deterioration of the winter browse component on feeding sites (Peterson and Messmer 2007).

As more fawns remain on winter range for extended periods (Peterson and Messmer 2007) the proportion of resident deer will likely increase (McClure 2001). This will result in increased utilization of winter range during summer, and reduce the carrying capacity of winter range during winter. Thus, small-scale responses initially considered trivial may actually have important long-term impacts that result from interactions among history (of the deer), necessity (due to environmental vagaries), and chance (short- and longer term weather events).

The feeding program in winters 2001–2006 not only increased the numbers of deer congregating and feeding near the feed distribution site (Fig. 1a), but also affected how deer used the surrounding zones. Fed deer tended to browse repeatedly over the same trails as they approached and left feed stations (Fig. 1b). In addition, fed deer traveled further from bed sites to feed. After feeding at the stations, fed deer moved up into areas near the feed sites, where they bedded and continued to browse. Density of deer in bedding areas on feed sites was greater than on nonfeed sites. Increased herd density limits forage selectivity and affects plant structure and cover (Augustine and McNaughton 1998). The numbers and activities of nonfed deer were more evenly distributed across study sites.

Figure 1. Increased numbers of mule deer congregated near feed stations as they waited for distribution of feed (a), and tended to browse repeatedly over the same trails as they approached and left feed stations (b) during each winter of a mule deer winter-feeding study, northern Utah, USA, 2001–2007.

Both fed and nonfed groups increased feeding activity through the season in winter 2002. Although winter 2005 was more severe than winter 2002, the feeding program was not implemented. Still, deer on the former feed sites increased feeding activity, whereas deer on nonfeed sites decreased feeding activity through the season. As increased snow depth restricted access to browse and decreased the nutrient:cost ratio (Parker et al. 1996), nonfed deer may have reduced the costs by decreasing the time spent feeding (Nudds 1980). However, on feed sites the higher production of bitterbrush possibly resulting from higher utilization in winter 2001, increased availability and provided a higher nutrient:cost ratio than on nonfeed sites. Thus, deer on these former feed sites continued to maximize their nutrient intake through increased feeding (Mautz 1978*a*,*b*; Schmitz 1990). Although the increased availability of nutrients on feed sites supports this theory, the increased snow depths in winter 2005 may have affected our ability to see and count bedded deer.

Winter forage selection by deer has different effects on sagebrush and bitterbrush (Welch and Wagstaff 1992, Bilbrough and Richards 1993, Bergman 2001). Due to placement and numbers of terminal growth buds, and resource allocation patterns, sagebrush declines with heavy utilization, whereas bitterbrush, more tolerant of increased use, may initially respond with higher production (Wandera et al. 1992, Bilbrough and Richards 1993, Wambolt et al. 1998, Bergman 2001) that gradually declines over time. However, if utilization of bitterbrush remains high for multiple years, production may decrease due to increased decadence and mortality. In this study, because of the high deer densities in winter 2001, browse utilization was likely much heavier than during the following years. This possibly led to the relatively higher production of bitterbrush and lower production of sagebrush on feed sites in 2002. Production of bitterbrush relative to sagebrush gradually decreased the following years, probably due to reduced utilization resulting from reduced numbers of deer, and increased response of sagebrush to greater precipitation (Shultz 1986). If deer populations and utilization remained high, decadence and mortality would decrease production of bitterbrush, resulting in decreased carrying capacity for mule deer.

During winter 2002, lower utilization of bitterbrush on feed sites was possibly because fed deer replaced part of their normal intake of bitterbrush with feed rations, whereas nonfed deer had no such replacement. However, in the more severe winters 2003 and 2004, fed deer may have utilized nutrients in rations to detoxify tannins in bitterbrush, and so utilization of bitterbrush increased on feed sites (Provenza et al. 2003). Multiple years of heavy use may ultimately decrease productivity of bitterbrush (Bilbrough and Richards 1993), and result in decreased carrying capacity for mule deer (Franzmann and Schwartz 1985, Boer 1992).

Utilization of both species varied annually, with mule deer selection of sagebrush possibly related to the availability of bitterbrush and feed rations, as well as deer density. Deer selected very little of either subspecies of sagebrush until deep snow or heavy utilization reduced the availability of bitterbrush, and/or increased nutrients from feed rations possibly enabled deer to detoxify terpenes from sagebrush (Provenza et al. 2003). However, much of the sagebrush on the study sites was located where snow accumulated in some years, possibly blocking utilization that otherwise might have occurred. With the reduced numbers of deer and variable snow cover in winters 2002–2004, neither utilization nor production of sagebrush varied.

The treatment × year effect on production, and the treatment × year and treatment × zone effects on utilization of bitterbrush may, in part, have resulted from deer congregating on feed sites and continuing to browse, as opposed to the more dispersed use of habitat by nonfeed deer (Cooper et al. 2006). However, these interactions may also be, in part, due to the increased nutrients of feed rations enabling deer to detoxify tannins in bitterbrush, increased duration on these winter sites by fed deer (Peterson and Messmer 2007), the greater preference of deer for bitterbrush over sagebrush (Bilbrough and Richards 1993), and the changing accessibility of browse due to variable snow depths and deposition sites each year.

MANAGEMENT IMPLICATIONS

Prolonged and repeated use of the same sites to feed deer as part of emergency winter-feeding programs altered mule deer habitat use and migration in northern Utah. Our results suggest that feeding programs could potentially decrease the carrying capacity of the winter range in developed landscapes by increasing deer year-round use of already limited winter range. Managers must be cognizant of these impacts and be prepared to implement alternative measures, such as rotating feed sites, to mitigate habitat impacts if winter-feeding is implemented.

If the goal of a winter-feeding program is to increase survival, the efficacy of the program would be increased by assessing site-specific factors such as weather conditions, browse production, deer condition, and the potential for increased mortality because of anthropogenic factors such as DVCs. Thus consistent localized monitoring of deer numbers, range condition, mortality, and weather conditions in areas historically prone to weather events must be conducted prior to implementation of winter-feeding policy in developed landscapes.

The increasing effect of DVCs on the productivity of this herd warrants increased management attention. Over one-third of the recorded mortalities in our study population were attributed to DVCs. Sullivan et al. (2004) suggested that the use of novel temporary signage in combination with increased enforcement of speed restrictions can provide a viable option to reduce DVCs. This effort will require increased coordination on the part of wildlife managers with local communities and law enforcement.

ACKNOWLEDGMENTS

We thank S. Durham, M. Conner, and N. Roberts for statistical advice. This project was funded by the Utah Division of Wildlife Resources, Sportsmen for Fish and Wildlife, Sportsmen for Habitat, the Pope and Young Club, Bridgerland Outdoor Coalition, the Utah Chapter of the Wildlife Society, Jack H. Berryman Institute for Wildlife Damage Management, Quinney Professorship for Wildlife Management, S. J. and Jesse E. Quinney Foundation, Utah State University Wildland Resources Department, and Utah State University Extension. The U.S. Forest Service granted access to several of the study sites.

LITERATURE CITED

Anderson, A. E. 1981. Morphological and physiological characteristics. Pages 27–98 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

Anderson, A. E., D. E. Medin, and D. C. Bowden. 1972. Mule deer numbers and shrub yield-utilization on winter range. Journal of Wildlife Management 36:571–578.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.

Austin, D. D. 2010. Mule deer. A handbook for Utah hunters and landowners. Utah State University Press, Logan, USA.

Austin, D. D., and P. J. Urness. 1983. Overwinter forage selection by mule deer on seeded big sagebrush–grass range. Journal of Wildlife Management 47:1203–1207.

Baker, D. L., and N. T. Hobbs. 1985. Emergency feeding of mule deer during winter: tests of a supplemental ration. Journal of Wildlife Management 49:934–942.

Bergman, M. 2001. Ungulate effects on their food plants: responses depending on scale. Dissertation, Swedish University of Agricultural Sciences, Umea, Sweden.

Bilbrough, C. J., and R. J. Richards. 1993. Growth of sage brush and bitterbrush following simulated winter browsing: mechanisms of tolerance. Ecology 74:481–492.

Boer, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Supplement 1:1–10.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carpenter, L. H. 1998. Deer in the West. Pages 1–10 *in* J. C. deVos, editor. Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

Carrel, W. K., R. A. Ockenfels, and R. E. Schweinsburg. 1999. An evaluation of annual migration patterns of the Paunsaugunt mule deer herd between Utah and Arizona. Arizona Game and Fish Department Research Branch, Technical Report no. 29, Phoenix, USA.

Conner, M. M. 2004. Estimation of mule deer population size, survival, and a description of movements in Rocky Mountain National Park. In collaboration with N. T. Hobbs and M. W. Miller. Report Prepared for Rocky Mountain National Park, Colorado, USA.

Cooper, S. M., M. K. Owens, R. M. Cooper, and T. F. Ginnett. 2006. Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. Journal of Arid Environments 66:716–726.

deCalesta, D. S., J. G. Nagy, and J. A. Bailey. 1975. Starving and refeeding mule deer. Journal of Wildlife Management 39:663–669.

DelGiudice, G. D., K. D. Kerr, L. D. Mech, and U. S. Seal. 2000. Prolonged winter undernutrition and the interpretation of urinary allantoin:creatinine ratios in white-tailed deer. Canadian Journal of Zoology 78:2147–2155.

DelGiudice, G. D., K. E. Kunkel, L. D. Mech, and U. S. Seal. 1990. Minimizing capture-related stress on white-tailed deer with a capture collar. Journal of Wildlife Management 54:299–303.

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.

Doenier, P. B., G. D. DelGiudice, and M. R. Riggs. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin 25:235–243.

Doman, E. R., and D. I. Rasmussen. 1944. Supplemental feeding of mule deer in northern Utah. Journal of Wildlife Management 8:317–338.

Flueck, W. T. 1994. Effect of trace elements on population dynamics: selenium deficiency in free-ranging black-tailed deer. Ecology 75:807–812.

Franzmann, A. W., and C. C. Schwartz. 1985. Moose twinning rates: a possible condition assessment. Journal of Wildlife Management 49:394–396.

Gill, R. B., and L. H. Carpenter. 1985. Winter feeding—a good idea? Proceedings of the Western Association of Fish and Wildlife Agencies 65:57–66.

Gill, J. D., and D. C. O'Meara. 1965. Estimating time of death in white-tailed deer. Journal of Wildlife Management 29:471–486.

Harris, D. 1945. Symptoms of malnutrition in deer. Journal of Wildlife Management 9:319–322.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101.

Jeffries, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71:193–206.

Kautz, M. A., G. M. Van Dyne, L. H. Carpenter, and W. W. Mautz. 1982. Energy cost for activities of mule deer fawns. Journal of Wildlife Management 46:704–710.

Kistner, T. P., C. E. Trainer, and N. A. Hartmann. 1980. A field technique for evaluating physical condition of deer. Wildlife Society Bulletin 8: 11–17.

Langenau, E. E. 1996. Artificial feeding of Michigan deer in winter. Wildlife Division Report no. 3244, Lansing, Michigan, USA.

Lyon, L. J. 1968. Estimating twig production of serviceberry from crown volumes. Journal of Wildlife Management 32:115–119.

Manier, D. J., and N. T. Hobbs. 2006. Large herbivores influence the composition and diversity of shrub–steppe communities in the Rocky Mountains, USA. Oecologia 146:641–651.

Mautz, W. W. 1978*a*. Nutrition and carrying capacity. Pages 321–348 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole, Harrisburg, Pennsylvania, USA.

Mautz, W. W. 1978*b*. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

Mayer, M. S., T. K. Fuller, R. D. Deblinger, and J. E. McDonald. 2002. Can low-precision population and survival estimates of deer be accurate? Wildlife Society Bulletin 30:440–448.

McClure, M. F. 2001. Energy, fractal movement patterns, and scale-dependent habitat relationships of urban and rural mule deer. Thesis, Utah State University, Logan, USA.

McDowell, L. R. 1992. Minerals in animal and human nutrition. First edition. Academic Press, New York, New York, USA.

Millspaugh, J. J., M. A. Coleman, P. J. Bauman, K. J. Raedeke, and G. C. Brundige. 2000. Serum profiles of American elk, *Cervus elaphus*, at the time of handling for three capture methods. Canadian Field Naturalist 114:196–200.

Moen, A. N. 1968. Energy balance of white-tailed deer in the winter. Transactions of North American Wildlife and Natural Resources Conference 33:224–236.

Murden, S. B., and K. L. Risenhoover. 1993. Effects of habitat enrichment on patterns of diet selection. Ecological Applications 3:497–505.

Nudds, T. D. 1980. Forage preference: theoretical considerations of diet selection by deer. Journal of Wildlife Management 44:735–740.

Olson, R., and A. Lewis. 1994. Winter big game feeding: an undesirable wildlife management practice. Department of Range Management, Cooperative Extension Service, University of Wyoming, Report B-1003, Laramie, USA.

Ouellet, J.-P., M. Crete, J. Maltais, C. Pelletier, and J. Huot. 2001. Emergency feeding of white-tailed deer: test of three feeds. Journal of Wildlife Management 65:129–135.

Ozoga, J. J., and L. J. Verme. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. Journal of Wildlife Management 46:281–301.

Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Zoology 74:442–450.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Pechanec, J. F. 1937. A comparison of some methods used in determining percentage utilization of range grasses. Journal of Agricultural Research 54:753–765.

Peterson, C. C., and T. A. Messmer. 2007. Effects of winter-feeding on mule deer in northern Utah. Journal of Wildlife Management 71:1440–1445.

Peterson, C. C., and T. A. Messmer. 2010. Can public meetings accurately reflect public attitudes about wildlife management. Journal of Wildlife Management 74:1588–1594.

Provenza, F. D., J. J. Villalba, L. E. Dziba, S. B. Atwood, and R. E. Banner. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Ruminant Research 49:257–274.

Ransom, A. B. 1965. Kidney and marrow fat as indicators of white-tailed deer condition. Journal of Wildlife Management 29:387–399.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, San Diego, California, USA.

Robinette, W. L. 1976. Probable causes of the recent decline of mule deer in western U.S. summary. Pages 125–127 *in* G. W. Workman and J. B. Low, editors. Mule deer decline in the West: a symposium. Utah State University, Logan, USA.

Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:3112–3325.

Rongstad, O. J., and R. A. McCabe. 1984. Capture techniques. Pages 655–676 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.

SAS Institute, Inc. 1999–2001. SAS procedures guide, release 8. Second edition. SAS Institute, Cary, North Carolina, USA.

Sawyer, H., and F. Lindzey. 2001. Sublette mule deer study. Final report. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.

Schmitz, O. J. 1990. Management implications of foraging theory: evaluating deer supplemental feeding. Journal of Wildlife Management 54:522–532.

Schoonveld, G. G., J. G. Nagy, and J. A. Bailey. 1974. Capability of mule deer to utilize fibrous alfalfa diets. Journal of Wildlife Management 38:823–829.

Shultz, L. M. 1986. Taxonomic and geographic limits of Artemisia subgenus tridentatae (Beetle). Pages 20–28 *in* E. D. McArthur and B. L. Welch, compilers. Proceedings of symposium on the biology of Artemisia and Chrysothamnus, July 9-13, Provo Utah. U.S. Department of Agriculture, General Technical Report INT-200, Intermountain Forest Service Research Station, Provo, Utah, USA.

Smith, B. L. 2001. Winter feeding of elk in western North America. Journal of Wildlife Management 65:173–190.

Sonant, K., and D. Maestro, editors. 2006. Baiting and supplemental feeding of game wildlife species. The Wildlife Society Technical Review 06-1. The Wildlife Society, Bethesda, Maryland, USA.

Sullivan, T. L., A. F. Williams, T. A. Messmer, L. A. Hellinga, and S. Y. Kyrychenko. 2004. Effectiveness of temporary warning signs in reducing deer–vehicle collisions during mule deer migrations. Wildlife Society Bulletin 32:907–915.

Tarr, M. D., and P. J. Pekins. 2002. Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, U.S.A. Canadian Journal of Zoology 80:6–15.

Trainer, C. E., J. C. Lemos, T. P. Kistner, W. C. Lightfoot, and D. E. Toweill. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968–1979. Oregon Department of Fish and Wildlife, Wildland Research Report 10, Salem, USA.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, R. L. Covert, and W. T. Magee. 1975. Consumption of artificial browse supplements by penned white-tailed deer. Journal of Wildlife Management 39:699–704.

Underwood, E. J. 1977. Trace elements in human and animal nutrition. Academic Press, New York, New York, USA.

Unsworth, J. W., D. F. Pac, and G. C. White. 1999. Mule deer survival in Colorado, Idaho and Montana. Journal of Wildlife Management 63:315–326.

Urness, P. J. 1980. Supplemental feeding of big game in Utah. Utah Division of Wildlife Resources, Publication 80-8, Salt Lake City, USA.

Utah Division of Wildlife Resources [UDWR]. 2003. Statewide management plan for mule deer. Utah Division of Wildlife Resources, Salt Lake City, USA.

Verme, L. J., and J. J. Ozoga. 1980. Effects of diet on growth and lipogenesis in deer fawns. Journal of Wildlife Management 4:315–324.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122–127.

Wambolt, C. L., W. W. Fraas, and M. R. Frisina. 1998. Bitterbrush (*Purshia tridentata Pursh*) growth in relation to browsing. Great Basin Naturalist 58:28–37.

Wandera, J. L., J. H. Richards, and R. J. Mueller. 1992. The relationship between relative growth rate, meristematic potential and compensatory growth of semiarid-land shrubs. Oecologia 90:391–398.

Ward, D. 2006. Long-term effects of herbivory on plant diversity and functional types in arid ecosystems. Pages 142–164 *in* K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, New York, New York, USA.

Welch, B. L., and F. J. Wagstaff. 1992. 'Hobble Creek' big sagebrush vs. antelope bitterbrush as a winter forage. Journal of Range Management 45:140–142.

Welsh, S. L., and G. Moore. 1973. Utah plants: tracheophyta. Third edition. Brigham Young University, Provo, Utah, USA.

West, N. E. 1983. Temperate deserts and semi-deserts. Pages 321–471 *in* N. E. West, editor. Ecosystems of the world. Volume 5. Elsevier Science, Amsterdam, Netherlands.

White, G. C., and R. M. Bartmann. 1998. Mule deer management—what should be monitored? Pages 104–120 *in* J. C. deVos, Jr., editor. Proceedings of the 1997 Deer/Elk Workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement 46:120–138.

Williams, E. S., and E. T. Thorne. 1996. Exertional myopathy (capture myopathy). Pages 181–193 *in* A. Fairbrother, L. N. Locke, and G. L. Hoff, editors. Non-infectious diseases of wildlife. Iowa State University Press, Ames, USA.

Associate Editor: Nielsen.