REVIEW

A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America

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ABSTRACT

1. Mule deer and black-tailed deer *Odocoileus hemionus* have exhibited marked population fluctuations throughout their range over the past century. The relative contributions of predation, forage availability and weather to observed population changes remain unclear and controversial.

2. We reviewed 48 studies on *Odocoileus hemionus* survival and predation from the past 30 years and quantified age-specific vital rates, population growth rates (λ) and causes of mortality. We also evaluated the effect of environmental variables on variation in vital rates and the contribution of age-specific survival to population growth.

3. Age-specific survival (ϕ) was the most frequently studied population parameter. *Odocoileus hemionus* have lower and more variable fawn survival than other ungulate species ($\phi_{summer} = 0.44$, CV = 0.42; $\phi_{annual} = 0.29$, CV = 0.67). Adult female survival conversely appeared to be high and stable throughout the geographical range of the species ($\phi_{annual} = 0.84$, CV = 0.06). Observed low fawn survival appears to be compensated for by high fecundity rates.

4. Predation was the primary proximate cause of mortality for all age classes, and was an important source of summer fawn mortality and of mortality in multi-prey, multi-predator systems. However, predator removal studies suggest that predation is compensatory, particularly at high deer densities, and that nutrition and weather shape population dynamics.

5. We propose three models to explain local population dynamics of *Odocoileus hemionus*: (i) populations are limited by forage availability and weather; (ii) adult females are limited by forage availability, fawns are limited by forage availability and predation, and population growth is constrained by fecundity and fawn predation; and (iii) large changes in the abundance of predators or alternative prey change predation risk and destabilize population dynamics.

6. Future research should be focused on: the effects of age-specific survival on population growth; possible interactions between predation, forage availability and weather; and the importance of multiple predator and prey species in shaping the population dynamics of *Odocoileus hemionus*.

INTRODUCTION

Population dynamics of ungulates are complex, and how predation and resource availability affect observed growth rates has long been a focus of much debate (Peek 1980, Gaillard et al. 2000, Sinclair & Krebs 2002). The effect of predation on ungulate dynamics is particularly controversial (Gaillard et al. 1998, 2000), especially in North America where ungulates are important game animals still coexisting with native predators, and where managers face demands to

maintain high population densities (Connolly 1978). While early studies of ungulate populations were based on competing hypotheses of bottom-up effects caused by food limitation vs. top–down effects from predation (Connolly 1978, Peek 1980), it is now acknowledged that both bottom–up and top–down mechanisms simultaneously affect ungulate dynamics and often interact (Sinclair & Krebs 2002, Sinclair 2003). The interactions between forage and predation are also likely to be mediated by environmental conditions such as weather (Hopcraft et al. 2010). Finally, ungulate body size and the diversity of both predator and prey communities are also critical factors, e.g., ungulate size simultaneously affects predation risk and nutritional demands (Hopcraft et al. 2010), and small-bodied ungulates in Africa tend to have more predators and higher predation rates than do larger ungulates (Sinclair et al. 2003).

To understand mechanisms underlying observed demographic variation caused by predation, resources and environmental conditions requires identifying temporal changes in age-specific vital rates caused by these factors, as well as the relative contributions of vital rates to population growth (Gaillard et al. 1998, 2000, 2010). Ungulate populations typically are characterized by high and stable survival rates of prime-aged females, moderately variable fecundity rates, widely variable fawn survival and lower survival and fecundity in senescent adults (Gaillard et al. 1998, 2000). In addition, population models have shown that population growth is affected by both variability and elasticity of vital rates, and variable fawn survival typically has a larger effect on population change than stable adult survival (Gaillard et al. 1998). However, because of the high elasticity of adult survival, small changes in adult survival can have large effects on population growth. Senescent adults generally have lower survival and fecundity, but the degree of variation in and causes of the reductions are poorly understood (Loison et al. 1999), although declines in body mass with age are the most likely explanation for observed reductions (Nussey et al. 2011).

Despite these recent theoretical advances, observed temporal variations in many ungulate populations remain unpredictable and poorly understood. For example, mule deer *Odocoileus hemionus*, including Columbian black-tailed deer *Odocoileus hemionus columbianus* and Sitka black-tailed deer *Odocoileus hemionus sitkensis* have exhibited large population fluctuations throughout their range in the last century (Connolly 1978, Wallmo 1981, Unsworth et al. 1999). These mid-sized members of the deer family indigenous to western North America occur in ecosystems ranging from deserts to coastal rain forests. Efforts to explain observed population fluctuations have focused on habitat conditions, although the effect of predation has received considerable attention and generated the most controversy (Connolly 1978, Ballard et al. 2001). The focus on

habitat and predation across a range of environmental variables has resulted in a large array of differing explanations for observed population fluctuations, including habitat changes caused by changing weather and land use, as well as suspected high predation rates (Connolly 1978, 1981, Ballard et al. 2001).

Uncertainty concerning the relative contributions of predation, forage and environmental conditions to mule deer population fluctuations has caused challenges for the management of the species (Heffelfinger & Messmer 2003). We reviewed studies on mule deer survival and predation published in the past 30 years, and quantified age-specific vital rates, population growth rates (λ) and causes of mortality. We highlight data needed to predict mule deer population dynamics more accurately and thus improve both management and conservation. We used this information to test the following hypotheses: (i) age-specific vital rates for mule deer, specifically high and stable adult survival and low and variable fawn survival, are similar to those reported for other ungulates; (ii) predation is the dominant cause of mule deer fawn mortality in summer but is replaced by poor nutrition in winter; (iii) predation and poor nutrition are equal causes of mortality in adult females; and (iv) age-specific interactions between predation and nutrition drive mule deer dynamics.

METHODS

Although there are currently 10 recognized subspecies of mule deer, we follow Wilson and Reeder (2005) and use mule deer to refer to all 10 collectively (i.e. to *Odocoileus hemionus*). Where appropriate, we separately refer to the black-tailed deer subspecies *Odocoileus hemionus columbianus* and *Odocoileus hemionus sitkensis* as black-tailed deer. The separation of black-tailed deer is supported by phylogenetic analyses of mitochondrial DNA (Latch et al. 2009) and differences in various life history traits and behaviour between the two groups (Wallmo 1981).

We used Web of Knowledge and Google Scholar to search all major wildlife and ecological journals using the search terms 'mule deer', 'black-tailed deer' and '*Odocoileus hemionus*' combined with the keywords 'predation' and 'survival', in both topics and titles. We also searched references of published articles to find additional publications, including government reports and unpublished theses. We included all studies in which survival rates (ϕ), fecundity, cause-specific mortality, population growth rate, kill rates or prey nutritional condition were reported (Fig. 1, Table 1). Following earlier authors (Ballard et al. 2001) we excluded predator diet studies, as these do not provide sufficient data to evaluate the effect of predation on prey populations.

Fig. 1. The geographical ranges of mule deer *Odocoileus hemionus* (light and dark grey areas) and black-tailed deer *Odocoileus hemionus columbianus* and *Odocoileus hemionus sitkensis* (dark grey area only) in western North America (Mackie et al. 2003). The 48 studies included in the review are shown as grey squares (mule deer not including black-tailed deer) and black triangles (black-tailed deer).

Definitions

We define additive mortality as an increase in one mortality factor that increases the total mortality rate, while compensatory mortality occurs when an increase in a mortality factor does not cause changes in the overall mortality rate (Bartmann et al. 1992a). We also attempted to determine the importance of different causes of mortality by comparing proximate, or immediate, causes of mortality with ultimate causes of mortality, the factors likely to be driving observed mortalities. Following these definitions, predation was considered the proximate cause of mortality of deer that were killed were in poor body condition, while nutrition was considered the ultimate cause.

Following Sinclair (1989) and Messier (1991), we refer to regulation as the density-dependent processes that move a population towards equilibrium, and limitation as any factor that causes a reduction in population growth rate. We define fecundity as the average number of young per female

per year; high snowfall as occurring in a winter with snowfall greater than the upper tail of the 99% confidence interval of a 15-year mean; and summer drought as occurring in a summer with rainfall lower than the 99% confidence interval of the 15-year mean. We chose the 15-year timeframe due to data availability.

Survival

We searched the literature for age-specific survival estimates. We included studies in which survival rates were reported from marked animals as well as those in which estimates were based on herd composition surveys. We included results from observational studies and from non-manipulated populations in experimental studies for summaries of survival estimates. We did not include male survival since mule deer have a polygynous mating system, and fluctuations in male survival do not affect population dynamics nearly as much as fluctuations in female survival

Table 1. The 48 studies of mule deer *Odocoileus hemionus* population dynamics reviewed, and the vital rates and causes of deer mortality presented in each

Study	Vital rates reported				Cause of mortality	
	Adult survival	Fawn survival	Fecundity	λ (growth rate)	Cause of mortality	Other data on predation
Atwood et al. 2007						✓
Atwood et al. 2009						✓
Bartmann et al. 1992a	✓	✓			✓	✓
Bender et al. 2007	✓				✓	
Bishop et al. 2005	✓	✓			✓	
Bishop et al. 2009	✓	✓	✓	✓	✓	✓
Bleich & Taylor 1998	✓				✓	✓
Bleich et al. 2006	✓	✓	✓		✓	
Bowyer et al. 1998						✓
Brown 2009						✓
Cooley et al. 2008						✓
Darimont et al. 2007						✓
Farmer et al. 2006	✓	✓			✓	✓
Hamlin et al. 1984		✓			✓	✓
Harrington & Conover 2007						✓
Hatter 1988		✓	✓		✓	
Hatter & Janz 1994	✓			✓		✓
Hornocker 1970						✓
Hurley et al. 2011	✓	✓	✓		✓	✓
Johnstone-Yellin et al. 2009		✓	✓	✓	✓	
Krumm et al. 2010						✓
Laundre et al. 2006						✓
Lawrence et al. 2004	✓	✓			✓	
Lingle 2000						✓
Lingle 2002						✓
Lingle et al. 2005						✓
Lingle et al. 2008						✓
Lomas & Bender 2007		✓			✓	
Lukacs et al. 2009	✓	✓				
Matthews & Coggins 1997	✓				✓	
McConnell & Dalke 1960				✓		
McCorquodale 1999	✓			✓		
McCoy & Murphie 2011		✓				
McNay & Voller 1995	✓				✓	✓
Miller et al. 2008						✓
Monteith et al. 2010	✓	✓			✓	
Nicholson et al. 1997	✓					
Peek et al. 2002				✓		
Pierce et al. 2000						✓
Pierce et al. 2004						✓
Pojar & Bowden 2004		✓			✓	
Robinson et al. 2002	✓		✓	✓		✓
Smith & Lecount 1979						✓
Unsworth et al. 1999	✓	✓			✓	
White & Bartmann 1998	✓			✓		
White et al. 1987	✓				✓	
Whittaker & Lindzey 1999		✓			✓	✓
Zager et al. 2007	✓					✓

(Wallmo 1981, Gaillard et al. 1998). Furthermore, mule deer sexes segregate outside the mating season (Bowyer 2004). Thus, the winter and summer competition for food and ensuing changes to the female body condition are the primary results of intraspecific competition among females.

We summarized annual adult female survival using a weighted mean approach, with sample size as the weighting variable (Cooper et al. 2009). We reported variation within studies as standard errors (SE), thus incorporating sample size in the error estimate, and, after testing whether data were normally distributed, used the mean SE from all studies to calculate confidence intervals for weighted means.

We summarized fawn survival independent of sex in three different categories: summer survival (0–6 months of age), winter survival (6–12 months) and first-year survival (0–12 months). These categories allowed us to evaluate proximate causes of mortality during biologically critical periods (Wallmo 1981, Gaillard et al. 2000). Most researchers reported survival in one or more of these categories. When average monthly survival rates were reported instead, we used a Kaplan–Meier estimator (Pollock et al. 1989) to adjust these rates to match the most appropriate of our three fawn survival categories. We only included first-year survival rates from studies in which fawns were followed for their entire first year of life. We report weighted means and SE for each category using the same methods as for adult survival. If rates were reported in a single study from more than one category (e.g. summer and first-year survival) we used both for summary purposes.

To determine potential bias in reported rates we used simple linear regression to quantify the effect of small sample sizes on age-specific survival estimates. In addition, we calculated the coefficient of variation (CV) in age-specific survival rates to determine variability among mule deer populations and provide comparisons to values reported for other ungulate species by Gaillard et al. (2000).

Ecoregional variation in survival

We distinguished studies by ecoregions designated by the Mule Deer Working Group of the Western Association of Fish and Wildlife Agencies, to investigate possible regional variation in survival obscured by our general summary. Although these regions contain variable habitats, the broad similarities in environmental conditions, land use histories and management concerns within ecoregions provide a useful framework for spatial comparison. Ecoregions include: Southwest Deserts, California Woodland Chaparral, Colorado Plateau Shrublands and Forests (CO Plateau), Northern Forests, Coastal Forests, Intermountain West and the Great Plains (Fig. 2; Heffelfinger et al. 2006, Sommer et al. 2007, Watkins et al. 2007, Hayden et al. 2008, Nelson et al. 2008, Cox et al. 2009, Fox et al. 2009).

Other vital rates

We report the weighted mean fecundity of non-captive mule deer, using sample size as the weighting variable and the mean SE as a measure of variance. Effects of senescence on survival and fecundity have been reported for other ungulates (Loison et al. 1999) and we searched for evidence of senescence effects on survival and fecundity in mule deer. We found insufficient data on the effects of senescence on adult female survival to provide a quantitative summary, but we summarize reported qualitative evidence.

Factors affecting survival

We summarized the proportion of mortalities due to predation, malnutrition/disease, other causes (e.g. accidents, vehicle collisions) and unknown causes from each study in which cause-specific mortality for both fawns and adult females was reported. We pooled malnutrition and disease because several researchers did not distinguish between the two. We then tested whether predation or malnutrition/disease mortalities were evenly distributed in adult female and summer and winter fawn populations, and for differences between annual fawn and adult female survival, using a chi-square goodness-of-fit test. We assigned other and unknown causes of mortality a value of 10% in the expected distributions based on results from previous reviews (Connolly 1978, Ballard et al. 2001) and data we collected for this review. We then assigned half of the remaining expected distribution to predation and malnutrition/disease mortality (40% each) and tested the actual distribution from each survival category against these values. We used these expected values to provide realistic analyses of proximate causes of mortality due to predation and malnutrition/disease while accounting for variation due to other and unknown causes of mortality.

We summarized results of studies of experimental predator removal and food supplementation, and observational studies conducted during large changes in predator numbers or alternative prey populations, and compare these results to the proximate causes of mortality reported in observational studies. We qualitatively summarized these results because marked animals were followed, and cause-specific mortality reported, in only three studies.

We evaluated the potential effect of weather on survival by testing both regional and local weather effects. The mean value of the southern oscillation index is correlated with regional weather patterns in the western United States (Stenseth et al. 2003). We used simple linear regression to compare the summer (June–September), winter (December–March) and annual mean southern oscillation index values with all reported fawn summer, winter and annual adult female survival, and to evaluate the relation-
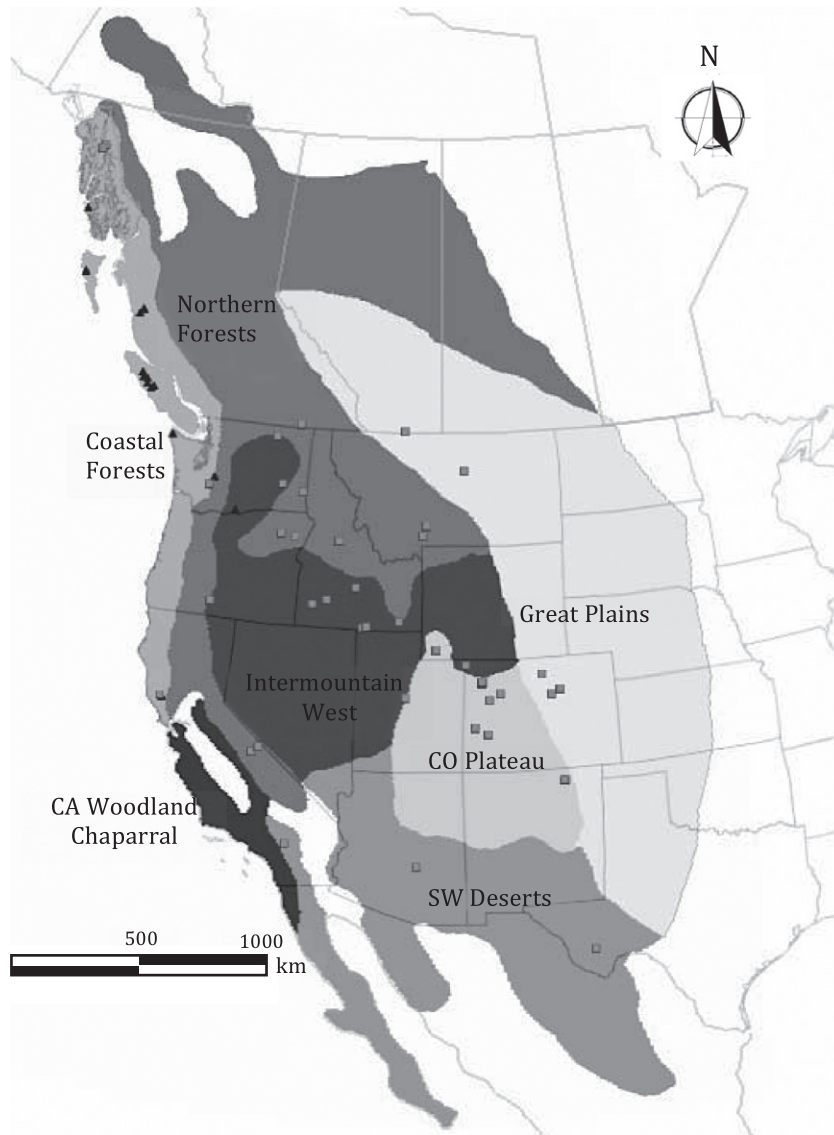
Fig. 2. Mule deer habitat ecoregions: Southwest Deserts, California Woodland Chaparral, Colorado Plateau Shrublands and Forests (CO Plateau), Northern Forests, Coastal Forests, Intermountain West, and Great Plains. Locations of studies are shown, as in Fig. 1.

ship between regional weather and mule deer survival. We also compared annual adult female and fawn overwinter survival during winters with high snowfall to survival during normal winters in the same study areas using local weather data. We obtained weather data, for all studies in which extreme weather was reported, from National Oceanic and Atmospheric Administration weather stations. We did not examine the effects of summer drought, because survival during drought years was quantified in few studies. We report the effect size of winter weather on survival, the reduction in survival during high snowfall winters $E_{h\phi}$, as: $E_{h\phi} = \phi_i - \phi_{avg}$ where ϕ_i is the study-specific survival for high snowfall winters, and ϕ_{avg} is the mean survival during normal weather in that study. We then calculated the weighted mean effect size for each category using study sample size as the weighting variable. We determined confidence intervals of effect size, after confirming survival data were normally distributed, using the mean SE of survival estimates from each study. We tested if the effect size of high snowfall winters was different from zero using a one-sample mean comparison test. To examine any potential lag effects of high snowfall, we also tested the difference between survival the year after a high snowfall winter and average survival. We examined effect size for bias across studies by regressing calculated effect size against sample size and the length of the study in years (Cooper et al. 2009). If periodic high snowfall winters have a biological effect, then longer and larger sample sizes should show increased effects, but if winter weather effects are due to sampling error, then longer and larger sample studies should show a reduced effect size.

All statistical tests were conducted in STATA (Anonymous 2011).

Population growth rates

We report population growth rates from studies in which it was estimated. For studies in which changes in deer densities over multiple years were reported, we estimated λ in two ways: as the slope of the regression of the log transformed counts, and as the tth root of the ratio of the initial and the final count, $\lambda = \left(\dfrac{N_t}{N_0}\right)^{\frac{1}{t}}$ where N_t equals population size in the last year of the study, N_0 equals population size in the first year of the study and t is the duration of the study in years (Largo et al. 2008). When these estimates were different we took the average of the two values. We also report results from studies in which the contribution of adult and fawn survival to λ was calculated.

RESULTS

We review a total of 48 studies containing information on survival, fecundity or causes of mortality of mule deer (Table 1), from throughout the geographical range of mule deer in North America (Fig. 1), although there appeared to be a reporting bias by ecoregion (Fig. 2). This may indicate a bias in data available in the public domain rather than a true bias in the amount of research conducted in these areas. Most reported research took place in the CO Plateau and the Intermountain West ecoregions; most reported black-tailed deer research was conducted on Vancouver Island (Fig. 2). The Southwest Deserts and Northern Forests (particularly in Canada) ecoregions are underrepresented. Data on the dynamics of mule deer in the desert areas of Nevada, Utah, and Wyoming as well as in Mexico are virtually unavailable. There was no detectable variation in adult female survival among ecoregions where survival was reported [Coastal Forests, CO Plateau, Intermountain West, Northern Forests, Southwest Deserts; $\chi^2 = 1.46$, degrees of freedom (d.f.) = 4, $P = 0.834$]. Annual fawn survival was insufficiently reported to test for ecoregional variation.

Survival and factors affecting survival

Fawn survival was the most frequently reported parameter of mule deer ecology ($n = 30$, Table 2), with data presented in 17 studies (Table 1). Most data were based on encounter histories of individuals fitted with telemetry devices (summer: $n = 10$ of 11 studies; winter: $n = 12$ of 12; first year: $n = 5$ of 7). The weighted mean summer fawn survival was 0.44 (CV = 0.42), winter survival was 0.61 (CV = 0.31) and first year survival was 0.29 (CV = 0.67; Table 2).

Sample size explained a small proportion of variance in reported summer or winter fawn survival ($R^2 = 0.06$ and $R^2 = 0.08$, respectively). However, a large proportion of variance in first year fawn survival was explained by sample size ($R^2 = 0.85$): first year survival was low in studies with large sample sizes. Estimates of first year fawn survival may have been biased low due to the small number of studies from which data were available.

Proximate causes of mortality for fawns were recorded in 16 studies (summer: $n = 8$, winter: $n = 7$, first year: $n = 4$). Predation and malnutrition/disease were the most common causes of mortality, and both were different than expected by chance (summer: $\chi^2 = 17.63$, d.f. = 3, $P < 0.001$; winter: $\chi^2 = 9.16$, d.f. = 3, $P = 0.01$; first year: $\chi^2 = 12.53$, d.f. = 3, $P = 0.006$; Fig. 3, Table 2). Predation was a more frequent, and malnutrition/disease a less frequent cause of mortality than expected for all fawn survival categories, although this difference was smallest in the first year survival category. A diverse suite of species was reported to prey on fawns. Primary fawn predators included coyotes *Canis latrans* ($n = 6$), mountain lions *Puma concolor* or bobcats *Lynx rufus* ($n = 3$), wolves *Canis lupus* ($n = 2$), and black bears *Ursus americanus* ($n = 1$). The weighted mean proportions of predation and malnutrition/disease mortality were not different between the summer and winter survival categories (predation: $\chi^2 = 0$, d.f. = 1, $P = 1$; malnutrition/disease: $\chi^2 = 1.59$, d.f. = 1, $P = 0.21$).

Adult female survival was the second most frequently reported parameter of mule deer ecology in the studies we reviewed ($n = 21$, Table 1); the weighted mean adult female annual survival was 0.84 (CV = 0.06). Adult female survival estimates were remarkably constant throughout the entire mule deer range and over the 30 plus years of mule deer research we summarized. Sample sizes and study durations explained little of the reported variation in adult female survival ($R^2 = 0.09$ and $R^2 = 0.01$, respectively) and did not appear to bias reported survival estimates.

Causes of adult female mortality were reported in 12 studies (Table 3). Predation was the largest reported proximate cause of mortality and was larger than expected by chance ($\chi^2 = 19.6$, d.f. = 3, $P < 0.001$; Fig. 3). The percentage of mortality caused by predation in adult females was highly variable and ranged from 22% to 66% (Table 3, Fig. 3). All other causes of mortality made up smaller percentages of total mortality which did not differ significantly from each other ($\chi^2 = 0.46$, d.f. = 2, $P = 0.80$; Table 3). Mountain lions were the main reported predator of adult female mule deer, although wolves were an important predator in British Columbia, Canada (Hatter 1988).

Weather effects on mule deer survival depended on age class. High winter snowfall effect sizes for adult females were heavily correlated with sample size and study length ($R^2 = 0.42$ and $R^2 = 0.33$, respectively): larger studies that

Table 2. Mule deer fawn survival rates (in three categories: summer, winter and first year) and causes of mortality

Study	Sample size	Fawn survival rates Summer	Cause of mortality as a percentage (%) of total mortality Predation	Malnutrition/disease	Other	Unknown
Bishop et al. 2009*	241	0.482	NR	NR	NR	NR
Bleich et al. 2006*	R	0.28‡	NR	NR	NR	NR
Hamlin et al. 1984	91	0.608	90	0	10	0
Hatter 1988*	28	0.616	64	21	14	0
Hurley et al. 2011*	250	0.452	64	22	7	7
Johnstone-Yellin et al. 2009	30	0.266	56	6	6	31
Lomas & Bender 2007*	100	0.210	27	34	6	33
McCoy & Murphie 2011*	228	0.514	NR	NR	NR	NR
Monteith et al. 2010	114	0.337	60	12	17	11
Pojar & Bowden 2004	230	0.501	44	38	9	10
Whittaker & Lindzey 1999	83	0.341	79	0	6	15
Weighted mean		0.440	58	21	9	12
95% Confidence interval		0.33–0.55	53–63	14–28	8–10	7–10
		Winter				
Bartmann et al. 1992b	241	0.300	25	66	9	0
Bartmann et al. 1992c	247	0.250	72	19	9	0
Bishop et al. 2005	295	0.526	44	30	26	0
Bishop et al. 2009*	241	0.684	65	27	8	0
Bleich et al. 2006*	109	0.859	NR	NR	NR	NR
Farmer et al. 2006*	19	0.714	NR	NR	NR	NR
Hurley et al. 2011*	301	0.561	67	16	3	14
Lawrence et al. 2004	72	0.795	35	26	26	13
Lukacs et al. 2009	2030	0.721	NR	NR	NR	NR
Unsworth et al. 1999	72†	0.44	45	39	16	0
White & Bartmann 1998	330†	0.610	NR	NR	NR	NR
White et al. 1987	426	0.473	NR	NR	NR	NR
Weighted mean		0.610	58	30	12	0
95% Confidence interval		0.51–0.71	51–65	25–35	8–16	0
		First year				
Bishop et al. 2009*	241	0.330	NR	NR	NR	NR
Farmer et al. 2006*	19	0.51	22	67	11	0
Hatter 1988*	28	0.39	35	15	12	38
McCoy & Murphie 2011*	228	0.33	74	19	2	4
Robinson et al. 2002	R	0.21‡	NR	NR	NR	NR
Smith & Lecount 1979	R	0.39‡	NR	NR	NR	NR
White et al. 1987	426	0.224	48	45	2	5
Weighted mean		0.287	55	36	3	6
95% Confidence interval		0.187–0.387	49–61	33–39	2.4–3.6	5.5–6.5

Weighted means and 95% confidence intervals are shown for each category.
R = calculated from recruitment measures such as composition counts.
NR, not reported.
*Survival was reported in multiple survival categories.
†Not reported; calculated from general information in study.
‡Calculated from recruitment measures.

ran for more years showed reduced effect sizes. Consequently we did not report adult effect sizes since it is highly likely that results are biased. Effect sizes of winter fawn survival showed no relationship with sample size ($R^2 < 0.01$) or study length ($R^2 = 0.11$). Regional weather patterns, as indicated by southern oscillation index values, were not related to summer ($R^2 < 0.01$) or winter fawn survival ($R^2 = 0.07$). However, local snowfall had a large impact on overwinter fawn survival. The weighted mean effect size of high snowfall on winter fawn survival was −0.29 (SE = 0.06) and was significantly different from 0 (one sample $t_7 = -11.33$, $P < 0.001$). Fawn survival was reduced by up to 42% during
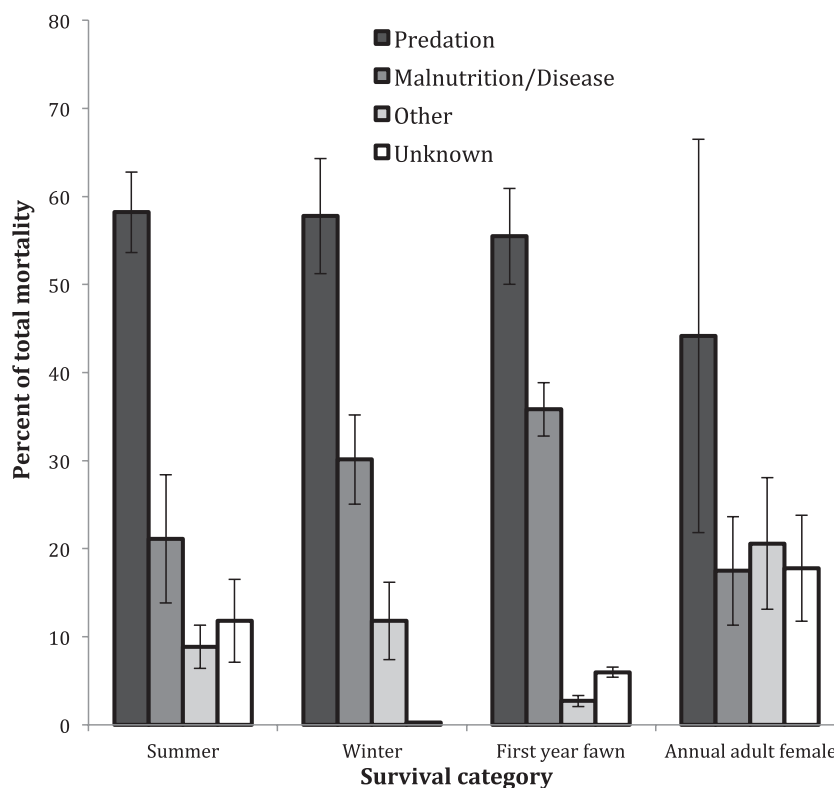
Fig. 3. Proximate causes of mule deer mortality (predation, malnutrition/disease, other and unknown) as percentages of reported total mortality for all age classes (error bars represent 95% confidence intervals; winter and summer mortality is calculated over 6 months, first year and annual rates are per year).

high snowfall winters (Fig. 4). To evaluate whether high snowfall enhanced subsequent summer forage, we compared fawn winter survival the year after high snowfall winters with average winter survival for the same area. We found that the weighted mean effect size was not significantly different from zero (one sample $t_7 = 1.17$, $P = 0.28$).

Other vital rates and senescence

Fecundity estimates were only reported in six studies: the weighted mean was 1.70 (SE = 0.12) fawns per female. Captive feeding studies have shown that fecundity appears to be positively associated with nutritional status of does (Robinette et al. 1973, Tollefson et al. 2010) and this has been confirmed in some non-captive populations (e.g. Monteith et al. 2010).

Almost all researchers reported survival for adults grouped into a single age class, and evidence of senescence on female survival was reported in only four studies (Table 3). In these studies, lower survival in females over eight years old was attributed to both increased susceptibility to predation and malnutrition/disease (White et al. 1987, Bishop et al. 2009, Hurley et al. 2011).

Population growth

Population growth rates were reported in only eight studies, and the weighted mean value of λ was 0.99 (SE = 0.04). In

five of these studies, effects of variation in age-specific survival on λ were also estimated. In four studies, fawn survival and recruitment were the largest contributors to changes in λ (Hatter & Janz 1994, White & Bartmann 1998, Lomas & Bender 2007, Bishop et al. 2009); in one study, adult survival had the largest effect on λ (Robinson et al. 2002). Hatter and Janz (1994) and Bishop et al. (2009) also found that adult survival was an important secondary factor in changes in population growth.
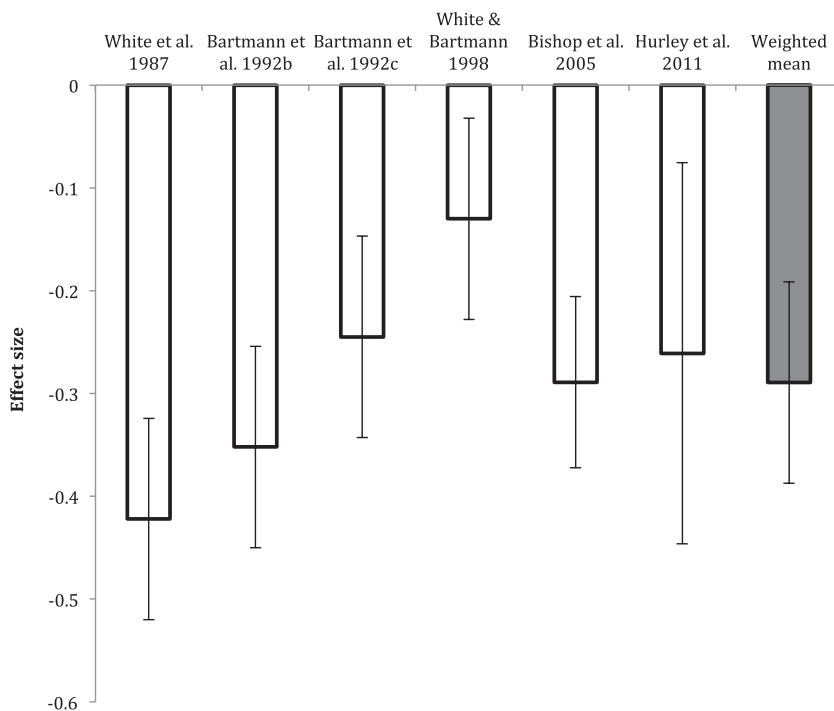
Experimental studies

We found six studies (five on predator control, one on predator reintroduction) in which vital rates of mule deer were reported following human-caused changes in predator densities (Table 4). In three of the five predator control studies, coyotes were removed, in one, coyotes and mountain lions were removed, and in one, wolves were removed. Results of predator control studies remain variable, but were more conclusive than results of earlier research (Ballard et al. 2001). Coyote removal generally had no effect. In one study slight increases in deer density occurred following efforts to control coyotes, but immigration into the treatment area, rather than an increase in fawn survival, was suspected (Harrington & Conover 2007). Overall, evidence showed that both coyote and mountain lion predation was compensatory rather than additive (Table 4).

Table 3. Annual adult female mule deer survival rates and causes of mortality, with weighted means and 95% confidence intervals

Study	Region	Survival	Cause of mortality as a percentage (%) of total mortality			
			Predation	Malnutrition/disease	Other	Unknown
Bartmann et al. 1992a	CO Plateau	0.86	NR	NR	NR	NR
Bender et al. 2007	CO Plateau	0.81	13	61	9	17
Bishop et al. 2005	Intermountain West	0.81	23	7	36	34
Bishop et al. 2009	CO Plateau	0.91 (S)	35	16	35	16
Bleich & Taylor 1998	Intermountain West	0.75	63	9	4	24
Bleich et al. 2006	Intermountain West and Northern Forest	0.86	NR	NR	NR	NR
Farmer et al. 2006	Coastal Forest	0.80	45	25	30	0
Hatter & Janz 1994	Coastal Forest	0.84	NR	NR	NR	NR
Hurley et al. 2011	Intermountain West and Northern Forest	0.89 (S)	73	6	6	15
Lawrence et al. 2004	SW Desert	0.86 (S)	32	41	18	9
Lukacs et al. 2009	CO Plateau	0.84	38	13	25	25
Matthews & Coggins 1997	Northern Forest	0.85	12	28	48	12
McCorquodale 1999	Intermountain West	0.80	61	6	22	11
McNay & Voller 1995	Coastal Forest	0.74	73	6	6	15
Monteith et al. 2010	Intermountain West	0.89	NR	NR	NR	NR
Nicholson et al. 1997	SW Desert	0.81	NR	NR	NR	NR
Robinson et al. 2002	Northern Forest	0.72	62	10	10	19
Unsworth et al. 1999	CO Plateau, Intermountain West, Northern Forest	0.85	NR	NR	NR	NR
White & Bartmann 1998	CO Plateau	0.87	NR	NR	NR	NR
White et al. 1987	CO Plateau	0.83 (S)	11	37	17	34
Zager et al. 2007	Unknown	0.85	NR	NR	NR	NR
Weighted mean		0.84	44	17	21	18
95% confidence interval		0.745–0.935	22–66	11–23	14–28	12–24

S = senescence effects on survival are reported.

NR, not reported.

Fig. 4. Effect of high snowfall on winter fawn survival rates, as quantified in six studies, plus the weighted mean effect size (error bars represent 95% confidence intervals).

Table 4. Results from experimental studies of mule deer population dynamics, showing effects of changes in predators and nutrition

Study	Study type	Predator species	Temporal scale (years)	Spatial scale (km²)	Predation additive or compensatory?	Short-term population change	Long-term population change
Atwood et al. 2007	Predator recolonization	Wolf	3	680	Unknown	↓ Predation risk	Unknown
Bartmann et al. 1992c	Predator removal	Coyote	7	140	Compensatory	None	Not measured
Bishop et al. 2009	Nutritional supplement	Mountain lion, coyote, bear	4	7700	Compensatory	↑ Survival ↓ Mortality – all types	Not measured
Brown 2009	Predator removal	Coyote	2	10518	Possibly compensatory	None	Not measured
Harrington & Conover 2007	Predator removal	Coyote	2	1900	Possibly additive	↑ Density ≡ Fawn : doe ratio	Not measured
Hatter & Janz 1994	Predator removal	Wolf	20	2400	Additive	↑ Population	Stable at higher level
Hurley et al. 2011	Predator removal	Coyote	6	14700	Compensatory	↑ Fawn survival (only in certain conditions)	No change in growth rate
Hurley et al. 2011	Predator removal	Mountain lion	6	14700	Compensatory	↑ Survival ↑ Fawn : doe ratio	No change in growth rate

The only conclusive evidence of additive predation was found on Vancouver Island, British Columbia, as a result of increasing wolf populations (Hatter & Janz 1994; Table 4). Wolf removal on Vancouver Island led to increased adult female mule deer survival, fawn to doe ratios, and population growth rate (Hatter & Janz 1994). However, an observational study in Montana, USA, during wolf recolonization showed that higher wolf populations actually resulted in lower predation risk for mule deer (Atwood et al. 2007, 2009), and the overall impact of wolves on mule deer remains unresolved. The reduced predation was probably due to a preference of wolves for elk *Cervus elaphus*, and changes in spatial overlap between elk and mule deer in the area after wolf recolonization.

Supplemental feeding during winter over large areas resulted in decreased mortality due to all causes, including predation, even though there was no evidence that predators were preying on mule deer in poor condition in control areas (Bishop et al. 2009).

DISCUSSION

Mule deer population dynamics match the general pattern of variable fawn survival and recruitment together with high and stable adult survival reported for other ungulates (Gaillard et al. 1998, 2000). However, results from our review indicate that mule deer may experience comparatively lower (mule deer = 0.44 vs. other ungulates = 0.64) and more variable (mule deer CV = 0.42 vs. other ungulates CV = 0.27) summer fawn survival (Gaillard et al. 2000).

Higher observed fecundity rates (1.70 in mule deer vs. 0.82 for all ungulates) apparently enable mule deer to compensate for reduced summer fawn survival over longer time scales. As expected, observed variation in adult female survival (CV = 0.06) is considerably lower than variation in fawn survival, and is close to the mean variation in adult survival for all ungulates (CV = 0.09). Thus our results indicate that mule deer may depend more than other ungulates on high fecundity and on high and stable survival of adult females to prevent long-term population declines.

The contribution of environmental variables to vital rates is affected by population density (Kie et al. 2003), and it is important to note that most studies we reviewed seemingly occurred at high density relative to nutritional carrying capacity (K). This assessment is supported by general poor or average body condition of adults, an increase in survival after density reduction (i.e. Bartmann et al. 1992a), compensatory predation (Table 4), and low reporting of high litter sizes (Kie et al. 2003). Therefore, our conclusions predominantly relate to high-density populations, since both predation and nutrition have different effects at different populations densities. In particular, predation at low ungulate densities can be density dependent or even inversely density dependent (McLellan et al. 2010). At higher densities, predation is often limited by handling time and predator territoriality, and so becomes density independent (e.g. Messier 1991, Bartmann et al. 1992a, Sinclair 2003).

Our review confirms that the proximate and ultimate causes of mule deer mortality are often different, and that assessing proximate causes of mortality alone results in a

poor predictor of mule deer dynamics. Predation was the largest proximate cause of mortality in both adults and fawns in all studies, including in fawns during winter. However, there was little evidence that predation mortality was additive, or that predation drove mule deer declines. Most predator removal studies showed that predation was compensatory (Table 4); one provided the first evidence of compensatory predation on adult mule deer by mountain lions (Hurley et al. 2011). The single large-scale nutritional supplementation study provided evidence for an increase in survival of both fawns and adults due to feeding (Bishop et al. 2009). These findings indicate that nutritional condition is likely to be the largest ultimate cause of mortality for adult females and fawns, with the exception of early summer fawn mortality (see below). This matches our hypothesis for fawn mortality but is different than we expected for adults. Nutrition seems generally more important for setting equilibrium population levels than predation, although predation appears to be the mortality source that keeps populations near equilibrium density.

Nutrition further influences mule deer dynamics since fecundity and fawn birth weight are driven by nutritional status (Parker et al. 2009). Mule deer seem to depend on higher fecundity to stabilize populations, and populations are likely to be sensitive to changes in available nutrition and have a higher intrinsic growth rate than populations of most other ungulates in good nutritional condition, because of the ability of mule deer to give birth to twins and triplets (Anderson 1981). Mule deer are highly selective feeders that depend on forage quality more than quantity (Wallmo 1981), and so annual weather effects on vegetation quality should affect year-to-year mule deer dynamics (Parker et al. 2009). However, while we found evidence of high winter snowfall lowering winter fawn survival, we found no evidence of precipitation affecting survival in the following year, indicating that increases in forage in summers following high snowfall years did not compensate for lower survival in high snowfall winters. We also found that high snowfall only had a small effect on adult female survival, contrary to predictions for high-density populations of deer with relatively poor body condition (Kie et al. 2003). Fecundity was too sparsely reported for us to examine nutritional effects on birth rates in non-captive populations.

The two notable exceptions to the pattern of compensatory predation mortality were summer fawn mortality and predation in multi-predator, multi-prey systems. Predation is the largest proximate cause of summer fawn mortality, and it is unlikely that early fawn predation is linked to maternal or fawn body condition, since mule deer fawns employ a hiding strategy to escape predators during the first 2–4 weeks following birth (Wallmo 1981). Even fawns with higher birth weights discovered by predators while hiding would thus be unable to escape. Most mule deer popula-

tions also coexist with a larger suite of fawn predators (including mountain lions, bobcats, bears, and coyotes) than adult predators. However, the true effect of summer fawn predation on mule deer dynamics is currently hard to identify because few researchers have followed fawns for their entire first year of life ($n = 5$ studies).

Predation also plays a larger role in declines of mule deer in multi-prey, multi-predator systems that have experienced large and recent changes in predator or alternative prey populations (Hatter & Janz 1994, Robinson et al. 2002, Cooley et al. 2008). Population declines in two mule deer populations in Washington, USA, and British Columbia were strongly linked to apparent competition with increasing white-tailed deer Odocoileus virginianus, mediated by mountain lion predation on adult females (Robinson et al. 2002, Cooley et al. 2008). Increasing wolf populations in Vancouver Island also caused a decline in a high-density black-tailed deer population, and the predator removal study that was conducted was successful in increasing deer populations (Hatter & Janz 1994). Fawn predation, especially during summer, is also sensitive to availability of alternative prey species. Prey switching, both annually and seasonally, has been observed for coyotes at high densities of microtine rodents, lagomorphs, or ground squirrels, and may result in reduced fawn predation rates (Hamlin et al. 1984, Lingle 2000). In one study, coyote removal only led to increased fawn survival when populations of alternative prey were high (Hurley et al. 2011). In some areas where white-tailed deer and mule deer overlapped, coyotes preyed more heavily on white-tailed deer fawns in summer, probably because white-tailed deer fawns are born earlier (Whittaker & Lindzey 1999) and because mule deer mothers show more defensive behaviour (Lingle et al. 2005).

The importance of mortality from predation, nutrition and weather depends on both mule deer age class and on the community of predator and prey species, but at this time there are not enough data to evaluate whether these interactions are driving dynamics, and further investigation is needed. Some modelling suggests that predation may exacerbate population declines caused by unfavourable weather (Laundré et al. 2006). In this case nutrition and weather were the ultimate causes of mortality, and managers should be cautious when assessing populations, because finding additive mortality in a declining deer population is not proof that predation is driving the decline. Weather is likely to interact with predation through behavioural mechanisms. Ungulates in poor body condition take greater risks to forage (Sinclair & Arcese 1995) and prey selection of many predators can be influenced by prey body condition (e.g. Sinclair & Arcese 1995, Krumm et al. 2010) although results depend on predator species (Hornocker 1970, McLellan et al. 2012). Other mechanisms may also be operating, since nutritional supplementation lowered predation

mortality even though predators were not selecting nutritionally stressed adults in control populations (Bishop et al. 2009).

The reliance of mule deer populations on high and stable adult survival rates shows that suppression of both fawn and adult survival simultaneously from predation and other mortality sources can lead to marked and sustained population declines. Such patterns may contribute to the declines of other ungulates including bighorn sheep *Ovis canadensis* (Johnson et al. 2010). The fact that the predator and prey community can have a large effect on mule deer survival rates shows that community ecology greatly influences appropriate interventions for mule deer management. Although evidence for predators holding deer populations far below K is scarce, we did find evidence that mule deer populations may be held slightly below K in communities with changing predators and alternative prey. The concept of a 'community carrying capacity' may have a high heuristic value to guide managers to make interventions (i.e. allowing hunters to shoot a proportion of invading white-tailed deer, in order to stabilize mule deer populations) and manage for multi-species objectives, but the role of predation in multi-prey, multi-predator systems at varying deer population densities needs further investigation.

The role of disease appears to be minor in most mule deer declines, but has affected mule deer locally in several ecoregions (e.g. adenovirus outbreak in California; Woods et al. 1996). Examples of disease interacting with other mortality factors are: hair loss syndrome increasing predation risk and death from malnutrition of black-tailed deer fawns in Washington (McCoy & Murphie 2011), and chronic wasting disease increasing risk of predation by mountain lions in Colorado (Krumm et al. 2010).

Competition between ungulates may also affect dynamics, but links between vital rates and these interactions are currently unclear.

Feedback patterns driving mule deer population dynamics

We identify three feedback patterns which are likely to drive mule deer population dynamics, depending on the ecological context of the deer population:

1. In high-density populations near K, nutrition, interacting with weather, determines population equilibrium density. Predation is primarily compensatory and, together with malnutrition/disease, acts as a regulating force.

This pattern is most likely in food webs that are relatively stable in terms of predator species and alternative prey levels. Long-term population cycles will be mainly driven by changes in nutrition because of weather and habitat change, and compensatory predation and malnutrition/disease will regulate populations around this shifting equilibrium point. Extreme weather events may destabilize dynamics by causing large and abrupt changes in survival that linger through cohort effects (Forchhammer et al. 2001, Coulson et al. 2006).

2. In systems with diverse predator communities, or large populations of alternative prey or predators, fawns are limited by predation and nutrition interactions, adult females are limited by nutrition, and population growth is constrained by both fawn predation and nutritional effects on fecundity.

In this scenario, fawn survival and recruitment are affected both by nutrition (mainly acting through birth weight) and by summer fawn predation, while adult survival is mostly affected by nutritional status and possibly senescence effects, depending on population age structure. Maternal nutritional condition affects both the birth weight of fawns and fecundity, resulting in complex interactions between nutrition and predation, which determine recruitment and population rate of increase. These interactions and the importance of predation change depending on predator diversity and the density of the deer population. More evidence is needed to determine the importance of predation of fawns, in particular by bears (e.g. Monteith et al. 2010).

3. Anthropogenic changes to habitat lead to lower nutritional capacity and/or large changes in predator and/or alternative prey species, which modify mule deer carrying capacity and predation risk, and are likely to destabilize mule deer population dynamics.

This pattern is likely to occur where human activities alter the landscape in a way that lowers nutritional carrying capacity (i.e. by development) or changes species interactions within food webs (e.g. by expanding agriculture resulting in invasion by white-tailed deer). Mule deer are particularly susceptible to any alteration resulting in lower survival of adults (Robinson et al. 2002). Both food web and community composition and the spatial distribution of species are likely to be important in this scenario. In today's rapidly changing world, this pattern will become more important in the future.

Recommendations for research

In today's rapidly changing socio-ecological landscapes, there is an increasing need for scientific knowledge to guide wildlife management. We therefore recommend research in several areas, to improve our understanding of mule deer population dynamics:

1. Interactions between predation, forage, and weather need to be studied, and it is highly unlikely that we will develop a predictive understanding of mule deer dynamics without understanding these interactions. The relationship between nutrition, fecundity, and predation risk is particularly interesting because of the high growth potential of mule deer populations.

2. Fecundity in free ranging populations is under-reported, and is needed to estimate population growth rates. In most studies we reviewed (20 out of 28), λ was not reported, lowering our ability to measure effects of environmental variables on vital rates and population growth quantitatively.

3. Much insight into general ungulate dynamics has come from long-term studies of marked individuals, and long-term mule deer research projects with marked individuals would probably yield substantial insights into population dynamics.

4. We need to understand the effects of senescence on survival and fecundity in mule deer. These effects may influence management, particularly in populations in which female and young male deer are not hunted (i.e. in populations without antlerless harvests). In these populations, adult female age distribution is likely to be skewed toward older adults. Effects of senescence on survival and fecundity could be investigated by a formal meta-analysis and better data reporting.

5. Collaborations between resource management agencies and universities would result in increased reporting of data and opportunities for future meta-analyses. Much of the mule deer literature is restricted to government reports, so there are likely to be large amounts of research we were not able to access. Collaborations would help to address this problem.

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