Top-down versus bottom-up forcing: evidence from mountain lions and mule deer

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We studied mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) inhabiting a Great Basin ecosystem in Round Valley, California, to make inferences concerning predator–prey dynamics. Our purpose was to evaluate the relative role of top-down and bottom-up forcing on mule deer in this multiple-predator, multiple-prey system. We identified a period of decline (by 83%) of mule deer (1984–1990), and then a period of slow but steady increase (1991–1998). For mule deer, bitterbrush (*Purshia tridentata*) in diets, per capita availability of bitterbrush, kidney fat indexes, fetal rates (young per adult female), fetal weights, and survivorship of adults and young indicated that the period of decline was typical of a deer population near or above the carrying capacity (K) of its environment. Numbers of mountain lions also declined, but with a long time lag. The period of increase was typified by deer displaying life-history characteristics of a population below K, yet the finite rate of growth ($\lambda = 1.10$) remained below what would be expected for a population rebounding rapidly toward K ($\lambda = 1.15$–1.21) in the absence of limiting factors. Life-history characteristics were consistent with the mule deer population being regulated by bottom-up forcing through environmental effects on forage availability relative to population density; however, predation, mostly by mountain lions, was likely additive during the period of increase and thus, top-down forcing slowed but did not prevent population growth of mule deer. These outcomes indicate that resource availability (bottom-up processes) has an ever-present effect on dynamics of herbivore populations, but that the relationship can be altered by top-down effects. Indeed, top-down and bottom-up forces can act on populations simultaneously and, thus, should not be viewed as a stark dichotomy.

Key words: density dependence, limitation, mountain lion, mule deer, nutrition, *Odocoileus hemionus*, predation, *Puma concolor*, regulation, Sierra Nevada

The concepts of top-down and bottom-up forcing are central to the development of modern ecological theory (Hunter and Price 1992; Power 1992; Strong 1992). These processes influence trophic cascades (Berger et al. 2001; Terborgh et al. 2001, 2006), ecosystem structure and function (McNaughton 1977; Molvar et al. 1993), biodiversity (Jacobs and Naiman 2008; Ripple and Beschta 2008; Stewart et al. 2009), and the conservation of rare or endangered species (Aaltonen et al. 2009). Large mammalian herbivores and their predators are important for studying top-down and bottom-up relationships because theory developed from small animals may not apply to large ones (Caughley and Krebs 1983; Sinclair and Krebs 2002).

Density-dependent mechanisms play an important role in population dynamics of large herbivores (Boyce 1989; Kie et al. 2003; McCullough 1979; Stewart et al. 2005). Diet quality and niche dimensions vary with population density (Kie and Bowyer 1999; Mobæk et al. 2009; Nicholson et al. 2006; Stewart et al. 2011), and life-history characteristics of large herbivores are influenced strongly by density dependence (Fowler 1981; McCullough 1999). The degree of resource limitation (proximity to carrying capacity [K]) determines the

relative importance of top-down and bottom-up influences on population dynamics (Bowyer et al. 2005; Kie et al. 2003). The classic definition of K is when a population is at equilibrium with its environment (Caughley 1977; McCullough 1979). We extend that definition to include the long-term ability of a particular environment to support viable populations of large herbivores, wherein the population fluctuates around some mean point of equilibrium. There may be, however, directional changes in K as a result of long-term environmental change (Kie et al. 2003).

There is considerable debate over the terms limitation and regulation (Berryman 2004; White 2007); we argue that all mortality factors are limiting, but only those resulting in a density-dependent feedback are regulating. Herbivore populations near K are characterized by females attempting to produce more young than can be recruited successfully into the population (Bartmann et al. 1992; McCullough 1979), resulting in mortality from predators that is primarily compensatory (i.e., the prey population remains near K)—the population is limited by predation, but regulated by density-dependent factors associated with K. Conversely, in populations backed far away from K, attempts to recruit young can be more successful if predation was reduced because resources are not limiting; in such situations mortality from predation tends to be additive—the population is not limited by resources, but is regulated by predation. We contend that information on kill rates or predation rates (Vucetich et al. 2011) are less meaningful than data concerning the life-history characteristics of ungulates in understanding predator–prey dynamics, because of the differences in the consequences of mortality as a function of the proximity of the prey population to K.

The long-term investigations necessary to understand these complex predator–prey relationships for large mammals are uncommon, although several examples do exist (Jędrzejewska and Jędrzejewski 2005; Vucetich et al. 2002). Nonetheless, factors underpinning dynamics of large herbivores continue to be debated, especially the role that large predators play in affecting vital rates and demographics (Frank 2008; Terborgh and Estes 2010; Terborgh et al. 2006). A lack of understanding of the role of top-down forcing in ecological systems as a result of the loss of large apex predators (Estes et al. 2011) and the predator-centric focus of numerous predator–prey models (Bowyer et al. 2005; Person et al. 2001) likely has hampered our understanding of top-down and bottom-up processes for these large mammals.

The theoretical development and debate over effects of top-down and bottom-up forcing on large herbivores largely began with the "world is green" or Hairston, Smith, and Slobodkin hypothesis (Hairston et al. 1960), which predicted that herbivores were seldom limited by food and were, thus, regulated by predation. In support of that hypothesis, cascading effects of the absence of large predators are well documented (Estes et al. 2011; Ripple and Beschta 2006, 2008; Terborgh and Estes 2010; Terborgh et al. 2006), and in multiple-predator, multiple-prey systems, predation can regulate prey at low densities relative to K (Bowyer et al. 1998; Dale et al.

1994; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994). Nonetheless, the occurrence of predation does not necessarily equate to top-down regulation; the degree of predation and the interaction between the herbivore population and its food supply determine the potential for top-down regulation (Bartmann et al. 1992; Bowyer et al. 2005). Assessing the relative strengths of top-down and bottom-up forcing on regulation of populations, however, is of greater theoretical value than debating which force is operating, because both processes can occur simultaneously (Bowyer et al. 2005; Boyce and Anderson 1999; Hunter and Price 1992).

We used a long-term data set on mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) that inhabited a Great Basin ecosystem to evaluate the relative influences of top-down and bottom-up forcing, because shifting dynamics of this predator–prey system allowed for unique insights into the role of large carnivores in regulating their ungulate prey. We cast our predictions based on a conceptual model of life-history characteristics for large herbivores proposed by Bowyer et al. (2005; Table 1). In populations of mule deer regulated by top-down forcing, the population would be held far away from K, mortality would be mostly additive, intraspecific competition would be reduced, and individuals would have a more-nutritious diet, resulting in better physical condition and, thus, greater reproductive rates and higher survival. Conversely, in populations regulated by bottom-up forcing, animals would be at or near K, mortality would be largely compensatory, intraspecific competition would be intensified, and a less-nutritious diet would lead to poor physical condition and, thereby, lower reproductive rates and decreased survival (Table 1). In the absence of the aforementioned dichotomy, some degree of nutritional limitation and effects of predation may co-occur, especially at intermediate densities in relation to K.

MATERIALS AND METHODS

Study area.—Round Valley (37°24′N, 118°34′W), located east of the Sierra Nevada in California, is the winter range for a migratory population of mule deer, and the mountain lions that prey upon them (Kucera 1992; Monteith et al. 2011; Pierce et al. 1999). Mule deer inhabiting this Great Basin ecosystem are the primary prey for mountain lions (Bleich et al. 2006; Pierce et al. 2000b, 2004; Villepique et al. 2011). Annual precipitation in the region was highly variable, and ranged from 5.3 to 25.2 cm. Precipitation was strongly seasonal, with about 72% occurring during November–March, and mean monthly temperatures ranged from 0°C to 16°C.

The predominant vegetation type in Round Valley is sagebrush steppe (Pierce et al. 2004), and includes stands of sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus nauseosus*); patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) also were common. Forbs, which were generally unavailable to deer in winter, included *Eriogonum kennedyi* and *Lomatium* sp. Common grasses were *Stipa speciosa*, *Oryzopsis hymenoides*, *Sitanion jubatum*, *Sitanion*

TABLE 1.—Life-history characteristics, measures of physical condition, and vital rates of large herbivores, including predictions tested in this study based on populations characterized by top-down forcing by large carnivores or bottom-up forcing through nutritional limitation (adapted from Bowyer et al. [2005]).

Life-history characteristic	Top-down forcing	Bottom-up forcing	Predictions tested in this study
Physical condition of adult females	Better	Poorer	Yes
Pregnancy rate of adult females	Higher	Lower	Yes
Fetal rate	Higher	Lower	Yes
Weight of neonates	Heavier	Lighter	Yes
Mortality of young	Additive	Compensatory	Yes
Diet quality	Higher	Lower	Yes
Pause in annual production by adult females	Less likely	More likely	No
Yearlings pregnant	Usually	Seldom	No
Corpora lutea counts of adult females	Higher	Lower	No
Age at 1st reproduction for females	Younger	Older	No
Age at extensive tooth wear	Older	Younger	No

hystrix, and *Bromus tectorum. Salix* spp., *Rosa* spp., and *Betula occidentalis* occurred in riparian areas (Kucera 1988).

Most mule deer inhabiting Round Valley during winter migrated to high elevations (>2,500 m) on the west side of the Sierra Nevada (Kucera 1992; Monteith et al. 2011; Pierce et al. 1999), where they used high-quality forage during summer (Kucera 1997). Summer ranges were typified by high mountain meadows associated with a variety of coniferous species including Jeffrey (*Pinus jeffreyi*) and lodgepole (*P. contorta*) pine. Deer remained on summer range until autumn, when winter storms pushed them eastward over the Sierra crest and downward to the valley floor (Monteith et al. 2011).

The population of mule deer overwintering in Round Valley declined steadily from about 6,000 animals (66 deer/km^2) in 1985 (Kucera 1988) to 939 (10 deer/km^2) in 1991. Subsequently, the deer population rose to 2,165 (24 deer/km^2) by January 1999 (Fig. 1). The deer decline was associated with a severe drought during 1987–1990, when water content of winter snowpack was 27% of the long-term mean.
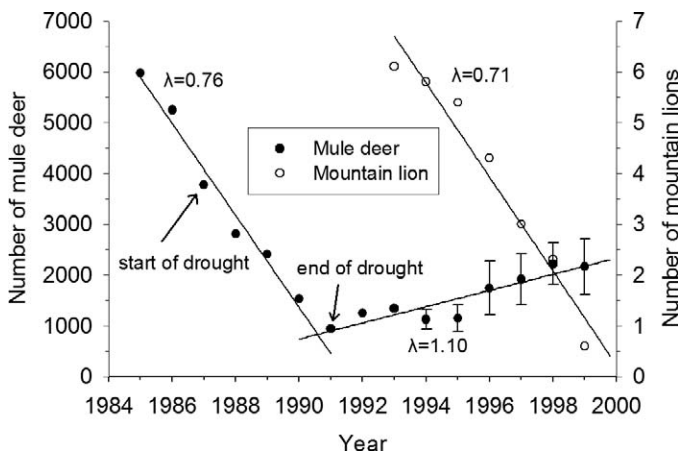

FIG. 1.—Phases of population trajectory for mule deer (*Odocoileus hemionus*) defined by piecewise regression, 1985–1999, and population trajectory for mountain lions (*Puma concolor*), 1993–1999, during winter in Round Valley, California. Error bars for the deer population from 1994 to 1999 are 95% confidence intervals. Adapted from Bowyer et al. (2005).

In winter 1984, hunters killed 200 female mule deer (~3.3% of the population) on the northern one-half of the study area (Kucera 1988). Limited sport hunting for male mule deer occurred during autumn in all years of our study. Hunting opportunity on winter range in Round Valley resulted in the harvest of approximately 15 males per year, but harvest of male mule deer on summer range was difficult to estimate because deer from Round Valley mingled with deer from other populations. Nevertheless, limited harvest of males would have had a negligible influence on population dynamics of deer (Kie et al. 2003; McCullough 1979, 2001). No sport hunting of mountain lions occurred during our study, and mountain lions were killed only if they preyed on pets or livestock (depredation), endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), or posed a threat to human safety (Torres et al. 1996), a policy that had been in place for >1 decade prior to the onset of our investigation.

Data collection.—In many instances, we used results from earlier investigations (Kucera 1988, 1991, 1997) combined with our data to evaluate characteristics of this mule deer population during a declining phase and the subsequent increasing phase. We tested for differences in diets of deer (percent of bitterbrush), per capita availability of bitterbrush, physical condition (kidney fat index [KFI]), fetal rate (young per adult female), fetal weight, survival of young, and survival of adults during the periods of decline and increase of the deer population. We also determined sources of mortality, and estimated population sizes of mule deer and mountain lions.

We used microhistological analyses of fecal pellets (Sparks and Malechek 1968) and digestibility of forages (Pierce et al. 2004) obtained monthly during winter to index percentage of bitterbrush occurring in diets of mule deer from the northern (*n* = 10 groups) and southern (*n* = 10 groups) parts of the study area. We collected only fresh (≤1-day-old) pellets, and composited samples, by area, each month. Microhistological identification of plant fragments was completed at the Composition Analysis Laboratory, Fort Collins, Colorado.

Current annual growth (leader lengths) for bitterbrush was sampled annually along 5 or 6 transects in autumn during most years by personnel from the United States Bureau of Land Management. Leader lengths were measured from ≥6 whorls

≤1.5 m above ground on 5 randomly selected plants along each transect. All leaders of current year growth from each whorl were measured until a minimum of 20 leaders on each plant was measured.

We collected 20 female mule deer annually in March 1991–1995, following methods described by Kucera (1997). We attempted to shoot only adult female deer, which were selected at random throughout the study area and age, weight, body condition, and fetal rate were recorded. Although we attempted to collect only adult (≥2 years old) females, a few yearling females were collected but differences in pregnancy and fetal rates between adults and yearlings were accounted for in subsequent analyses. We used 1 kidney from each deer to determine physical condition with the KFI (Riney 1955). We recorded weight of fetuses (± 1 g), but only of the heaviest if >1 were present (Kucera 1988).

We used a helicopter and net gun (Krausman et al. 1985) to capture mule deer (217 females and 93 males) in Round Valley and fitted them with very-high-frequency radiocollars each winter (∼7% of the population) from 1993 to 1997. We distributed collars among adult males and adult females in proportion to their occurrence in the population (1:3). In addition, we captured young (<1 year old; $n = 113$) at random and fitted them with expandable collars (Bleich and Pierce 1999). We intentionally avoided capturing deer from groups that contained animals collared during previous years. We monitored telemetered deer 6 or 7 times per week during winter to determine survival and cause-specific mortality, and monthly during summer to determine survival.

We conducted helicopter surveys each January to estimate the proportion of adult male, adult female, and young (<1 year old) mule deer on winter range, and obtain information on population size. Aerial transects were flown with 3 observers, and transects extended across the entire winter range to an elevation at which deer tracks in snow were no longer evident. In the early years (1984–1993), a total count of deer was conducted (Kucera 1988) and no measures of variance could be developed; nonetheless, the general trend of declining and subsequently increasing deer numbers was unequivocal (Bowyer et al. 2005). During 1994–1999, we used collared animals to estimate the deer population and associated variances (Chapman 1951); we used aerial telemetry 1 day before each of these surveys to determine the number of marked adult females within the survey area.

From 1994 to 1997, mule deer were evaluated for evidence of diseases capable of causing a marked decline: brucellosis ($n = 538$), infectious bovine rhinotracheitis ($n = 416$), parainfluenza-3 ($n = 397$), bluetongue ($n = 538$), epizootic hemorrhagic disease ($n = 538$), leptospirosis ($n = 532$), and anaplasmosis ($n = 535$). Those data yielded no evidence of pathogens that could have affected the population. Moreover, necropsy results ($n = 194$ deer) during 1984–1996, yielded no evidence of any ongoing disease.

During November 1991–April 1999, we used hounds and techniques described by Davis et al. (1996) to capture 21 adult mountain lions (12 females and 9 males) in Round Valley and

fitted them with very-high-frequency radiocollars. We conducted regular and intensive searches for mountain lions throughout the study area during 1991–1997, because these large felids are capable of dispersing long distances (Thompson and Jenks 2010). These intensive searches provided strong evidence that all mountain lions that regularly used winter range in Round Valley (i.e., resided for >30 days) were fitted with radiocollars by 1993, and that immigrants were detected and collared within 1 month of their arrival on winter range. Detailed descriptions of searches for mountain lions and mule deer killed by predators were provided previously (Pierce et al. 1998, 2000b, 2004).

We determined the mean number of collared mountain lions on the study area during telemetry flights at weekly intervals during November–March, and used that value to index the number of adult mountain lions on winter range each year. We excluded winter 1991–1992, because we captured the 1st mountain lion during November 1991 and continued to capture new, unmarked lions in Round Valley until November 1992, by which time we had captured 12 adults. From then on our ability to detect and capture new, unmarked lions was constant from year to year (Pierce et al. 2000a, 2000b).

We also evaluated the number of depredation permits issued for mountain lions to provide information on the annual abundance of lions prior to 1992; number of permits issued, however, does not represent the number of lions killed. We assumed that depredation permits would be positively associated with lion abundance, because additional conflicts are expected as lion density increases (Torres et al. 1996). All research methods were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks, and complied with guidelines published by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

Analyses.—We estimated number of deer born on summer range by multiplying fetal rates in March by the estimated number of adult females in the population. Survivorship of young to 6 months-of-age was calculated from the number of young estimated to have been born on summer range, and the number of those young that arrived on the winter range, based on composition counts conducted in early winter (Bleich et al. 2006). Survivorship of adult deer with radiocollars was calculated with the Kaplan–Meier estimator (Pollock et al. 1989) and proportions of cause-specific mortality during winter were determined according to Heisey and Fuller (1985).

We used piecewise regression (Neter et al. 1990) to define periods of population change, although an estimate for the population was not available for 1990; thus, we used regression analysis to estimate the value for 1990 for use in subsequent analyses. We calculated the finite rate of population growth (λ) as the inverse log of the slope of the regression on the natural log of population size through time (Caughley 1977). We used analysis of covariance (Neter et al. 1990), with Julian date of collections as a covariate to adjust weight of fetuses among years for dates of collection. We developed a density-dependent index to the availability of bitterbrush as an

indication of forage available to deer (mean leader-length per deer in the population during winter $\times$ 100); this index is influenced by changes in the number of bitterbrush leaders over time in relation to the density of the deer population.

We tested for effects of weather on forage availability and condition of mule deer, as well as the relationships between deer diet, body condition, reproduction, and λ using the Spearman rank correlation (r_s—Conover 1980). We also used r_s to test for the relationship between survivorship of young on summer range and λ for all years pooled, and for the same comparisons during periods of decline and increase in the deer population. Spearman rank correlations make no assumptions about the shape of relationships between variables (Conover 1980); thus, figures include lines of best fit only as an aid to interpret those relationships.

We used the Mann–Whitney U-test (Conover 1980) to examine differences in mean temperatures during December–February, leader length of bitterbrush, the index to the availability of bitterbrush, percent bitterbrush in diets, KFI, fetal rates, fetal weights, and survivorship of young and adult mule deer between periods of decline and increase of the deer population. We maintained an $\alpha = 0.05$ for those comparisons, except analyses where KFI, fetal rate, and fetal weight were obtained from the same individual; for those tests, we corrected experiment-wide error with a sequential Bonferroni procedure (Rice 1989). We also used this correction for correlations between weather variables and life-history characteristics of deer. We used r_s to compare the number of depredation permits issued with our index to lion abundance from 1993 to 1999, and subsequently to evaluate the relationship between deer abundance and number of depredation permits issued during both phases of population change.

We used a life table with 3 age classes (0, 1, and 2–12 years of age) and sexes combined to estimate adult survivorship each year. We did not calculate survivorship of deer directly because those data were available for only 4 years; for consistency, we used the life-table analysis to calculate survivorship for the entire study period. We used fetal rates corrected for the entire population, survivorship of young on summer range, and the λ estimated for each year in the life-table analyses. We assumed survivorship for yearlings and adults to be similar, and survivorship was adjusted until a λ matching the observed value for a particular year was obtained. Violation of this assumption would have had negligible effects on resulting survival rates for adults because yearlings comprised a small component of the population relative to adults. For yearlings, fetal rates during the period of decline were set at 0; we used fetal rates of 0 during 1991–1993, and of 1 during 1994–1996, based on data from deer collections.

Life tables assume a stable age distribution, and can overestimate the importance of adult survivorship when λ is fixed (Bowyer et al. 1999; Caughley 1977; Eberhardt 1985); however, calculating parameters repeatedly on an annual basis minimized that potential bias. Moreover, we did not use that analysis to determine the relative role of adult survivorship on population growth, but only to compare survivorship between

2 periods for which it was estimated in the same manner. Thus, any upward bias in the importance of adult survivorship should not have affected our results markedly.

Testing predictions for whether top-down or bottom-up forcing occurred in this population of mule deer involved a variety of statistical procedures, all of which were directed at a similar hypothesis (Table 1). Consequently, we combined probabilities from those statistical tests using the method of Sokal and Rohlf (1981):

$$\chi^2 = -2\sum \ln P,$$

with $2k$ degrees of freedom, where k is the number of separate tests. We recognize that our tests were not completely independent; accordingly, we reduced alpha for this analysis to 0.02 (Bowyer et al. 2007). Meta-analyses using this approach have been increasingly recognized as valuable tools in ecology when probabilities used in the analyses are focused on single hypotheses (Arnqvist and Wooster 1995; Osenberg et al. 1999).

RESULTS

Predation and population trajectory.—Piecewise regression identified 2 trajectories of population size for mule deer: a declining phase (1984–1990) and an increasing phase (1991–1998; Fig. 1). The λ of the deer herd in Round Valley during the drought of the late 1980s reflected a marked decline ($r^2 = 0.98$, $P < 0.001$) followed by a phase of slow population growth ($r^2 = 0.82$, $P < 0.001$) in the 1990s (Fig. 1).

Mean number of adult mountain lions inhabiting Round Valley during winter declined from 6.1 in winter 1992–1993 to 0.6 in winter 1998–1999 ($r^2 = 0.95$, $P < 0.001$; Fig. 1). During that period, we documented 20 mortalities of radiocollared lions: 10 males and 10 females. Sources of mortality included malnutrition ($n = 3$), killed because of depredation on domestic sheep or Sierra Nevada bighorn sheep ($n = 6$), intraspecific strife ($n = 2$), illegal killing ($n = 3$), vehicle collision ($n = 1$), and causes that could not be determined ($n = 5$). Of the 6 mountain lions killed on depredation permits, 3 were in poor physical condition. The population of mountain lions tracked mule deer numbers downward, but with a time lag of about 8 years (based on data from 1992 to 1999; Fig. 1). In addition, the number of depredation permits was strongly correlated with lion abundance from 1993 to 1999 ($r_s = 0.81$, $P = 0.027$); this outcome substantiated the annual number of depredation permits as an index to the abundance of mountain lions.

Despite the directional change in the trajectory of the deer population in 1991 (Fig. 1), and with the exception of an outlier in 1985, depredation permits issued for mountain lions declined from 1986 to 1999 (Fig. 2). Prior to 1985, when the deer population was probably high or increasing, few annual permits for lion depredation from 1972 to 1984 were issued ($\bar{X} = 1.3$, $SE = 0.44$). During the declining phase of the deer population, lion abundance was not related to deer numbers ($r_s = 0.29$, $P = 0.27$), even though substantially more permits for lion depredation were issued annually ($\bar{X} = 11.6$, $SE = 1.03$).

The increased killing of mountain lions had no discernible effect on the continued decline of mule deer through 1990 (Fig. 2), a pattern contrary to expectations if top-down forcing occurred. Following the crash of the deer population, number of depredation permits issued continued to decline ($\bar{X} = 7.6$, $SE = 1.44$), with the exception of 1996 when an abnormally high number of permits was issued (Fig. 2). Nevertheless, number of depredation permits issued was negatively related to deer abundance ($r_s = -0.63$, $P = 0.069$). Predation by mountain lions was the most significant cause of mortality for mule deer in all years (Fig. 3) except 1998, when predation by coyotes (*Canis latrans*) surpassed that of mountain lions.

Diet, animal condition, reproduction, and survival.—Per capita availability of bitterbrush and the percent of bitterbrush in diets of mule deer were significantly greater during the period of population increase than during the period of decline (Table 2). We identified a strong relationship between leader length of bitterbrush and total water content of snowpack measured in April (Fig. 4). That relationship was positive during the period of decline ($r_s = 0.83$, $P = 0.010$), and waned during the period of increase ($r_s = 0.43$, $P = 0.29$). A strong positive relationship also existed between per capita availability of bitterbrush and body condition of deer (as indexed by KFI) during the declining phase ($r_s = 1.0$, $P < 0.001$); this relationship weakened during the increasing phase ($r_s = 0.2$, $P = 0.74$). As percent bitterbrush in the diet in March increased from 2% to 10%, physical condition (as indexed by KFI) of mule deer rose exponentially and became asymptotic when bitterbrush in diet was >30% (Fig. 5). Mean winter temperature also was positively related to KFI, but not significantly so following a Bonferroni correction ($r_s = 0.62$, $P = 0.05$), and did not differ between periods of population decline and increase ($U_{11} = 33.0$, $P = 0.9$).
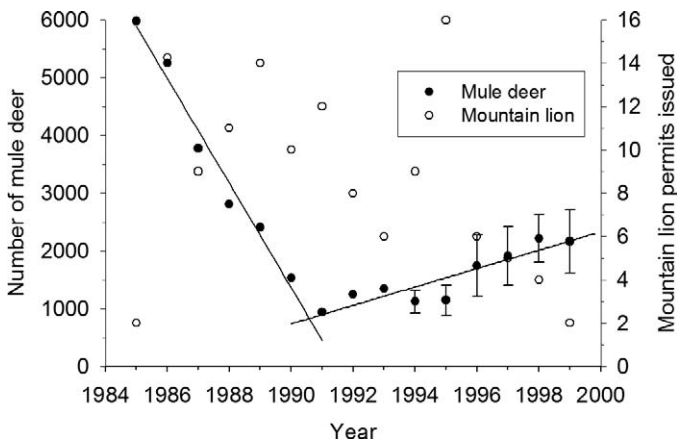

FIG. 2.—Phases of population trajectory for mule deer (*Odocoileus hemionus*) and the number of mountain lion (*Puma concolor*) depredation permits issued in Inyo and Mono counties, 1985–1999, Round Valley, California. Error bars for the deer population from 1994 to 1999 are 95% confidence intervals. Depredation permits were positively correlated with number of lions present in Round Valley and, hence, provided a viable index to mountain lion abundance.
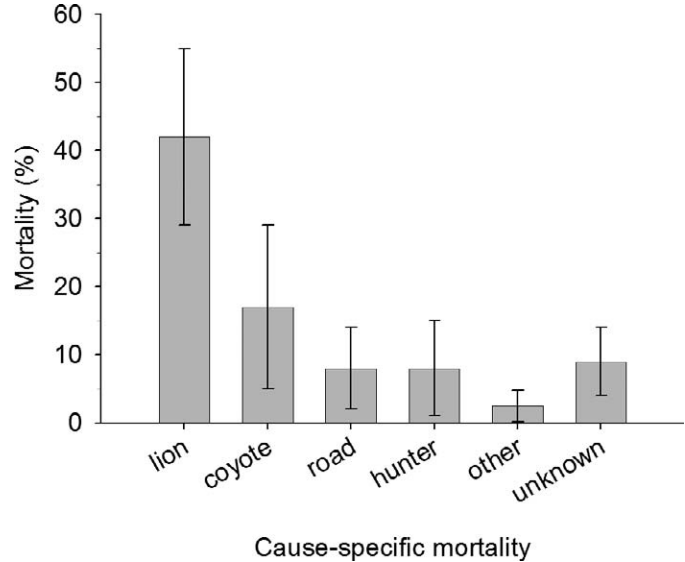

FIG. 3.—Cause-specific mortality ($n = 115$) of mule deer (*Odocoileus hemionus*) during winter in Round Valley, California, during the increasing phase, 1993–1998 (error bars are 95% confidence intervals).

Fetal rates were 13% lower during the period of population decline than when the population was increasing (Table 2). Following a Bonferroni correction, fetal rates were related positively to KFI of female mule deer, which was significant during the increasing phase ($r_s = 0.94$, $P = 0.005$) but not during the decline ($r_s = 0.83$, $P = 0.05$). Mean weight of fetuses adjusted for age also was 14% less during the period of decline than during the period of increase (Table 2). The relationship between KFI and fetal weight was not significant during the decline ($r_s = 0.20$, $P = 0.8$), but was strongly negative during the period of increase ($r_s = -0.89$, $P < 0.001$). That negative relationship, however, more likely was driven by the higher fetal rate during the period of population increase ($r_s = -0.94$, $P < 0.001$) than during the decline ($r_s = 0.52$, $P = 0.2$; Table 2).

Mean annual survivorship of adults differed significantly and was 24% lower during the period of decline than the period of increase (Table 2). Reduced survivorship among adult females was likely the underlying demographic cause of the population crash from 1985 to 1990. In contrast, survivorship of young on summer range was statistically similar between periods of decline and increase (Table 2). Following Bonferroni corrections, meta-analysis indicated that characteristics of mule deer differed during periods of population increase and decline ($\chi^2_{14} = 38.8$, $P < 0.001$).

Finite rate of increase (λ).—When population trajectories of mule deer were considered separately, in all instances, λ was <1.0 when the mean percent of bitterbrush in diets of mule deer in March was $\leq 10\%$. Although KFI of mule deer was positively correlated with λ, that relationship was not significant ($r_s = 0.31$, $P = 0.36$). No significant relationship ($r_s = 0.32$, $P = 0.38$) existed between winter temperature and λ for the deer population across years. A significant relationship

TABLE 2.—Population characteristics of a wintering population of mule deer (*Odocoileus hemionus*) in Round Valley, California, during decreasing and increasing trajectories of population size. *P*-values are results of Mann–Whitney *U*-tests for differences in characteristics of the population between decreasing and increasing phases. Results from the declining phase are from Kucera (1988). All *P*-values ≤ 0.02 are significant following a Bonferroni correction.

Population characteristic	Declining phase (1984–1990)			Increasing phase (1991–1998)			*P*-value
	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	
Bitterbrush in deer diets (%)	5.40	1.10	2.5–10.0	43.40	13.20	7.3–78.9	0.006
Per capita availability of bitterbrush (cm/deer × 100)	0.13	0.05	0.01–0.34	0.56	0.12	0.12–1.24	0.007
Kidney fat index	28.00	8.70	12.0–68.0	33.30	7.70	10.4–56.0	0.750
Fetal rate (young/adult)	1.40	0.08	1.2–1.72	1.60	0.08	1.4–1.8	0.100
Fetal weight (g)[a]	156.70	13.10	116.3–202.2	182.10	18.60	126.1–258.8	0.260
Survivorship of young	0.22	0.01	0.16–0.25	0.26	0.03	0.16–0.38	0.390
Survivorship of adults	0.65	0.03	0.59–0.73	0.86	0.04	0.69–1.0	0.012

[a] Weight was adjusted by Julian day of collection.

between λ and survival of young during the period of decrease ($r_s = 0.90$, $P = 0.04$) did exist, but not when the population was increasing ($r_s = -0.21$, $P = 0.65$).

DISCUSSION

Our approach was to evaluate the relative role of top-down and bottom-up forcing in a mule deer population using a conceptual model (Bowyer et al. 2005; Table 1) based on the life-history characteristics of ungulates (Eberhardt 1985; Gaillard et al. 2000) linked with their nutritional condition (Parker et al. 2009) to parameterize deer population characteristics in relation to *K*. The conceptual model was developed in reference to directional changes in important life-history characteristics that are expected under top-down or bottom-up regulation, but does not necessarily make assumptions about the magnitude of change for a particular variable. The significance of a single variable in this interpretation is less important than the overall pattern and direction of an influential set of life-history characteristics. Therefore, we used a weight-of-evidence approach (sensu Bowyer et al. 2003), wherein information from a single variable is insufficient to draw conclusions, but when multiple variables are considered in concert, a strong and clear pattern may emerge.

Although some of the individual population characteristics in Table 2 did not differ between periods of decline and increase, all differences were in the predicted direction based on the physical condition of deer. Characteristics were consistent with bottom-up forcing regulating the population of mule deer through environmental effects on forage availability relative to population density; however, top-down forcing (i.e., predation) had a modest, but negative effect (a reduction of 5–11% per annum) on population growth while the population was recovering from the crash (Fig. 1; Table 2). These outcomes align with the premise that variation in
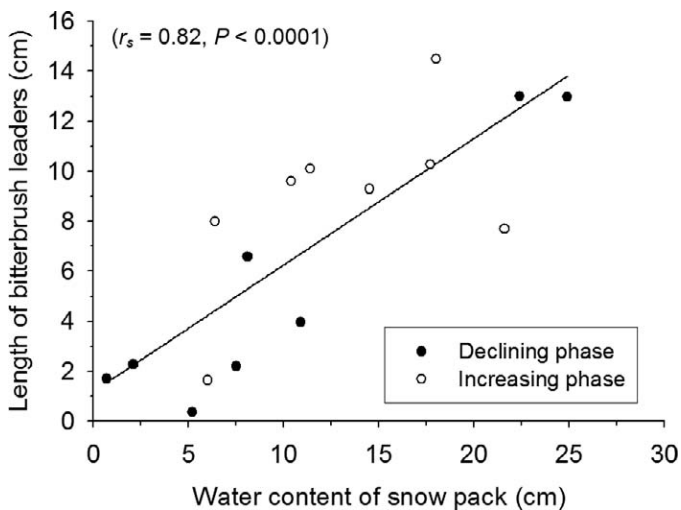

FIG. 4.—Length of annual growth of bitterbrush leaders (important winter forage for mule deer [*Odocoileus hemionus*]) in relation to water content of snowpack measured in April during the declining phase (1985–1990) and increasing phase (1991–1998) of the population of mule deer in Round Valley, California.
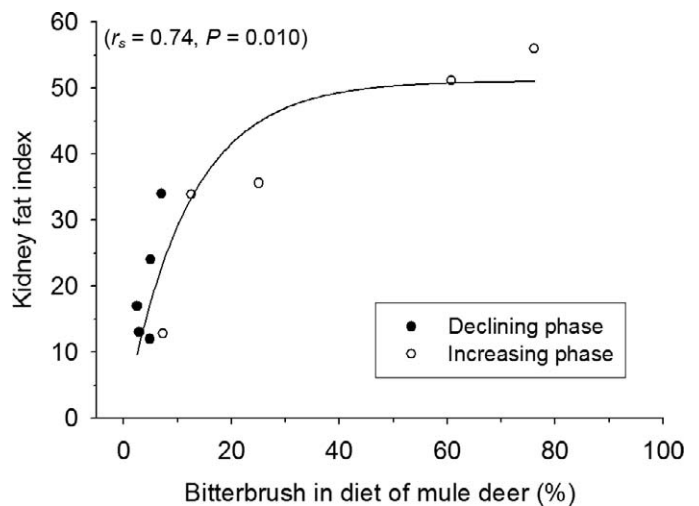

FIG. 5.—Percent bitterbrush in diet of mule deer (*Odocoileus hemionus*) during March in relation to mean kidney fat index of female mule deer collected in March during the declining phase (1985–1990) and increasing phase (1991–1998) of the population of mule deer in Round Valley, California. Results from the decreasing phase are from Kucera (1988).

resource availability (bottom-up) permeates through the system and has an ever-present effect, which may be altered by top-down effects (Hunter and Price 1992). Indeed, top-down and bottom-up forces can act on populations simultaneously and, thus, should not be viewed as a stark dichotomy (Bowyer et al. 2005; Boyce and Anderson 1999), an outcome that is inconsistent with expectations of the Hairston, Smith, and Slobodkin hypothesis.

Our results illustrate the importance of obtaining long-term information on the physical condition and vital rates of the prey population, which also has been emphasized by others (Barboza et al. 2009; Bishop et al. 2009; Parker et al. 2009). Considering only the size or density of the population of mule deer (and in later years the number of mountain lions) would have supported a conclusion that mountain lions regulated mule deer in the declining phase and failed to do so during the increasing phase (Figs. 1 and 2)—a supposition contradictory to our conclusions. Studies assessing the degree of top-down and bottom-up forcing typically have not included data on physical condition of prey, an omission that may cloud interpretation of results. Furthermore, a less lengthy investigation might have concluded that forcing was either from below or above, depending on the phase of the population trajectory sampled (Fig. 1).

The population decline of mule deer probably was not the result of severe winter weather in this Great Basin ecosystem; we documented only positive effects of snowpack on mule deer via increased forage growth (Fig. 4) that, in turn, resulted in improved physical condition. During the period of increase, we observed limited effects of snowpack on forage consumption or λ, likely because deer were released from severe nutritional limitation (Table 2). Bitterbrush in diets of deer was positively correlated with the KFI during the decline, but not when the deer population was increasing. Consequently, density-independent factors (e.g., severe weather) likely were not responsible for the population decline via effects on the energy budget of deer, and were unrelated to population characteristics during the period of increase. Moreover, no evidence existed that diseases were responsible for the decline in numbers of mule deer, or for slowing their rate of recovery.

If predation was an additive source of mortality during the decline, the condition of deer should not have been strongly correlated with their food supply (Bowyer et al. 2005; Kie et al. 2003; McCullough 1979). Indeed, we would not have expected mortality to be additive (i.e., top-down forcing) when levels of bitterbrush in diets of deer were low (<10%), deer were in comparatively poor physical condition, and reproductive rates were low—all characteristic of a declining and nutritionally regulated population. Primarily top-down forcing should have resulted in deer being in good physical condition, because they would have been better buffered against, and less influenced by, slight fluctuations in their food supply, particularly during the period of decline. Bitterbrush in diets of deer, per capita availability of bitterbrush, KFIs, fetal rates, fetal weights, survivorship of young, and survivorship of adult females all were lower during the period of decline than the period of

increase for mule deer (Table 2). These results clearly indicate that mule deer in Round Valley were at or near K of the winter range—conditions that precipitated the population decline—and that mortality during that time, regardless of the proximal cause, was largely compensatory.

The prolonged drought during the period of decline likely lowered K for mule deer. This deer population, however, was in decline before the start of the drought, which commenced in 1987 (Fig. 1). Similarly, McCullough (2001) demonstrated that strong density-dependent processes continued to operate for a population of deer during the course of a 6-year drought. Although we cannot determine conclusively what caused the initial crash in mule deer numbers, an overshoot of K followed by a severe drought is a plausible explanation. Populations of large herbivores exhibit strong density dependence (Kie et al. 2003; McCullough 1999; Stewart et al. 2005), and population irruptions with overshoots of K are well documented (Forsyth and Caley 2006; Klein 1968; McCullough 1979).

Several lines of reasoning indicate that top-down forcing was operating during the period when mule deer numbers were increasing. Although a proximal cause of mortality is insufficient evidence to interpret the consequences of mortality (Bartmann et al. 1992; Bleich et al. 2006), mountain lions were the primary source of winter mortality for mule deer during the increase (Fig. 3). We obtained little evidence that food was limiting during the period of increasing numbers of mule deer (Table 2). Indirect effects of predation risk (Berger 2010) were likely minimal because deer selected habitat that simultaneously reduced predation risk and enhanced forage benefits (Pierce et al. 2004). Christianson and Creel (2010) reported a similar situation for North American elk (*Cervus elaphus*) preyed upon by gray wolves (*Canis lupus*). Moreover, the stress and associated physiological responses to predation risk should have been strongest after the population crash when mountain lion abundance lagged behind the deer population (Creel et al. 2007). In contrast to that presumption, fetal rates and nutritional status were greater during the period of increase than during the declining phase (Table 1).

In June 1995, a fire burned 22 km^2 (24%) of the winter range dominated by sagebrush and bitterbrush. The loss of winter habitat associated with the fire in 1995 did not markedly affect variables associated with the physical condition or life-history characteristics of mule deer, because the deer population was relatively low (Fig. 1) and forage availability remained high (Table 2). Therefore, predation by mountain lions likely was an additive source of mortality during the period of increase. Moreover, λ for mule deer was only 1.10 during the increase, whereas mule deer can attain λ = 1.15–1.21 when not limited by food or predation (Kie and Czech 2000). Top-down forcing by mountain lions and other carnivores likely slowed, but did not prevent, recovery of mule deer in this Great Basin ecosystem. Whether the deer population ultimately will return to the 6,000 animals present on the winter range in the 1980s, and how changes in available resources will alter K, is a topic for future research.

We encountered several challenges while conducting our research. We combined our results with those reported by Kucera (1988, 1991, 1997) to obtain a sufficient number of years to encompass the trajectories of this population of mule deer. As a result, we often had access to only mean values with no associated measures of variance, which necessitated the use of nonparametric statistics for most analyses. Our approach also required that we duplicate the methods of Kucera (1988) as closely as possible to allow meaningful comparisons. These methodologies led to some inconsistencies in our results. For example, KFI is less sensitive to changes in physical condition when cervids have high fat reserves (Cook et al. 2007), which explains why KFI exhibited a curvilinear pattern with increasing bitterbrush in diets (Fig. 5) and did not differ markedly between periods of differing population trajectories (Table 2).

Sampling only the largest fetus may have caused us to underestimate the total weight of fetuses from females with twins. Fetal rates were higher during the period of increase than decline and, consequently, twins were more plentiful (Table 2). Singletons often weigh more than individuals from a set of twins (Kucera 1991), which likely introduced a bias into our data; total fetal weight might have produced a greater difference between phases of population decline and increase. Another factor reducing the difference in fetal weights and associated survivorship of young between periods of population decline and increase could be a residual maternal effect (Monteith et al. 2009). Indeed, survivorship of young increased only slightly during the increasing phase (Table 2). Intergenerational maternal effects caused by severe nutritional limitation during the decline may have resulted in lags in population response, and thereby have the potential to mask expected patterns related to top-down or bottom-up forcing from the body size of animals (Monteith et al. 2009).

Grange and Duncan (2006) reported that populations of plains zebras (*Equus quagga*) were more resistant to drought than were populations of other grazing ruminants such as blue wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Those authors concluded that zebras were more likely to be influenced by top-down forcing by African lions (*Panthera leo*), whereas populations of wildebeest and buffalo were limited principally by their food supply. Moreover, Wilmers et al. (2007) concluded that stalking predators, such as mountain lions, were more effective at suppressing fluctuations in their prey than were cursorial hunters, such as wolves and coyotes. Even an effective stalking predator such as the mountain lion (Knopff et al. 2010; Pierce et al. 2000a, 2000b), however, only slowed the recovery of the mule deer population in Round Valley. The resistance of the prey population to food shortages, and the type of predator and its hunting style, hold potential to influence the magnitude of bottom-up and top-down forcing.

Our results demonstrate that top-down forcing from multiple predators may limit population growth but does not always regulate prey populations. Mountain lions and other large carnivores in our study area slowed, but did not regulate, the growth of a mule deer population. More attention needs to be given to the specific conditions that lead to equilibria or disequilibria between populations of large mammalian predators and their prey (Hunter and Price 1992), and whether those factors lead to population irruptions and overshoots of K with subsequent effects on ecosystem structure and function. This approach is likely to be critically important for the conservation of large mammals in a changing climate, where directional changes or dramatic variation in K may become the norm.

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