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Life-History Characteristics of Mule Deer: Effects of
Nutrition in a Variable Environment

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(Top) Deer ID479 within a few hours of birth during the day of her initial capture on 20 June 2008. (Bottom) Deer ID479 and her mother ID256 in Round Valley, California, USA during autumn 2008. Deer ID256 was first captured on 20 November 2002, and remained in our study through the last capture event of our study in March 2009. During that time she resided on the east side of the Sierra crest during summer and was captured a total of 12 times. She failed to recruit young during 2005, but she was a successful mother and recruited a single young during 2006, 2007, and 2008, and twins during 2004. Our long-term, individual-based study revealed the importance of nutritional condition in understanding life-history characteristics and population regulation of large herbivores. Photos by Kevin L. Monteith

Life-History Characteristics of Mule Deer: Effects of Nutrition in a Variable Environment

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ABSTRACT Vital rates of large herbivores normally respond to increased resource limitation by following a progressive sequence of effects on life-history characteristics from survival of young, age at first reproduction, reproduction of adults, to adult survival. Expected changes in life-history characteristics, however, should operate through changes in nutritional condition, which is the integrator of nutritional intake and demands represented primarily by the deposition and catabolism of body fat. Elucidating seasonal patterns of nutritional condition and its relative influence on individual and population performance should improve our understanding of life-history strategies and population regulation of ungulates, provide insight into the capacity of available habitat to support population growth, and allow assessment of the underlying consequences of mortality on population dynamics. We acquired longitudinal data on individual female mule deer (*Odocoileus hemionus*), and linked those data with environmental and population characteristics. Our goal was to provide a nutritional basis for understanding life-history strategies of these large mammals, and to aid in the conservation and management of large herbivores in general. We studied a migratory population of mule deer that overwintered in Round Valley on the east side of the Sierra Nevada, California, USA, and was subject to a highly variable climate and predation from a suite of large carnivores. We intensively monitored nutritional and life-history characteristics of this population during 1997–2009 as it recovered from a population crash, which occurred during 1985–1991. Deer in Round Valley migrated to high-elevation summer ranges on both sides of the crest of the Sierra Nevada (Sierra crest), where a rain shadow resulted in a mesic and more forested range on the west side compared with xeric conditions east of the Sierra crest. Average survival of neonatal mule deer to 140 days of age during 2006–2008 was 0.33 (SE = 0.091), but was lower for neonates on the west side (0.13, SE = 0.092) compared with those on the east side (0.44, SE = 0.11) of the Sierra crest. Birth mass and nutritional condition of mothers had a positive effect on survival of young; however, those effects were evident only for neonates born east of the crest where predation pressure was less intense compared with the west side. Black bear (*Ursus americanus*) predation was the main cause of mortality for west-side young (mortality rate = 0.63, SE = 0.97) compared with canid and felid predation for east-side young (0.29, SE = 0.076). Mean autumn recruitment of young during 1997–2008 was lower for females on the west side (0.42, SE = 0.037) than for females on the east side (0.70, SE = 0.041) of the crest, and was affected positively by March ingesta-free body fat (IFBFat) of individual females. At the level of the population, ratios of young-to-adult females (1991–2009) were highly variable and strongly related to March IFBFat of adult females during the current and preceding year. Reproduction by yearling females was sensitive to per capita availability of forage during summer (as 1-yr-old individuals), thereby influencing whether a sufficient body mass for ovulation was obtained. Litter size remained high (1.69, SE = 0.027) during the study, but was influenced positively by forage availability, negatively by summer temperature, and was greater for females that resided on the west side of the Sierra crest during summer than those on the east side. In contrast, pregnancy rates remained unchanged across years of study (0.98, SE = 0.005). Survival of prime-age (2- to 9-yr-old) females was 0.90 (SE = 0.021) in summer, 0.94 (SE = 0.012) in winter, and 0.87 (SE = 0.025) annually. Although relatively stable across years, both winter and summer survival

were influenced positively by the preceding April snowpack relative to the density of the population. Mean IFBFat of adult females was 7.2% (SE = 0.077) in March 1997–2009 and 9.7% (SE = 0.23) in November 2002–2008. Nutritional condition offered a mechanistic link between factors that influence resource limitation and population performance, because condition of adult females in autumn and late winter was sensitive to the nutritional history of individual animals as related to forage growth, population density, migratory tactic, reproductive costs, and nutritional carryover. Nutritional condition of adult females in March also was the most parsimonious predictor of finite rate of population growth (λ) during the forthcoming year. The relative magnitude of effect of nutritional condition on survival and reproduction was mostly in accordance with the predicted changes of vital rates in response to resource limitation for populations of large herbivores. Our results indicate that management and conservation of large herbivore populations could be improved by integrating indices of nutritional condition into current monitoring and research programs. We offer a method to estimate the proximity of a population to nutritional carrying capacity (NCC) that is based on nutritional status of the population relative to population performance (termed animal-indicated NCC). The proximity of the population to animal-indicated NCC represents the short-term capacity of the environment to support population growth. A nutritional approach to monitor and manage populations offers a direct link to the capacity of the habitat, and reduces the need to estimate population abundance or set goals according to population size. We also propose that the consequences of mortality (degree of additive or compensatory mortality) on population dynamics can be assessed by comparing the estimated nutritional capacity for survival and recruitment of young to that measured empirically, because more young are produced than what the habitat can support when nutrition is limiting. Our approach is useful for quantifying effects of predation, and provides a basis for determining the efficacy of predator control to enhance ungulate populations. © 2014 The Wildlife Society.

KEY WORDS additive mortality, California, carrying capacity, compensatory mortality, density dependence, environmental stochasticity, migration, nutritional condition, *Odocoileus hemionus*, predation, Sierra Nevada.

Características de Historia de Vida del Ciervo Mulo: el Efecto de la Nutrición en Presencia de un Medio Ambiente Variable

RESUMEN Normalmente, la respuesta de las estadísticas vitales de los grandes herbívoros a una mayor restricción de recursos es una secuencia progresiva de efectos en las características de la historia de vida, que van desde la supervivencia de los juveniles y la edad de la primera reproducción, hasta la reproducción de los adultos y la supervivencia de estos. Los cambios previstos en las características de la historia de vida, sin embargo, deben experimentarse a través de cambios en el estado de nutrición (niveles de grasa corporal), constituido por la ingesta y las necesidades alimenticias, representadas principalmente por la deposición y el catabolismo de la grasa corporal. El esclarecimiento de los patrones estacionales del estado de nutrición y su influencia relativa, tanto en el desempeño individual como en el de la población, debe mejorar la comprensión de las estrategias de historia de vida y de la regulación de las poblaciones de ungulados, así como también, dar una idea de la capacidad del hábitat disponible para sustentar el crecimiento de la población y permitir la evaluación de las consecuencias subyacentes que tiene la mortalidad en la dinámica demográfica. Adquirimos datos longitudinales sobre individuos de ciervo mulo (*Odocoileus hemionus*), y vinculamos estos datos con las características ambientales y demográficas. Nuestro objetivo era ofrecer una base nutricional para la comprensión de las estrategias de historia de vida de estos grandes mamíferos y ayudar en la conservación y gestión de los grandes herbívoros en general. Se estudió una población migratoria de ciervo mulo que habitó, por un período que sobrepasó el invierno, en Round Valley, al este de la Sierra Nevada en California, EE.UU., la cual estuvo sujeta a un clima muy variable y a la depredación de un conjunto de grandes carnívoros. Monitoreamos intensamente las características nutricionales y de historia de vida de esta población durante el período 1997–2009, período durante el cual, dicha población se recuperaba del drástico descenso experimentado durante el período 1985–1991. En el verano, los ciervos emigraron de Round Valley a las cordilleras de gran altitud a ambos lados de la cima de la Sierra Nevada (cima de la Sierra), en cuya parte oeste, como resultado de una sombra pluviométrica, se desarrolló una cordillera mesofítica y más boscosa, si se la compara con las condiciones xerófilas al este de la cima de la Sierra. Durante el período de 2006–2008 la supervivencia promedio del ciervo mulo neonatal hasta los 140 días de edad fue de 0,33 (ES = 0,091), sin embargo; la supervivencia de los recién nacidos en el lado oeste fue menor (0,13, ES = 0,092), en comparación con los del lado este de la cima de la Sierra (0,44, ES = 0.11). La masa corporal al nacimiento y el estado de nutrición de la madre afectaron positivamente la

supervivencia de los jóvenes, sin embargo; estos efectos sólo se evidenciaron en los neonatos nacidos al este de la cima, donde estuvieron expuestos a una depredación menos intensa en comparación con los del lado oeste. La actividad depredadora del oso negro (*Ursus americanus*) fue la principal causa de mortalidad en los juveniles en el lado oeste (tasa de mortalidad = 0,63, ES = 0.97) si se la compara con la actividad depredadora de los cánidos y félidos en el lado este (0,29, ES = 0.076). El nivel de agregación medio de los juveniles para el otoño durante el perído 1997–2008 fue menor para las hembras en el lado oeste de la cima (0,42, ES = 0.037) que para las hembras en el lado este (0,70, ES = 0.041), y se vio afectada positivamente por la medida, para marzo, de la grasa corporal con exclusión de sustancias ingeridas (siglas en inglés, IFBFat), de las hembras. A nivel de la población, la proporción de juveniles por hembra adulto (1991–2009) fue muy variable y estuvo fuertemente relacionada con el IFBFat para marzo de las hembras adulto durante el año en curso y los años anteriores. La reproducción de las hembras juveniles (de un año de edad) fue susceptible a la disponibilidad de forraje per cápita durante el verano (en su condición de individuo de 1 año de edad), influyendo, en consecuencia, en el logro o no de masa corporal suficiente para la ovulación. Durante el estudio, el tamaño de las crías se mantuvo alto (1.69, ES = 0.027), pero se vio afectado positivamente por la disponibilidad de forraje, negativamente, por la temperatura durante el verano, y fue mayor para las hembras que residían en el lado oeste de la cima de la Sierra durante el verano, que para las del lado este. Por el contrario, la tasa de preñez se mantuvo relativamente estable durante años de estudio (0,98, ES = 0.005). La supervivencia de las hembras de edad óptima (2–9 años), fue 0,90 (ET = 0,021) en el verano, 0,94 (ES = 0,012) en el invierno, y 0,87 (ES = 0,025) al año. Aunque la supervivencia lo largo de los años ha sido relativamente estable, tanto en invierno como en verano, esta fue afectada positivamente por la nieve acumulada del abril precedente, en relación con la densidad de la población. El IFBFat medio para marzo de las hembras adulto fue de 7,2% (ES = 0,077) de 1997 a 2009, y de 9,7% (ES = 0.23) de noviembre de 2002 a 2008. El estado de nutrición permitió una relación mecánica entre los factores que influyen en la limitación de los recursos y el desempeño de la población, debido a que la condición de las hembras adulto en el otoño y a finales del invierno fue susceptible tanto a la historia nutricional de los individuos en relación con el crecimiento del forraje, como a la densidad de la población, la táctica migratoria, el costo de reproducción y el remanente nutricional. El estado de nutrición para marzo de las hembras adultas también fue la explicación más prudente para la tasa finita de crecimiento poblacional (λ) durante el año siguiente. La magnitud relativa del efecto que tiene el estado nutricional sobre la supervivencia y la reproducción estuvo generalmente conforme con los cambios previstos en la estadística vital de las poblaciones de grandes herbívoro, resultantes la restricción de recursos. Nuestros resultados indican que la gestión y la conservación de grandes poblaciones de herbívoros podrían mejorarse mediante la integración de los índices de estado de nutrición en los programas de investigación y supervisión en curso. Ofrecemos un método para estimar la inminencia de una población a alcanzar la capacidad de aporte nutricional (singla en inglés, NCC) con base en el estado nutricional de la población en relación con el desempeño de la población (denominado NCC de indicación animal). La proximidad de la población a la NCC de indicación animal representa la capacidad a corto plazo del medio ambiente para sustentar el crecimiento de la población. Un enfoque nutricional para el monitoreo y administración de las poblaciones ofrece un nexo directo con la capacidad del hábitat, y reduce la necesidad de estimar la abundancia de la población o establecer metas de acuerdo con el número de habitantes. También proponemos que las consecuencias de la mortalidad (grado de mortalidad agregado o compensatorio) sobre la dinámica demográfica pueden calcularse mediante la comparación de la estimación de la capacidad nutricional necesaria para la supervivencia y la agregación de juveniles, con aquellas calculadas empíricamente, debido a que se producen más juveniles de los que el hábitat puede sustentar cuando la nutrición es una limitante. Nuestro enfoque es útil para efectos de la cuantificación de la depredación, y proporciona una base para determinar la eficacia del control de la depredación en el aumento de las poblaciones de ungulados.

Traits Biodémographiques chez le Cerf Mulet: Effets de la Nutrition dans un Environnement Variable

RÉSUMÉ Les taux démographiques des grands herbivores répondent habituellement à une limitation croissante des ressources et cela, selon une séquence progressive d'effets sur les traits biodémographiques en débutant par des effets sur la survie des juvéniles, puis sur l'âge à la première reproduction, la reproduction des adultes et enfin, la survie des adultes. Les changements attendus des traits biodémographiques devraient toutefois se produire en fonction des changements dans la condition physique qui intègre l'apport et les besoins nutritionnels qui se traduisent principalement par l'accumulation et le catabolisme des réserves de gras corporel. L'étude des tendances saisonnières de la condition physique et de leur influence relative sur la performance individuelle et populationnelle

pourrait améliorer notre compréhension des stratégies d'histoire de vie et de la régulation des populations d'ongulés et cela, tout en déterminant la capacité des habitats disponibles à supporter la croissance de la population et en évaluant les conséquences sous-jacentes de la mortalité sur la dynamique de population. Nous avons acquis des données longitudinales sur des individus de cerfs mulets (*Odocoileus hemionus*), et avons relié ces données à des caractéristiques environnementales et populationnelles. Notre objectif était de fournir une base nutritionnelle pour comprendre les stratégies d'histoire de vie de ces grands mammifères et pour aider à la conservation et la gestion des grands herbivores en général. Nous avons étudié une population migratrice de cerfs mulets qui hiverne dans la Round Valley, dans la partie est du Sierra Nevada, Californie, USA. Cette population est sujette à des conditions climatiques très variables et à de la prédation par une large guilde de carnivores. Entre 1997 à 2009, nous avons suivi intensivement les caractéristiques nutritionnelles et les traits biodémographiques de cette population, alors qu'elle récupérait d'un déclin marqué s'étant produit entre 1985 et 1991. Les cerfs de la Round Valley ont migré vers les aires estivales situées à des élévations élevées sur les deux côtés de la crête de la Sierra Nevada (crête de la Sierra). Sur le côté ouest de la crête, la pluie et l'ombrage ont résulté en une aire mésique présentant un couvert forestier plus important comparativement aux conditions xériques retrouvées sur le côté est de la crête de la Sierra. La survie moyenne des faons de la naissance à l'âge de 140 jours était, entre 2006 et 2008, de 0.33 (SE = 0,091), mais était plus faible pour les faons sur le côté ouest (0.13, SE = 0,092) que sur le côté est (0.44, SE = 0,11) de la crête de la Sierra. La masse à la naissance et la condition physique maternelle avaient un effet positif sur la survie des jeunes; toutefois, ces effets étaient évidents seulement pour les faons nés sur le côté est de la crête où la pression de prédation était plus faible que sur le côté ouest. La prédation par l'ours noir (*Ursus americanus*) était la principale cause de mortalité des faons sur le côté ouest (taux de mortalité = 0,63, SE = 0,97) comparativement à la prédation par les canidés et les félidés pour les jeunes nés sur le côté est de la crête de la Sierra (0,29, SE = 0,076). Entre 1997 et 2008, le recrutement moyen des jeunes à l'automne était plus faible pour les femelles sur le côté ouest (0,42, SE = 0,037) que pour les femelles sur le coté est (0,70, SE = 0,041) de la crête, et était positivement influencé par le niveau de gras corporel en mars mesuré à partir de la masse éviscérée des femelles (IFBFat). À l'échelle de la population, le ratio de jeunes par rapport aux femelles adultes (1991–2009) était très variable et fortement relié à l'IFBFat en mars des femelles adultes pour l'année en cours et l'année précédente. La reproduction des femelles d'un an était sensible à la disponibilité de la nourriture *per capita* pendant l'été (en tant qu'individu d'un an) qui influençait ainsi l'atteinte d'une masse corporelle suffisante pour permettre l'ovulation. La taille de la portée est demeurée élevée (1,69, SE = 0,027) au cours de l'étude. Elle était positivement influencée par la disponibilité de la nourriture, mais négativement par la température estivale, et était plus élevée pour les femelles résidant sur le côté ouest de la crête de la Sierra pendant l'été que pour celles résidant du côté est. À l'opposé, le taux de gestation est demeuré relativement stable au cours de l'étude (0,98, SE = 0,005). La survie des femelles matures (2 à 9 ans) était de 0,90 (SE = 0,021) en été, de 0,94 (SE = 0,012) en hiver, et de 0,87 (ET = 0,025) pour l'année entière. Malgré une relative stabilité entre les années, la survie estivale et la survie hivernale étaient positivement influencées le rapport entre le couvert de neige en avril de l'année précédente et la densité de la population. La valeur moyenne de IFBFat des femelles adultes était de 7,2% (SE = 0,077) en mars 1997–2009 et de 9,7% (SE = 0,23) en novembre 2002–2008. La condition physique représente un lien mécanistique entre les facteurs influençant la disponibilité et la qualité ressources et la performance d'une population, puisque la condition des femelles adultes à l'automne et à la fin de l'hiver est sensible à l'histoire nutritionnelle individuelle qui est liée à la croissance de la végétation, à la densité de population, aux tactiques de migration, aux coûts de la reproduction et aux effets nutritionnels différés. La condition physique des femelles adultes en mars est la variable la plus parcimonieuse permettant d'expliquer le taux de croissance de la population (λ) au cours de l'année à venir. L'ampleur relative de l'effet de la condition physique sur la survie et la reproduction était généralement en accord avec les changements prédits des taux démographiques en réponse à une limitation des ressources chez les populations de grands herbivores. Nos résultats indiquent que la gestion et la conservation des populations de grands herbivores pourraient être améliorées en intégrant des indices permettant de mesurer la condition physique individuelle dans les programmes de suivis et de recherche actuels. Nous proposons une méthode permettant d'estimer la proximité d'une population à sa capacité de support nutritionnel (NCC) qui est basé sur le statut nutritionnel de la population par rapport à la performance de la population (nommé indice-animal NCC). La proximité de la population à l'indice-animal NCC représente la capacité à court terme de l'environnement à soutenir la croissance de la population. Une approche nutritionnelle pour suivre et gérer les populations propose ainsi un lien direct avec la capacité de support de l'habitat tout en réduisant la nécessité d'estimer l'abondance de la population ou d'établir des objectifs en fonction de la taille de la population. Nous suggérons également que les effets de la mortalité (niveau de mortalité additive ou compensatoire) sur la dynamique de population peuvent être évalués en comparant la capacité nutritionnelle estimée pour la survie et le recrutement aux données empiriques mesurées, puisqu'on s'attend à ce que le nombre de jeunes produits soit plus important que ce que peut supporter l'habitat lorsque la nutrition est limitante. Notre approche est utile pour quantifier les effets de la prédation et fournit une base permettant de déterminer l'efficacité du contrôle des prédateurs sur les populations d'ongulés.

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INTRODUCTION

Nutritional ecology, the science relating an animal to its environment through nutritional interactions (Parker et al. 2009), holds implications for understanding behavior, life-history strategies, and effects of climate and predation on demographics (Raubenheimer and Boggs 2009). Despite advances in the understanding of nutritional ecology of numerous large herbivores (Parker et al. 2009), the complex interactions between predation, climate, and density dependence on population dynamics continue to hamper identification of factors ultimately responsible for regulating population growth (Skogland 1991, Coulson et al. 2001, Sinclair and Krebs 2002, Sinclair et al. 2003). Concepts such as carrying capacity (K; McCullough 1979, McLeod 1997), additive and compensatory mortality (Errington 1946, 1967), and top-down or bottom-up forcing (Bowyer et al. 2005, Pierce et al. 2012) are all aspects known to affect population dynamics and life-history characteristics of large mammals, but often are of greater heuristic than practical value because those characteristics are difficult to quantify.

Vital rates of large herbivores generally respond to resource limitation in a predictable sequence, starting with decreased survival and recruitment of young, increased age of first reproduction, decreased reproduction by adults and, finally, decreased survival of adults (Gaillard et al. 1998, 2000; Eberhardt 2002). Reproduction demands resources above those necessary for maintenance (Monteith et al. 2014) and life-history theory predicts that when those resources are limited, long-lived, iteroparous mammals should favor their own survival over successful reproduction (Stearns 1992). In addition, young animals have fewer nutritional reserves, and thereby have a lower

tolerance for unfavorable conditions (Barboza et al. 2009). The sequential changes in reproduction and survival, therefore, are underpinned largely by nutrition (Cameron and Verhoef 1994, Testa and Adams 1998, Keech et al. 2000, Cook et al. 2004, Stewart et al. 2005, Bender et al. 2007), and the resources required to support each life-history component.

A better understanding of seasonal patterns of nutritional condition and its relative influence on population dynamics would improve our knowledge of life-history strategies and population regulation of ungulates (Stephenson et al. 2002, Cook et al. 2004, Parker et al. 2009, Monteith et al. 2013). Making inferences concerning effects of climate, density, or predation on vital rates and mortality factors without knowledge of seasonal deficiencies or surpluses in nutrition can be difficult (Bowyer et al. 2005, Brown et al. 2007). Nutritional condition integrates the balance of nutritional intake and expenditure, and is represented primarily by the deposition and catabolism of body fat (Parker et al. 2009). As a result, nutritional condition (i.e., percent body fat) ultimately should function as the mechanism through which intraspecific competition for resources is mediated, and should provide the most direct and sensitive measure of habitat quality and resource limitation.

Temperate and arctic herbivores follow seasonal cycles in nutrient intake according to seasonal changes in quality and quantity of food resources, activity levels, reproductive effort, and metabolic rate (Moen 1978, Parker et al. 1993, Taillon and Côté 2006, Barboza et al. 2009), with declines in all processes occurring during winter. Research typically has focused on nutrition during winter, likely because of the conspicuous effects of malnutrition during that season (Kucera 1997, Parker et al. 2005, Page and Underwood 2006). In contrast, forage

quality and quantity are highest during the growing season, and fat and protein deposition, thus, typically are greatest during spring and summer, and are thought to prepare animals for the food-limited winter (Moen 1978, Cook et al. 2013). Carryover of nutritional condition from one season to the next, however, underscores the importance of not considering a particular season in isolation (Monteith et al. 2013). For example, gestation and lactation are nutritionally taxing for large herbivores (Moen 1978, Pekins et al. 1998, Monteith et al. 2014). As a result, range conditions and reproductive status during summer directly influence nutritional condition of individuals entering winter (Chan-McLeod et al. 1999; Cook et al. 2004, 2013; Couturier et al. 2009).

Several investigators have identified proximate factors affecting survival and reproduction of large herbivores, but few have characterized the underlying mechanisms that influence vulnerability to mortality, or the ability to produce and successfully rear young (Pettorelli et al. 2011). The relative influence of nutrition (bottom-up) and predation (top-down) on the regulation of populations remains a common theme in ecological studies (Hairston et al. 1960, Skogland 1991, Estes et al. 2011, Pierce et al. 2012). Indeed, the reintroduction and expanding populations of large carnivores have fueled, and likely will continue to promote, the controversy behind the ecological consequences of their presence (Bangs et al. 1998, Pyare et al. 2004, Carroll et al. 2006, Kauffman et al. 2010, Smith et al. 2010). In systems where ungulates co-occur with large carnivores, predation is commonly the leading proximal cause of mortality among young ungulates (Linnell et al. 1995, Singer et al. 1997, Bowyer et al. 1998b, Ballard et al. 2001), but simply identifying cause of death is of little value without characterizing the implications or underlying basis of those mortalities (Bleich and Taylor 1998, Ballard et al. 2001, Bowyer et al. 2005). Errington (1967:235) forewarned against confusing "the *fact* of predation with the *effect* of predation." Understanding the nutritional basis for survival and reproduction has potential to reveal the compensatory or additive effects of mortality, and thereby the relative role of large carnivores in the population dynamics of their ungulate prey.

Studies at the population level have provided the basis for our understanding of the regulation of animal abundance (Lack 1954); most studies of large herbivores have focused on population-level phenomena because of the logistical challenges associated with acquiring sufficient data for individuals (McCullough 1979, Stewart et al. 2005, Clutton-Brock and Sheldon 2010). Data collection and analyses at the level of the individual are complementary to those at the population level, but provide greater insights into the mechanisms of population change and selection for particular life-history strategies (Stearns 1992, Lindström 1999, Testa 2004, Benton et al. 2006). Although few such investigations have been conducted for cervids in North America, individual-based studies have been the cornerstone for recent advances in understanding population ecology (Clutton-Brock and Sheldon 2010). Moreover, carryover of nutritional deficiencies or incomes can confound interpretation of dynamics at the population level (Testa 2004), and can only be elucidated by long-term, individual-based studies (Clutton-Brock and Sheldon 2010, Harrison et al. 2011).

Populations of mule deer have experienced periodic declines over the latter part of the last century; causes of those declines remain speculative and controversial (deVos et al. 2003, Connelly et al. 2012). Potential sources of declines include loss or fragmentation of habitat because of development, altered forage quality, competition with other ungulates, predation, disease, increased hunting mortality, poaching, severe winter weather, and droughts (deVos et al. 2003, Bishop et al. 2009, Hurley et al. 2011). Given high and consistent rates of pregnancy and fecundity (Andelt et al. 2004, Bishop et al. 2009), however, reduced survival of neonates during their first year-of-life is the most likely explanation for population declines (Gill et al. 2001, Andelt et al. 2004, Wasley 2004). Although predation is routinely identified as the proximate cause of mortality for neonatal mule deer, survival and recruitment of young mule deer also are sensitive to maternal nutritional condition and forage condition (Lomas and Bender 2007, Tollefson et al. 2011). Habitat quality is believed to have declined across most of the western United States because of successional changes in vegetation caused by altered fire regimes, noxious weeds, overgrazing, energy development, and habitat loss (Lutz et al. 2003, Bishop et al. 2009). Furthermore, alterations in temperature, snowpack, and hydrologic regimes as a result of recent changes in climate (Knowles et al. 2006, Barnett et al. 2008, Shuman 2011) likely are affecting the phenological patterns of forage growth and abundance. Failure to identify specific factors that regulate populations, however, has precluded the detection of the underlying causes, because habitat condition, weather, and predation interact with density dependence to affect population processes (Kie et al. 2003). Detailed and long-term investigations are needed to identify factors regulating populations of mule deer and to improve their conservation and management (Caughley 1977, deVos et al. 2003, Bleich et al. 2006, Connelly et al. 2012, Pierce et al. 2012). Results of 2 recent and comprehensive studies on mule deer in Colorado (Bishop et al. 2009) and Idaho (Hurley et al. 2011), USA, underscored the effects of nutrition and climate on dynamics of mule deer populations. Our research is an extension of those studies and melds population ecology with longitudinal data on nutrition and life history of individual mule deer in a variable environment.

We studied a population of mule deer that overwintered in Round Valley, located on the east side of the Sierra Nevada, California, USA. This population of mule deer has been subjected to a highly variable climate and receives predation pressure from a suite of large carnivores (Kucera 1988; Pierce et al. 2000, 2004). We intensively monitored the population of mule deer in Round Valley from 1997 to 2009, as it recovered from a population low in 1991 (Pierce et al. 2012). Deer that overwintered in Round Valley migrated to high-elevation summer ranges on both sides of the crest of the Sierra Nevada (hereafter Sierra crest), where a rainshadow caused by the Sierra Nevada results in a more xeric range on the east side of the crest compared with the mesic west side (Pierce et al. 1999, Storer et al. 2004, Bleich et al. 2006, Monteith et al. 2011).

The divergent migratory pattern of mule deer that overwintered in Round Valley afforded a unique opportunity to evaluate influences of summer range on factors influencing their recruitment and survival. Differential fitness between migratory

strategies may permit the coexistence of 2 strategies, but advantages of each tactic are sensitive to changes in reproductive success and survival (Kaitala et al. 1993). In 1987, Kucera (1988) determined that 87% of the population of mule deer in Round Valley migrated to the west side of the Sierra crest during summer. The mesic west side presumably offered better foraging opportunities for mule deer during summer, which likely supported high recruitment and survival favoring that migratory tactic.

Our objectives were to examine life-history characteristics of individual mule deer, including migratory tactic, to better understand interactions of those characteristics with nutritional ecology. We evaluated the influence of nutritional condition on survival and reproduction of female mule deer, factors that influenced nutritional condition, and the seasonal carryover of their nutritional state. We hypothesized that nutritional condition would serve as a sensitive metric of resource limitation, and function as the underlying mechanism of those life-history patterns in mule deer, thereby providing insights into population dynamics (Fig. 1). Accordingly, we predicted that nutritional condition would influence vital rates of mule deer in the same order proposed by their sensitivity to resource limitation (Eberhardt 2002), and that those vital rates would be influenced by seasonal patterns of climate, forage abundance, and animal density (Fig. 1). We also hypothesized that the migratory tactic employed by an individual would interact with other life-history components to determine patterns of nutritional condition and fitness within the population (Hebblewhite and Merrill 2009).

We expected nutritional condition of individuals to be sensitive to environmental factors including precipitation and growth of forage relative to population density, migratory tactic, season, and reproductive status (Fig. 1). We also assessed the degree of carryover effects on seasonal levels of nutritional condition and their influence on population characteristics (Fig. 1). Our overarching goal was to integrate nutrition with life-history theory in a free-ranging large mammal to provide a nutritional basis for understanding life-history strategies, and aid in the conservation and management of large herbivores.

STUDY AREA

The Sierra Nevada is a mountain range oriented northwest to southeast that extends about 250 km from the shore of Lake Almanor in the north, to Tehachapi Pass, east of Bakersfield (Storer et al. 2004), and lies entirely within California, USA, except for the Carson Range, which extends eastward into Nevada. This mountain range is a massive granitic block that tilts to the west with a gradual slope of 2–6%, extending 75–100 km from the crest to the San Joaquin or Sacramento valleys. Conversely, the precipitous east side of the Sierra crest is characterized by steep slopes rising abruptly from the bordering valleys that merge with the western edge of the Great Basin. The Owens Valley, extending from the Sherwin Grade north of the town of Bishop and southward about 120 km, is demarcated by elevations of 4,200 m at the mountain summits to 1,220 m at the
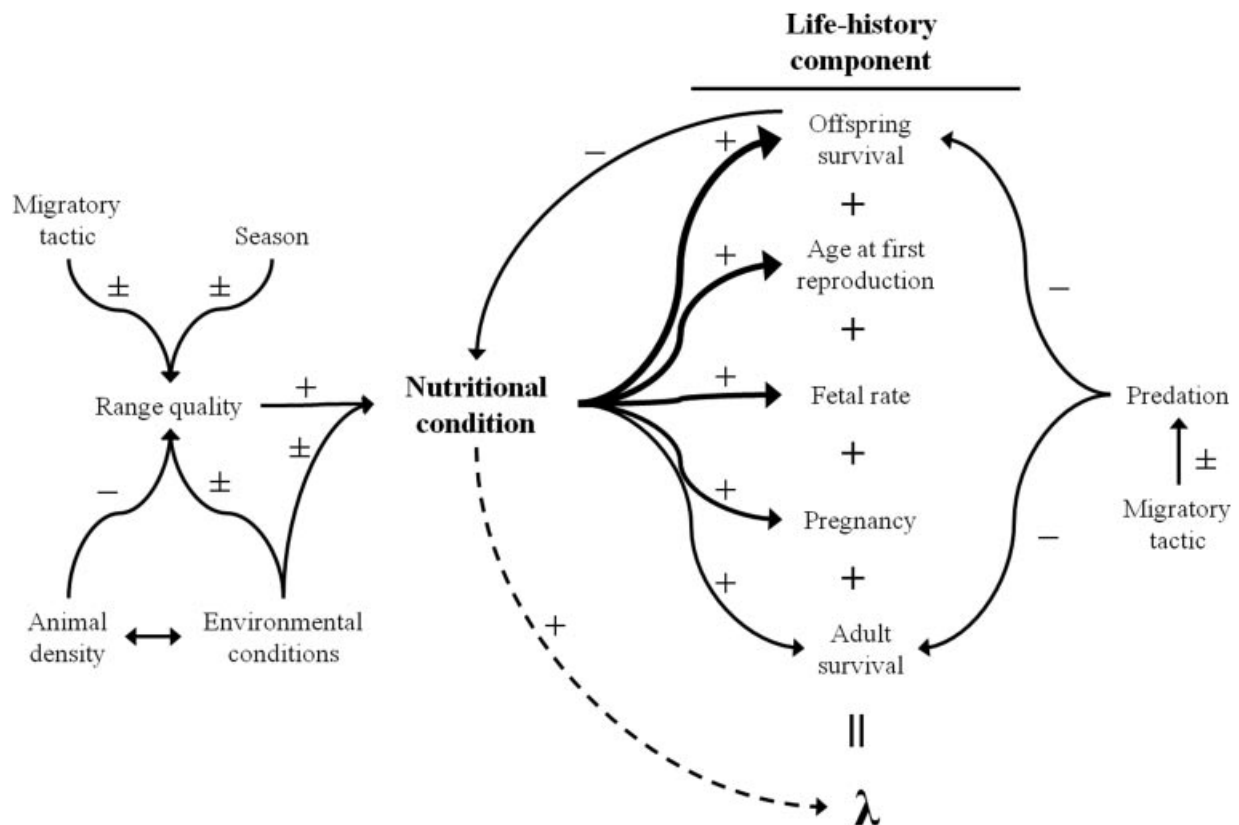
Figure 1. Conceptual model illustrating the predicted association between nutritional condition and life history, and the factors expected to influence nutritional condition. Weight of the arrows between nutritional condition and life-history component represent the expected sensitivity of each life-history component to resource limitation. Expected direction of relationships (i.e., positive, negative, or both) are indicated with each connection. Season refers to winter versus summer conditions and the feedback from offspring survival to nutritional condition refers to the cost of reproduction on autumn nutritional condition.
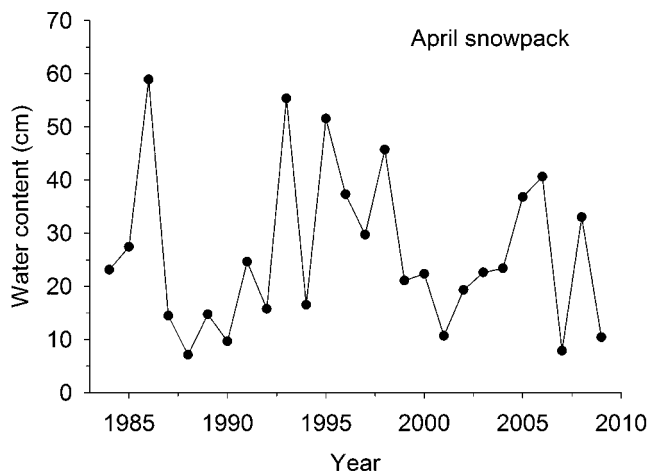
Figure 2. Water content (cm) of the snowpack during April in the Rock Creek drainage adjacent to Round Valley, Bishop, California, USA, 1984–2008 (Station ID: RC2, California Department of Water Resources).

Figure 3. Range occupied by migratory mule deer that share a common winter range in Round Valley and migrate to distinct summer ranges on both sides of the crest of the Sierra Nevada, California, USA with summer range locations of adult female mule deer monitored during 1984–1987 (Kucera 1988), 1998, and 2008.

valley floor over horizontal distances of <10 km (Kucera 1988). Few passes allow vehicular traffic over the Sierra crest; thus, most passes are accessible to humans only by foot or on horseback.

The Sierra Nevada is typified by dry, hot summers (Jun–Sep), short, mild autumns (Oct), and long, cool winters, with most annual precipitation accumulating as snow (Nov–Apr; Monteith et al. 2011). Within the region, 75% of the precipitation, including rain or snow, accumulates between November and March (Monteith et al. 2011). Snow accumulation measured by water content of the April snowpack in a drainage adjacent to Round Valley (Station ID: RC2, California Department of Water Resources) was highly variable during 1984–2009, and ranged from 7.1 cm to 58.9 cm (Fig. 2). The Sierra crest, which sharply delineates the western slope from the eastern slope of that range, causes a rain-shadow that results in >3× greater deposition of moisture on the west side and produces an arid landscape on the eastern slope, where the Great Basin Desert begins.

Mule deer inhabited approximately 90 km^2 of Round Valley (37°24′, 118°34′W) during November–April (Fig. 3), but the size of the area used was dependent on snow depth in any particular year (Kucera 1988). Most of these mule deer migrated northward and westward to high-elevation ranges in summer (Kucera 1992, Pierce et al. 1999); some migrated over passes to the west side of the Sierra crest, whereas others remained on the east side (Monteith et al. 2011).

Round Valley is bounded to the west by the eastern escarpment of the Sierra Nevada. Vegetation in Round Valley was characteristic of the western Great Basin and the sagebrush belt (Storer et al. 2004). Typical vegetation that characterized habitats used by mule deer in Round Valley included bitterbrush (*Purshia glandulosa*), sagebrush (*Artemesia tridentata*), blackbrush (*Coleogyne ramosissima*), desert peach (*Prunus andersonii*), rabbitbrush (*Chrysothamnus nauseosus*), and Mormon tea (*Ephedra nevadensis*). Riparian areas consisted of willow (*Salix* spp.), rose (*Rosa* spp.), and water birch (*Betula occidentalis*); forbs and graminoids were uncommon in Round Valley during winter (Kucera 1988, Pierce et al. 2004). Open pastureland comprised
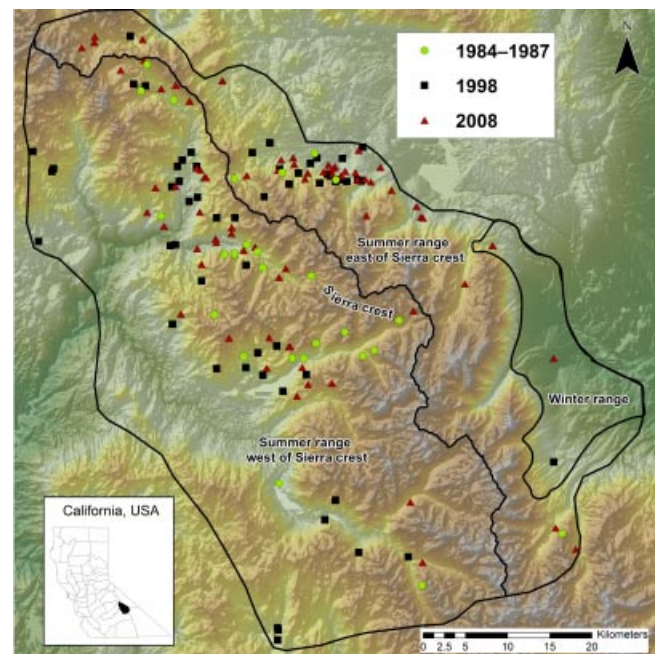
parts (18.3 km^2) of the eastern portion of the valley; however, deer used pastures only when heavy snows forced them from higher elevation areas dominated by bitterbrush, which was a primary winter forage for mule deer (Pierce et al. 2004, 2012).

Deer overwintering in Round Valley migrated in spring to summer ranges on both sides of the Sierra crest at elevations ranging from 2,200 m to >3,600 m (Monteith et al. 2011). The western slope of summer range for mule deer was dominated by the upper-montane and mixed-conifer vegetation zones (Storer et al. 2004) consisting of conifer stands with little understory, including red fir (*Abies magnifica*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), Jeffery pine (*Pinus jeffreyi*), and quaking aspen (*Populus tremuloides*). Montane chaparral, composed of dense stands of manzanita (*Arctostaphylos* spp.), ceanothus (*Ceanothus* spp.), and bush chinquapin (*Chrysolepis sempervirens*), occured at lower elevations within drainages on the western slope (Storer et al. 2004). The relatively common and dense pine-fir (*Pinus-Abies* spp.) stands and rivers on the west side contrast with the sparse forests (*Pinus* spp.) transitioning to sagebrush (*Artemesia* spp.) steppe on the east side. The eastern slope of the Sierra was characterized largely by the sagebrush vegetation zone (Storer et al. 2004). This zone was dominated by sagebrush, but also included other shrub species such as bitterbrush, ceanothus, manzanita, rabbitbrush, and mountain mahogany (*Cercocarpus betuloides*), and supported pure stands of Jeffrey pine in some areas (Storer et al. 2004).

Mule deer inhabiting winter range in Round Valley have been subjected to the vagaries of climate, coupled with influences of density dependence (Kucera 1988), and have exhibited marked variation in population size during the past quarter century. Coincident with a likely overshoot of *K* and a severe drought

during 1987–1990, when water content of winter snowpack was 27% of the long-term mean (Pierce et al. 2012), total numbers (based on minimum counts) declined from 5,978 (66 deer/km^2) animals in 1985 (Kucera 1988) to a low of 939 (10 deer/km^2) in 1991 (Pierce et al. 2012). During the population decline, pregnancy rates, fetal rates, fetal sizes, adult weights, and kidney fat varied with precipitation and forage growth on winter range (Kucera 1988, Pierce et al. 2012). Following the prolonged drought and population nadir in 1991, deer numbers increased to approximately 1,900 in 1997 (Pierce et al. 2012), when we initiated our research. With the exception of winter 1984, when an antlerless hunt removed 200 female mule deer (approx. 3.3% of the total population at that time) on the northern portion of the study area as part of a research project (Kucera 1988), only limited hunting of 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 the harvest of male mule deer on summer range was difficult to estimate because deer from Round Valley mingle with deer from other populations. Nevertheless, limited harvest of males would have had a negligible influence on population dynamics of deer (McCullough 1979, 2001; Kie et al. 2003).

Areas occupied by migratory mule deer include a full complement of other predators on both winter and summer ranges, including cougars (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*; Pierce et al. 2000, Villepique et al. 2011). Black bears (*Ursus americanus*) were abundant on summer ranges west of the Sierra crest, but were less common in the eastern Sierra Nevada. Grizzly bears (*Ursus arctos*) formerly existed west of the Sierra crest, but were extirpated by 1922 (Storer and Tevis 1955).

METHODS

Animal Capture and Handling

Adult females.—During March 1997–2009 and November 2002–2008, we captured adult (>1 yr old) female mule deer on winter range in Round Valley using a hand-held net gun fired from a helicopter (Barrett et al. 1982, Krausman et al. 1985). We hobbled and blindfolded each animal before transporting it via helicopter to a central processing station. We removed 1 incisiform canine using techniques described by Swift et al. (2002) to allow age estimation by cementum annuli (Matson's Laboratory, Milltown, MT). This procedure had no effect on body mass, percent body fat, pregnancy rate, or fetal rate in mule deer (Bleich et al. 2003). We measured body mass with an electronic scale (±1 kg). We fitted each animal with a standard very high frequency (VHF) radiocollar (Telonics, Inc., Mesa, AZ; Advanced Telemetry Systems, Isanti, MN) equipped with mortality sensor, and covered with orange tape or orange plastic to enhance visibility during mark-resight surveys. To obtain longitudinal data on individual females, we attempted to capture every radiocollared female in March and >50% of the radio-collared females during November. We captured new, unmarked females in an effort to maintain a sample of ≥75 adult females for the duration of the study. Our sample included 347 individual adult females, which we captured an average of 3.6 times each

(range = 1–20 times) on winter range in Round Valley during 1997–2009.

We conducted ultrasonography (Aloka 210 with 5-MHz transducer, Aloka, Inc., Wallingford, CT) to determine nutritional condition of captured animals using standard protocols developed for mule deer. We measured maximum thickness (to the nearest 0.1 cm) of subcutaneous fat at the thickest point cranial to the cranial process of the tuber ischium (Stephenson et al. 2002). We accompanied ultrasonography with palpation to achieve a body-condition score validated for mule deer (Cook et al. 2007) to aid in estimating nutritional condition of animals that had catabolized subcutaneous fat reserves (<5.6% ingesta-free body fat; IFBFat). We then combined body mass, body-condition score, and maximum thickness of rump fat to estimate percent IFBFat according to relationships ($r^2 = 0.81$, $P < 0.001$) and equations provided by Cook et al. (2010). When body mass was not available, we used measurements of chest girth to estimate body mass ($r^2 = 0.74$) for calculations of IFBFat (Cook et al. 2010). We also converted kidney-fat indices collected during 1985–1996 (Kucera 1988, Pierce et al. 2012) using standard equations (Cook et al. 2007) to obtain estimates of IFBFat during that period ($r^2 = 0.84$), which provided a long-term trend in nutritional condition of deer.

We also used ultrasonography during March to determine pregnancy and fetal rates of captured females (Stephenson et al. 1995). We shaved the left-caudal abdomen behind the last rib and applied lubricant to facilitate transabdominal scanning using a 3-MHz transducer. Upon completion of ultrasonography, we fitted numerous (approx. 60/yr) pregnant females with vaginal implant transmitters (VITs) during 2006–2008; we used VITs (M3930, Advanced Telemetry Systems) to facilitate locating and capturing neonatal mule deer. We inserted VITs using a technique similar to that described by Bishop et al. (2007). We placed VITs approximately 20 cm into the vaginal canal, or until the silicone wings of the VIT were pressed firmly against the cervix. We used a temperature-sensitive switch that increased pulse rate of transmissions from 40 pulses to 80 pulses per minute when the temperature decreased below 32° C, which was representative of the VIT being expelled by the deer and the subsequent birth of young. Vaginal implant transmitters have been employed without reproductive problems or effects on female survival, and are a practical technique for locating birth sites and neonates (Carstensen et al. 2003, Johnstone-Yellin et al. 2006, Bishop et al. 2007).

Neonates.—During 2006–2008, we located and captured 119 neonatal mule deer from 15 June to 20 July by searching for and observing females that exhibited postpartum behavior and by locating expelled VITs. We located radiocollared females and monitored VITs for evidence of parturition at first light each day during the period of parturition (i.e., 15 Jun–31 Jul) using a Cessna 180 fixed-wing aircraft (Cessna Aircraft Company, Wichita, KS) fitted with 2, 2-element H-antennas, and used ground-based telemetry to locate the VIT and radiocollared female as quickly as possible. We used the location of the VIT and the location and behavior of the female to identify search areas.

When our ground searches failed to produce neonates, we evaluated whether the location of the VIT was an actual birth

site, and confirmed that supposition by observing the pregnancy status and behavior of the radiocollared female. If the female appeared to have undergone parturition and personnel were available, we attempted to observe the female from a distance (≥300 m, depending upon terrain and cover) sufficient to avoid disturbance, and used postpartum behavior of the female to locate fawns (Monteith et al. 2007). In addition to radiocollared females with VITs, we opportunistically observed random females at first light with binoculars (6–15×) or spotting scopes (20–50×), and located neonates by focusing on adults that exhibited maternal behavior (Huegel et al. 1985, Carstensen et al. 2003). When we located a neonate, we hiked to the area where the neonate bedded, and conducted ground searches to locate and capture young mule deer.

We captured neonatal deer by hand and placed them in a cloth bag containing sagebrush to minimize scent transfer, although that likely would have had little influence on potential abandonment (Bowyer et al. 1998a, Carstensen et al. 2003). We determined sex of each neonate and acquired a measurement of new hoof growth using dial calipers (Robinette et al. 1973, Brinkman et al. 2004). We determined the body mass of each neonate within the cloth bag to the nearest 0.1 kg using a hand-held spring scale. We recorded the geographic coordinates of each capture site using a global positioning system (GPS) device, and processed all neonates quickly to minimize the potential for abandonment or attraction of predators (Livezey 1990). We fit all neonatal deer with an expandable radiocollar (Advanced Telemetry Systems, Inc.; Telemetry Solutions, Walnut Creek, CA) with a 4-hour mortality delay. Methods of research and animal capture were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (protocol: 650-0410), were in accordance with guidelines for research on wild mammals adopted by the American Society of Mammalogists (Gannon et al. 2007), and followed protocols of California Department of Fish and Game for restraint of ungulates.

Deer Monitoring and Cause-Specific Mortality
We endeavored to monitor all radiocollared mule deer with ground telemetry on winter range ≥3 days per week from October to April to determine survival and cause-specific mortality. During summer, we attempted to monitor radio-collared neonates daily from a fixed-wing aircraft and ground-based radiotelemetry from their time of capture until at least 31 August, when risk of mortality was greatest (Bishop et al. 2009); we monitored young deer approximately 3 days per week thereafter. The near absence of roads in the 2,800-km² summer range precluded frequent monitoring of most adult females on summer range. Therefore, we often did not detect mortality of adults during summer for ≥1 week, reducing the likelihood of ascertaining cause of death. We attempted to locate each animal at least once during 15 June–30 September to determine summer occupancy and migratory status. We grouped animals based on their summer residency, which we defined by their use of summer range on the east or west side of the Sierra crest. To illustrate the relative changes in density of individuals that migrated to the east versus west side of the Sierra crest, we developed a metric of relative change in density between decades using summer

locations of radiocollared females (i.e., single location per female each summer) obtained using aerial telemetry for summers of 1984–1987 (Kucera 1988), 1998, and 2008. With those summer locations, we calculated the Euclidian distance to the nearest female for each 30-m pixel within our study area. We then developed a map where the shading per pixel was based on the relative change in density, which we determined by subtracting the Euclidian distance for each pixel between 1998 and 1984–1987, and 2008 and 1998.

Frequent monitoring of animals on winter range and of neonates during summer typically allowed us to detect mortality early enough to determine proximate cause of death. When mortalities were detected, we used ground telemetry to locate carcasses as quickly as possible (<8 hr). We examined carcasses to estimate date of death based on decomposition and condition of the animal. We evaluated and recorded the location and arrangement of the carcass, presence and position of tooth marks, ante- and post-mortem bleeding or bruising, fractures, and remaining organs when present. We identified other physical evidence of predation including tracks and feces (Elbroch 2003), and collected hair for confirmation of the predator responsible (Moore et al. 1997). When we could not ascertain cause of death, we transported the carcass to the laboratory to be necropsied; we performed field necropsies when distance or a precarious location hindered transport of the carcass from the field.

We classified proximate causes of death as 1) predation; 2) malnutrition, which included small and emaciated neonates where the carcass remained intact with no signs of predation and adults with <25% femur marrow fat; 3) other natural causes if the carcass was intact, did not show signs of predation, malnutrition, or trauma, and post-mortem examination indicated potential infection or disease; 4) accident if a carcass was located mainly intact with broken bones or other premortem physical trauma, which included deer-vehicle collisions; or 5) undetermined if cause of death could not be placed in 1 of the aforementioned categories, or lack of evidence otherwise precluded determination of cause of death. For predation-related mortalities, we attempted to identify the predator responsible for the death.

For neonates, we included abandonment as a proximate cause of death if the neonate was apparently healthy and post-mortem necropsy revealed an abomasum that was empty or contained soil and vegetation rather than milk, an indication of the absence of nursing (Church 1988). When available, we collected femurs from mortalities and evaluated femur marrow from its appearance and texture; we also estimated femur-marrow fat based on percent dry weight (Neiland 1970). We considered the proximate cause of mortality as the ultimate cause except for those adult animals that had a visual score of 1 (marrow was red and fluid) and femur-marrow fat <25% (Neiland 1970). Femur-marrow fat <25% is indicative of malnutrition and depletion of the last remaining fat reserves (Mech 2008); we considered the cause of mortality to be malnutrition in those instances, regardless of proximate indicators of death (Ratcliffe 1980, Depperschmidt et al. 1987).

We defined recruitment status of radiocollared females by the number of young-at-heel identified each autumn, which we determined as females arrived on winter range in late-October through November, when mother–infant bonds were still intact

(Bonenfant et al. 2005). We located each radiocollared female and stalked to within ocular range (<200 m) aided by ground-based telemetry. We observed each female using binoculars or spotting scopes until we could determine the number of young-at-heel confidently, which we identified by observing nursing and other maternal behaviors (Monteith et al. 2011).

Population Surveys

We conducted 2 helicopter surveys during each January to estimate the number of deer wintering in Round Valley and the proportion of adult females, adult males, and young in the population. We conducted surveys in a Bell Jet Ranger 206 BIII (Bell Helicopter, Hurst, TX) with 3 observers; we removed the doors to improve visibility (Clancy 1999). Aerial transects overlapped the entire winter range to an elevation at which deer tracks were no longer evident in snow. We established the location of the initial transect randomly, but subsequent transects were parallel to the initial transect, and spaced at intervals of approximately 0.4 km. We also calibrated reference points on the door jambs of the helicopter to allow observers to estimate distances from the centerline out to 200 m.

For population-composition surveys, we flew aerial transects with 3 observers and classified deer as we encountered them. For each group or individual encountered, we identified the size and composition of each group, which included adult males, adult females, and young (<1 yr old). Visibility bias among sex and age classes were likely kept to a minimum (Bonenfant et al. 2005), because we collected our herd composition data with helicopter surveys on winter range, in open sagebrush-steppe habitat in January. Sample sizes were typically >1/3 of the population estimate. We calculated age ratios and their standard errors according to Bowden et al. (1984), which assumed sampling without replacement.

We obtained population size from a total count of deer before 1994 (Pierce et al. 2012), for which no measure of variance existed because these were censuses. Subsequently, we estimated population size using the marked deer in Round Valley (Chao and Huggins 2005). During those mark-resight surveys, we noted the number of marked female deer in each group, but did not classify deer with respect to age class or sex, thereby alleviating the need for the pilot to deviate from, and then attempt to return to, the transect line. The pilot tried to maintain an elevation of 25 m above ground level (AGL) and an air speed of approximately 75 km/hour.

We used the Chapman (1951) modification of the Lincoln–Petersen estimator to calculate unbiased estimates and the associated variance of population size for mule deer from the mark-resight data collected during the annual helicopter surveys. We assumed that marked animals had sightabilities similar to unmarked animals (White and Shenk 2001), and that the population was geographically and demographically closed during the survey period, based on aerial or ground-based telemetry immediately before each aerial survey to confirm the number of marked deer available within the survey area. We did not identify individually marked animals during the survey; therefore, we assumed homogeneity in sighting probability per individual. We recognize that if heterogeneity in sighting probabilities for individuals existed, our error estimates could be biased. Any bias caused by differences in sightability among individuals likely was minimal, however, because of the open habitat on winter range in Round Valley.

Statistical Analyses

Modeling approach.—We modeled neonatal and adult survival, cause-specific mortality, reproductive rates, nutritional condition, sex and age ratios, and the finite rate of population growth (λ) for mule deer as a function of predictor variables that were representative of 3 different levels: population, individual, and maternal. Population-level covariates were environmental factors or variables that corresponded to the entire population, or a large proportion of the population. Individual-level covariates were unique attributes of individuals, and maternal variables were characteristics of the mother of a particular neonate. We first evaluated effects of covariates at the population level and retained those variables identified as being influential in this first stage of analysis (Arnold 2010, Monteith et al. 2011, Grovenburg et al. 2012a), and used them for the same analysis with incorporation of variables at the individual level, and then at the maternal level when relevant. Therefore, we modeled response variables in 1–3 stages according to the aforementioned levels. We conducted our analyses in that 2- or 3-stage approach because covariates at the individual or maternal level were not available for every animal, and population-level and individual-level factors can affect life-history characteristics differently (Monteith et al. 2011, 2013). We also conducted an additional analysis that included only data from 2002 to 2008 to assess relationships related to life-history characteristics of females in autumn, because capture efforts in November occurred only during those years.

We used an information-theoretic approach to assess variable importance. In each stage of the analysis, we evaluated all possible combinations of predictor variables that we hypothesized to influence the response variable (Whittingham et al. 2006, Arnold 2010, Doherty et al. 2010). For each model, we calculated Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, and Akaike weight (w_i; Burnham and Anderson 2002). We then calculated model-averaged parameter estimates and the associated 90% confidence intervals, based on unconditional standard errors. Model averaging minimized effects of uninformative parameters, and thereby provided a conservative assessment of variable importance (Whittingham et al. 2006, Arnold 2010, Doherty et al. 2010). We determined if model-averaged parameter estimates differed from zero based on whether their 90% confidence intervals overlapped zero. We used importance weights, calculated as the sum of w_i across all models that contained that particular variable (Burnham and Anderson 2002, Arnold 2010, Doherty et al. 2010, Monteith et al. 2011), to evaluate the relative ranking of each predictor variable. We retained variables from the previous stage of an analysis if the parameter estimate differed from zero (i.e., 90% CI did not overlap 0) or had an importance weight >0.50 (Arnold 2010, Monteith et al. 2011). To best depict relationships between a specific predictor variable and a response variable in figures, we used the top model ($\Delta AIC_c = 0$) of all possible combinations of variables, and modeled expected effects (y-axis) of the variable of interest (x-axis) within the observed range,

while holding all other variables constant at their mean (or other values as specified).

We evaluated biologically meaningful interactions between predictor variables using the global model in each stage of the analysis based on whether confidence intervals of the parameter estimate for the interaction overlapped 0 and if the inclusion of the interaction term resulted in an improvement of model fit (<2 ΔAIC_c). We removed all interaction terms with confidence intervals that overlapped zero and did not result in an improvement of model fit from analyses because inclusion of those interaction terms can alter model-averaged estimates of the independent counterpart of those terms. In addition, for age-specific patterns, we evaluated both the inclusion of the quadratic effect of age (age^2) and a threshold model of age (ln[age]), because demographic and morphometric relationships with age may take many forms (Nussey et al. 2011). We retained age^2 or ln(age) if its inclusion resulted in improved model fit.

Predictor variables.—For each level of analysis, we developed a set of variables a priori based on the literature and that we expected would influence or be related to the response variable, with the overarching goal of assessing effects of nutrition on life-history characteristics of mule deer (see Appendices A–O for complete list of variables). Predictor variables at the population level (Table 1) included environmental variables such as weather, categorical variables that applied to a large portion of the population (e.g., summer residency), and annual metrics of the condition or performance of the mule deer population (e.g., mean Mar IFBFat). At the individual level, variables included life-history characteristics that corresponded to each individual (e.g., age, recruitment status, IFBFat; Table 2), and variables at the maternal level were characteristics of the mother of a specific neonate (e.g., age, IFBFat; Table 2). We evaluated multicollinearity among all predictor variables in each stage of analysis, and did not allow variables that were correlated ($r > |0.50|$) enter the same model.

Growth of bitterbrush, the primary winter forage for mule deer in the Sierra Nevada (Kucera 1997, Pierce et al. 2004), was influenced largely ($r^2 = 0.65$, $P = 0.001$) by the water content of the snowpack from the preceding April (Fig. 2; Pierce et al. 2012). Accordingly, seasonal nutrition was influenced by snowfall from the preceding year; however, per capita availability of forage was determined by the relationship of snowpack and number of individuals present in the subsequent year (Pierce et al. 2012, Monteith et al. 2013). Therefore, we calculated a density-dependent proxy to forage availability based on the quotient of the water content of the snowpack during the preceding April, and the estimated number of females for that year (per capita snowpack; cm/female). This variable integrated factors that affected growth of forage and population density to yield a density-dependent index to forage availability. Our per capita snowpack metric was similar to relationships established for African ungulates, where plant growth was strongly associated with rainfall, but the influence on demography depends on the current relative abundance of herbivores (i.e., animals per kg green grass; Sinclair et al. 1985). We included estimated number of females rather than a population estimate because males and females partition use of resources throughout much of the year (McCullough 1979; Bowyer 1984, 2004; Kie and Bowyer 1999). We assessed the relative importance of including either per capita snowpack, or snowpack and number of females, or their interaction based on ΔAIC_c for each separate analysis, and then included the most influential variable(s) in the remainder of model sets.

We also included location of summer residency as a predictor variable, because deer that overwinter in Round Valley reside on disparate ranges on opposite sides of the Sierra crest, and life-history patterns may differ between females residing in different areas (Monteith et al. 2011). We coded females occurring on the west side as 0 and females residing on the east side of the Sierra crest as 1 (Table 1).

Survival.—We used the known-fate model in Program MARK (White and Burnham 1999), which accommodated staggered entry and exit of radiocollared animals (Kaplan and Meier 1958, Pollock et al. 1989), to estimate survival and determine factors that influenced seasonal survival of adult (>1 yr) female mule deer. We first estimated winter (Nov–Apr) and summer (May–Oct) survival for prime-aged females (2- to 9-yr-

Table 1. Definitions of predictor variables used to assess factors that influence life-history characteristics of mule deer at the population level.

Level	Predictor	Units	Definition
Population	Summer residency	East or west	Side of the Sierra crest occupied during summer (east = 1; west = 0)
	Spring precipitation	cm	Total precipitation during May–June
	Spring temperature	° C	Mean temperature during May–June
	Summer precipitation	cm	Total precipitation during July–October
	Summer temperature	° C	Mean temperature during July–October
	Monthly precipitation	cm	Total monthly precipitation
	Monthly temperature	° C	Mean of daily temperature per month
	Snowpack	cm	Water content of snowpack during the previous April
	Number females	Estimate	Number of females on winter range
	Per capita snowpack	cm/female	Water content of the previous April snowpack divided by the estimated number of females in the population
	Mean litter size	Number/female	Mean number of fetuses per adult female in March
	Mean Mar IFBFat	%	Mean ingesta-free body fat (IFBFat) of adult females during March
	Mean Nov IFBFat	%	Mean IFBFat of adult females during November
	Stage	Category	Stage-specific variable allowing survival of neonates to vary during the first 4 weeks, with constant survival thereafter
	Month	Category	Nuisance parameter allowing response variable to vary as a function of month
	Year	Category	Nuisance parameter allowing response variable to vary as a function of year

Table 2. Definitions of predictor variables used to assess factors that influence life-history characteristics of mule deer at individual and maternal levels.

Level	Predictor	Units	Definition
Individual	Age and age^2	yrs	Age of individual females
	Mar IFBFat	%	Ingesta-free body fat (IFBFat) of individual females during March
	Nov IFBFat	%	IFBFat of individual females during November
	Mar body mass	kg	Body mass of individual females during March
	Nov body mass	kg	Body mass of individual females during November
	Litter size	Number	Number of fetuses as determined during neonate capture or March ultrasonography for individual females
	Recruitment status	Number	Number of young-at-heel in autumn for individual females
	Sex	Category	Male or female
	Julian birth	Julian date	Estimated date of birth via vaginal implants or hoof growth of neonate
	Deviation from mean birth	Days	Number of days prior to or post mean birth dates per year
	Birth mass	kg	Estimated body mass of neonates at birth
	Age at death	Days	Age at death based on estimated date of birth for neonates
Maternal	Age and age^2	yrs	Age of dam
	Mar IFBFat	%	IFBFat of dam the preceding March
	Mar body mass	kg	Body mass of dam the preceding March

old), without the addition of covariates, by allowing survival to vary monthly during each season and thereby estimate survival without heterogeneity introduced by different survivability of young or senescent females. We estimated annual survival as the product of summer and winter survival within years and used the delta method to calculate associated variances (Seber 1982). Thereafter, we modeled factors that affected survival during winter and summer separately for all females >1 year old. We expected environmental and individual factors to affect survival differently on seasonal ranges, because of differences in life-history patterns of deer between seasons. Therefore, we modeled monthly survival separately during 2 periods of 6 months as a function of environmental and individual-based covariates using the aforementioned modeling approach. We censored adult females that died within 14 days of capture to avoid under-estimating survival for individuals that perished as a result of capture-related causes.

We determined date of birth for each neonate from a combination of hoof, umbilicus, and behavioral characteristics (Haugen and Speake 1958, Brinkman et al. 2004, Haskell et al. 2007). We considered all neonates that we captured with wet pelage, wet umbilicus, or with the aid of an expelled VIT to be 0 or 1 day old, after assessing those characteristics. For all others, we estimated age for neonatal mule deer based on new-hoof growth with the equation of Robinette et al. (1973), where age (days) = mean hoof growth (mm) × 2.55–6.3. More recently, Haskell et al. (2007) provided an additional equation for estimating age of neonatal mule deer; however, we chose not to use their equation, because negative hoof growth is required for a neonate to be <5 days old. We assumed mass of neonates at capture was the birth mass for neonates ≤1 day old at capture. For older neonates, we back-calculated birth mass from the slope of the regression between body mass and age at capture for all neonates in our study (mass [kg] = 2.76 + age × 0.27; $r^2 = 0.67$, $P < 0.001$); growth rates were similar between sexes ($F_{1,110} = 1.39$, $P = 0.24$). We multiplied age of the neonate (based on new-hoof growth) by the slope from the previous equation, and subtracted the product from body mass at time of capture. We recognize that our estimates of birth mass for neonates >1 day old could be affected by low precision in hoof-growth equations or by differences in growth rate among

individual neonates (Haskell et al. 2007). Nevertheless, 76% of neonates in our sample were ≤2 days old and estimates of birth mass were nearly identical for neonates captured at birth ($\bar{x} = 2.76$ kg, SE = 0.089, range: 1.0–4.0) compared with older neonates for which we back-calculated birth mass ($\bar{x} = 2.75$ kg, SE = 0.075, range: 1.86–4.1). Consequently, estimating age at capture and birth mass should have a limited effect on our analyses.

We used the known-fate model in Program MARK (White and Burnham 1999) to estimate survival and determine factors that influenced survival of neonatal mule deer at population, individual, and maternal levels. We estimated preweaning survival of young mule deer weekly from birth until 20 weeks of age (140 days; approx. Jul–Oct), at which time we considered young mule deer to be weaned (Sadleir 1980). For encounter histories in the known-fate model, we placed all events, including capture, survival monitoring, mortality, and censors into 1-week intervals. Neonates that were ≤1 week old when captured entered the survival analysis in the first interval; neonates >1 week old and ≤2 weeks old when captured entered the analysis during the second interval, and so forth. We right-censored all animals that prematurely shed collars ($n = 4$), because censoring likely was independent of the fate of the neonate.

We first modeled summer survival of neonates through 20 weeks of age with a time-dependent model that allowed survival to vary randomly by week and plotted the resulting weekly estimates of survival to identify periods of time with consistent survival (Barber-Meyer et al. 2008). Survival varied during the first 4 weeks of life, but remained relatively constant thereafter, which was expected because of changing patterns of vulnerability of young to predation, activity of young deer, and degree of association with the dam (Haskell et al. 2010). Accordingly, we developed a model that was life-stage specific and allowed survival to vary during the first 4 weeks of life, with constant survival for the remaining 16 weeks. We selected that stage-specific model from among other models (i.e., constant survival and different survival each week) using AIC$_c$, because no other candidate models were within 2 ΔAIC$_c$. Subsequently, we used that stage-specific model, and added factors that we predicted to influence survival of neonates at the population ($n = 119$), individual ($n = 113$), or maternal ($n = 73$) levels using

the same modeling approach described previously to evaluate variable importance.

We hypothesized that effects of birth mass and maternal condition on neonatal survival would be age-dependent. We predicted that birth mass would be most influential during the first few weeks of life, because birth mass affects viability of neonates (Verme 1962, Sams et al. 1996, Keech et al. 2000, Carstensen et al. 2009), whereas effects of maternal condition on offspring development and survival should be stronger when maternal provisioning and the energetic costs of lactation rise (Sadleir 1982, Taillon et al. 2012). Therefore, we evaluated models that incorporated an age-dependent effect of birth mass by adding the covariate birth mass starting with only week 1, and then incrementally added weeks up to week 4, and compared those models against a model with an effect of birth mass from 1 week to 20 weeks of age. Similarly, at the maternal level, we incorporated an age-dependent effect of maternal nutritional condition from 1 week to 20 weeks of age, and then incrementally removed weeks from 1 to 4. Doing so allowed us to evaluate our hypothesis directly by developing models that included effects of birth mass within the first few weeks of life that transitioned to an effect of maternal condition as neonates grew older. We selected from among the differing structures for age-dependent parameterization of birth mass and maternal condition using AIC_c and included that structure in all subsequent models where the covariates birth mass or maternal condition were included.

Our data on survival for neonates probably were not fully independent (i.e., were overdispersed), because siblings share maternal resources and occupy similar environments in both space and time (Bishop et al. 2008); our sample contained 2 sets of triplets, 31 sets of twins, and 51 singletons. We used data-bootstrap analysis in Program MARK to estimate overdispersion by generating 10,000 replicate datasets by resampling our data with replacement (White and Burnham 1999, Bishop et al. 2008). We resampled within litters of adult females; thus, the number of samples within each replicate equaled the number of adult females with litters ($n = 84$) rather than the number of neonates ($n = 119$) in the original dataset. We used a time-dependent global model (year × week) for bootstrap analyses to avoid misinterpreting poor model fit as overdispersion (Burnham and Anderson 2002). We estimated overdispersion by dividing the theoretical variance estimates with empirical variance estimates calculated from the bootstrap analysis (Bishop et al. 2008). The estimate of overdispersion in our survival analysis for neonates was 1.18, which indicated only modest overdispersion, and was similar to that reported for mule deer in Colorado (1.25; Bishop et al. 2008). Therefore, for all neonatal survival analyses, we set the variance inflation factor ($\hat{c}$) to 1.18.

Cause-specific mortality.—We modeled causes of mortality for neonates (i.e., up to 20 weeks of age) during summer and winter as a function of population and individual factors predicted to influence cause of death using multinomial logistic regression (Bishop et al. 2009), and the same multi-stage modeling approach that we outlined previously with covariates at the population, individual, and maternal levels. For this analysis, we included only mortalities, because we were interested in evaluating factors that influenced cause of mortality and how those causes contributed to total observed mortality. We excluded all mortalities for which cause was undetermined, because those samples provided no information regarding cause of death and may simply be a combination of various sources of mortality (Bishop et al. 2009). We were unable to determine cause of mortality for 11% of all neonate mortalities. We only conducted the analyses on cause-specific mortality for neonates, because proportion of unknown mortalities for adults was high (41% of mortalities during winter and 55% during summer).

For multinomial models, we grouped response variables of cause-specific mortality into separate categories that were easily distinguishable to yield sufficient sample sizes. We assessed 4 categories of neonate mortality: bear predation ($n = 23$), malnutrition ($n = 9$), other predation ($n = 19$; composed mostly canid and felid predation), and other natural causes ($n = 12$; comprised of accident, injury, drowning, or undetermined disease). Following the analysis of cause-specific mortality, we calculated rates of mortality for neonates and adult females by combining those results with our survival analyses. We estimated rates of cause-specific mortality for neonates based on the product of the probabilities of each mortality cause and the overall mortality rate from our survival analyses, which we calculated from 1 to $\hat{S}$ (estimated survival rate). We used the delta method to estimate variances of rates of cause-specific mortality for each analysis (Seber 1982).

Reproduction and nutritional condition.—We modeled birth mass, timing of birth, pregnancy status, litter size, recruitment rate, March IFBFat, March body mass, November IFBFat, and November body mass of adult female mule deer as a function of population and individual-level covariates using the approach described previously (see Appendices C–O). We used linear mixed models (PROC MIXED, SAS Institute, Cary, NC) with a repeated-measures structure to avoid inflating degrees of freedom and account for potential autocorrelation from repeatedly sampling individual deer. For each analysis, we used AIC_c to select the best-fitting covariance structure for repeated measures (Ferron et al. 2002) from those deemed biologically appropriate (Verbeke and Molenberghs 2000, Yoccoz et al. 2001), and used the best covariance structure in subsequent models for a particular analysis. We considered models with covariance structures of variance components, compound symmetry, spatial power, spatial exponential, spatial Gaussian, and heterogeneous autoregressive (Littell et al. 1996).

We conducted separate analyses for pregnancy status of yearlings (1.5-yr-old), and pregnancy status and litter sizes of females ≥2.5 years old to avoid having low or more variable reproduction by yearling females unduly influence models of age-specific reproduction (Gaillard et al. 2000, Bonenfant et al. 2009). We modeled pregnancy status of yearling females using logistic regression (PROC LOGISTIC in SAS). For adult females ≥2.5 years old, we also modeled pregnancy status using logistic regression (PROC GLIMMIX in SAS), but with a Poisson distribution, because non-pregnant females were rare (McDonald and White 2010), and used a random effect with the RESIDUAL option to specify an R-side covariance structure (which is similar to repeated measures in PROC MIXED). We removed 2 adult females that were ≥2.5 years old because they were barren during every year of monitoring (>4 yrs) and, thus, may have confounded analyses on factors that influenced patterns

of fecundity. One was incapable of becoming pregnant because of the awkward position and abnormally small size of the vulva; the absence of pregnancy in the other deer occurred for unknown reasons.

Age ratios and population growth rate.—For population-level analyses of age ratios and lambda, we combined our data with those of Pierce et al. (2012) to lengthen our dataset and strengthen our statistical power for detecting relationships at the population level. We did not include data from Kucera (1988) for this set of models, with the exception of an additional post hoc analysis of lambda, because sample sizes were small and estimates of variance were not always available. Furthermore, data collection by Kucera (1988) occurred during a population crash; demographic patterns can be misleading during different trajectories of population growth when they are combined (Pierce et al. 2012). We estimated λ based on annual population estimates where: $\lambda_t = N_{(t+1)}/N_t$. We used general linear models (PROC GLM, SAS Institute) to determine population-level factors that influenced age ratios and λ. We weighted models based on the inverse of the variance around each annual metric to account for uncertainty in those estimates (Neter et al. 1996).

Consequences of mortality on population dynamics differ depending upon the proximity of a population to its food supply (nutritional carrying capacity; NCC) and, thus, the degree of density dependence (i.e., nutritional limitation) within a population determines the level of compensatory or additive effects of mortality (McCullough 1979, Boyce et al. 1999, Bowyer et al. 2005). The residuals of the relationship between the nutritional capacity for recruitment (i.e., model-based predictions) and actual recruitment should indicate the degree to which mortality is additive or compensatory, because the nutritional potential for survival determines the consequences of mortality for a population (Bartmann et al. 1992, Tveraa et al. 2003). More specifically, nutritional potential for recruitment reflects the point at which mortality transitions from being compensatory to additive with increasing rates of mortality (Fig. 4).

We employed this approach using 2 datasets from our long-term research in the Sierra Nevada: ratios of young-to-adult females and autumn recruitment of young (number of young at heel per radiocollared female). For each analysis, we incorporated variables that reflected the nutritional ability to support young (i.e., habitat and nutritional condition) and that were identified as being influential in previous analyses, and removed effects of variables that accounted for other external factors not related to nutrition. We estimated the nutritional capacity for recruitment (Fig. 4) of young mule deer using the same mixed models with repeated measures for recruitment rate, and mixed models weighted by the inverse of the variance in each estimate for age ratios. We then used the residuals between model-based predictions of the nutritional potential for recruitment and empirically measured recruitment to infer the relative consequences of mortality (i.e., amount of additive and compensatory mortality). Negative residuals reflect the amount of mortality that was additive because the nutritional potential for recruitment was greater than what was realized (Fig. 4). Conversely, residuals near zero or slightly positive would be indicative of recruitment equal to or greater than what was expected on a nutritional basis; thus, observed mortality was compensatory.
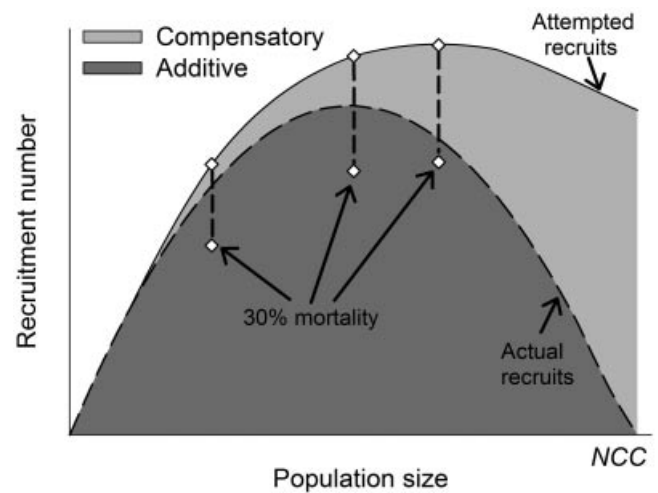

Figure 4. Changes in number of attempted recruits (number of young born) and actual recruits limited by density-dependent feedbacks relative to size of an ungulate population increasing towards its food supply (nutritional carrying capacity; NCC) in the absence of other external mortality factors (i.e., predation). Actual recruits represent the number of young that can be recruited given current habitat limitation via density-dependent feedback (i.e., nutritional potential for recruitment). The difference between the number of attempted and actual recruits therefore represents the component of mortality that is compensatory. Note that the position of the population relative to NCC and thus, the nutritional potential for recruiting young, determines the degree of compensatory or additive mortality even when mortality rates remain unchanged (0.30). Adapted from McCullough (1979) and Kie et al. (2003).

RESULTS

Mean size of the population of mule deer overwintering in Round Valley between 1985 and 2009 was 2,428 animals (range: 939–5978), but was highly variable (CV = 50%; Fig. 5). Winter precipitation also was highly variable; the coefficient of variation of water content of the April snowpack was 57% (Fig. 2). Mean
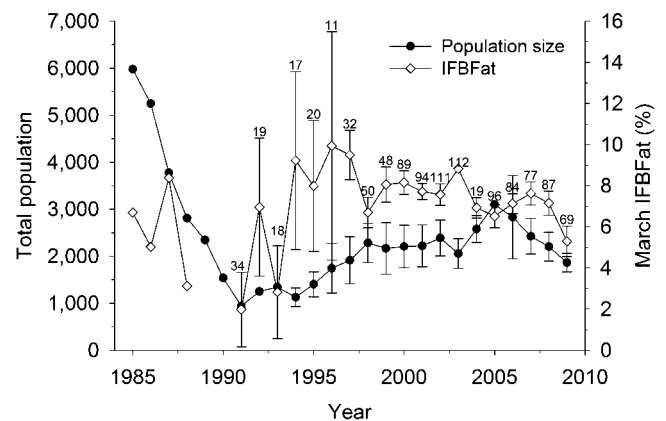
Figure 5. Annual population estimates (solid circles ± 95% CI) of mule deer in January and ingesta-free body fat (hollow diamonds ± 95% CI) of adult female mule deer in March on a winter range in Round Valley, Inyo County, California, USA. We determined population estimates from total counts before 1994 and from mark-resight surveys thereafter. We measured ingesta-free body fat (IFBFat) via kidney fat indices before 1997 and untrasonography thereafter. We obtained data before 1997 from Kucera 1988 and Pierce et al. (2012), and estimates since 1997 are estimates from this study. Sample sizes for IFBFat are displayed above means.
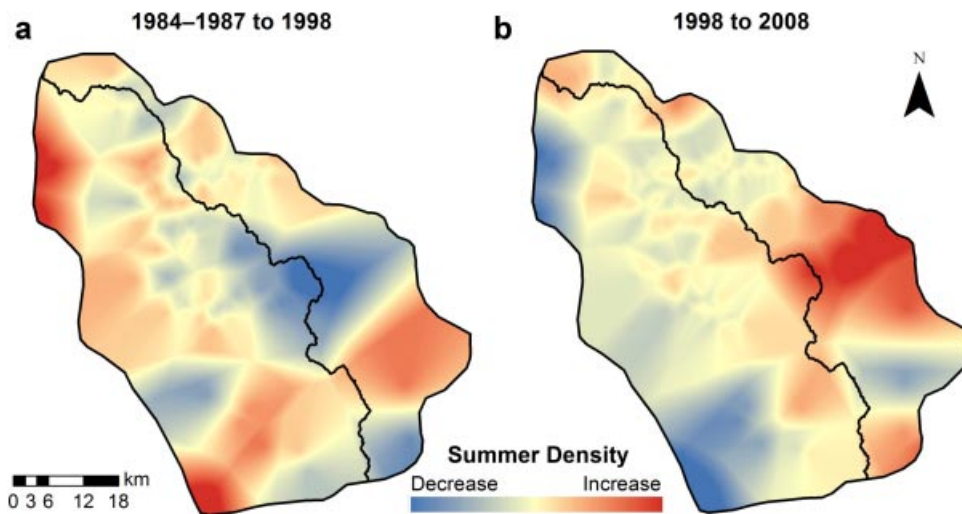
Figure 6. Relative change in density during summer from 1984–1987 to 1998 (a), and from 1998 to 2008 (b), with warm colors indicating increases in density and cool colors indicating declines in density of mule deer that migrate to summer ranges on both sides of the crest of the Sierra Nevada, California, USA. Relative change in density was measured as the change in distance to the nearest location of a female mule deer during summer between the aforementioned years.

nutritional condition (IFBFat) of adult females in March ranged from 2.0% to 9.9% with a coefficient of variation of 33%. Despite that variation in population size and nutritional condition, pregnancy (0.98; CV = 4.4%) and fetal rates (1.69; CV = 10.4%) of adult females remained high, with markedly less variation. The proportion of the population that migrated to the west side of the Sierra crest declined from 87% in 1985 to 58% when our study began in 1998, and was followed by further reductions to <50% of our marked sample of adult females by 2005 (Fig. 6). This shift in proportion of west-side migrants in the population occurred despite high fidelity to summer ranges, indicating the shift was caused by demographics rather than behavior. Of the 251 adult females that we monitored for >1 summer, females never switched summer ranges to the opposite side of the Sierra crest, and none of the young that we

monitored in subsequent years ($n = 26$) switched sides from where they were born.

Survival of Neonates

The stage-specific pattern of neonatal survival indicated low, but generally increasing survival during the first 4 weeks of age ($\bar{x} \pm$ SE; week $1 = 0.75 \pm 0.047$; week $2 = 0.88 \pm 0.039$; week $3 = 0.96 \pm 0.026$; week $4 = 0.90 \pm 0.041$), and relatively constant survival from 5 weeks to 20 weeks of age (0.97 ± 0.007 weekly). Average survival of neonatal mule deer to 140 days of age during 2006–2008 was 0.33 (SE = 0.091). Survival of young was influenced by the side of the Sierra crest on which a neonate was born (Table 3); survival of west-side neonates averaged 0.13 (SE = 0.092), whereas east-side neonates averaged 0.44 (SE = 0.11). At the individual level, we evaluated the hypothesis that

Table 3. Model-averaged parameter estimates, confidence interval, and Akaike importance weights of factors that influenced survival of neonatal mule deer to 20 weeks of age conducted at the population ($n = 119$), individual ($n = 113$), and maternal ($n = 73$) levels, Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendix A.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	0.98*	0.49	1.47	1.00
	Stage[a]				1.00
Individual	Summer residency	0.33	−0.45	1.10	1.00
	Stage[a]				1.00
	Deviation from mean birth	0.039	$−2.8 \times 10^{-3}$	0.081	0.68
	Birth mass[b]	0.73*	0.19	1.27	1.00
	Summer residency × birth mass[b]	1.19*	0.61	1.78	1.00
Maternal	Summer residency	−2.19	−4.64	0.24	1.00
	Stage[a]				1.00
	Birth mass[b]	0.25	−0.34	0.85	1.00
	Summer residency × birth mass[b]	1.82*	0.84	2.80	1.00
	Mar IFBFat[c]	−0.068	−0.46	0.32	1.00
	Summer residency × Mar IFBFat[c]	0.39*	0.089	0.68	1.00

[a] Stage-specific variable that allowed survival to vary during the first 4 weeks, with constant survival the remaining 16 weeks.
[b] Age-specific effect of birth mass on survival during the first 3 weeks of life.
[c] Age-specific effect of March ingesta-free body fat (IFBFat) of the mother on survival during 4–20 weeks old.
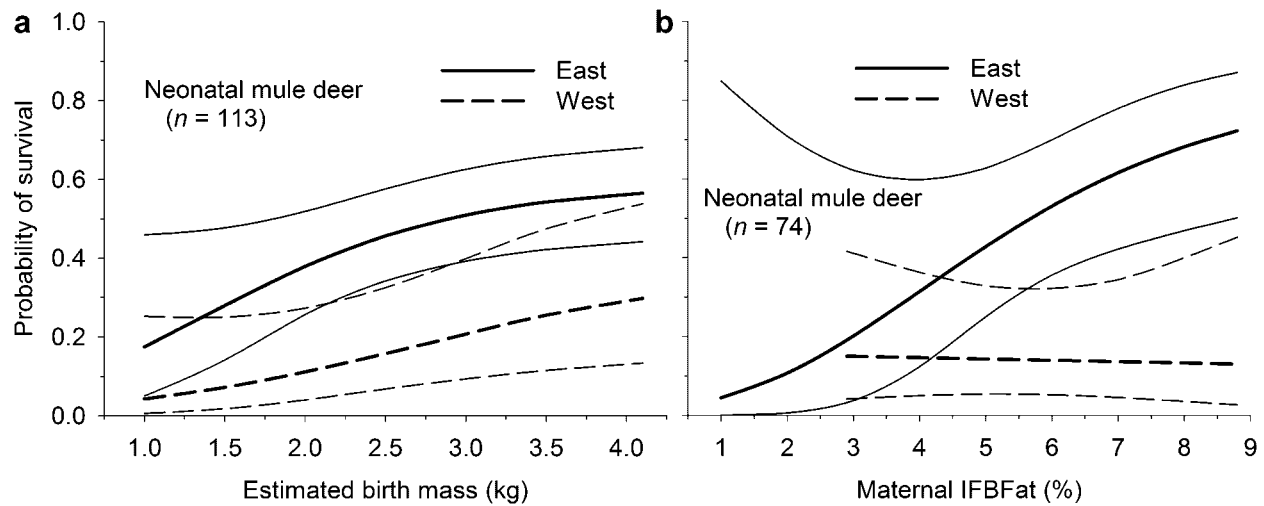
Figure 7. Estimated probability (±95% CI) of survival of neonatal mule deer from birth to 20 weeks of age during 2006–2008 as a function of estimated birth weight (a), and ingesta-free body fat of the mother in March (b), Sierra Nevada, California, USA. Results are based on best model at the individual level with stage, summer residency, deviation from mean birth, birth mass, and summer residency × birth mass (a), and at the maternal level with stage, summer residency (east or west), birth mass, summer residency × birth mass, maternal IFBFat, and summer residency × maternal March IFBFat (b). We constrained effects of birth mass to weeks 1–3, and effects of maternal IFBFat to weeks 4–20. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

effects of birth mass and nutritional condition of mothers on neonatal survival were age-dependent, with effects of birth mass on survival occurring early in life (<1 month old), and effects of maternal condition being most prominent when lactation demands increase (≥4 weeks old). By incrementally adjusting the temporal effect of each covariate and assessing model fit, we determined that birth mass was most influential during the first 3 weeks of life, whereas nutritional condition of the mother (IFBFat) affected survival from 4 weeks to 20 weeks. Nevertheless, the expected positive effect of birth mass and maternal IFBFat was evident only for young mule deer born on the east side of the Sierra crest (as evidenced by significant interactions of summer residency with birth mass and maternal IFBFat; Table 3). For east-side young, individuals that were large at birth and with mothers in good nutritional condition had a greater probability of survival during summer than those born small to mothers in poor nutritional condition (Fig. 7). Those effects were muted (birth mass) or non-existent (maternal IFBFat) for offspring born on the west side of the crest.

Distribution of cause-specific mortality for neonatal mule deer contrasted between the side of the Sierra crest on which an individual was born (Table 4). Neonates born on the west side of the Sierra crest were >6 times more likely to die of predation by black bears (0.72, SE = 0.093) than any other cause (Fig. 8). In contrast, the primary cause of mortality for neonates inhabiting the east side was predation by canids and felids (Fig. 8), with low probability of bear predation. At the individual level, the distribution of cause-specific mortality was influenced by birth mass (Table 4); small neonates (<2.0 kg) were most likely to succumb to malnutrition, whereas large neonates (>3.0 kg) had a low probability of dying from malnutrition, while being equally likely to die from either predation or other natural sources of mortality (Fig. 9a). Cause of mortality for neonatal mule deer also changed modestly as individuals grew older (Table 4), albeit the model-averaged parameter estimates overlapped 0. Deaths of neonates from malnutrition and bear predation were most likely to occur within the first 2 weeks of life (Fig. 9b). Conversely, probability of mortality of young caused by other sources of

Table 4. Model-averaged parameter estimates and Akaike importance weights for factors that influence cause of mortality of neonatal mule deer evaluated at the population ($n = 62$), individual ($n = 57$), and maternal levels ($n = 47$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendix B.

| Level | Parameter | Cause of mortality[a] | | | Importance weight |
		Bear	Other natural	Other predation	
Population	Summer residency	−2.39*	0.50	1.47	1.00
Individual	Summer residency	−2.67	1.91	2.86	1.00
	Age at death	0.26	0.25	0.25	0.64
	Birth mass	2.21*	3.16*	3.30*	1.00
Maternal	Birth mass	1.96*	2.47*	2.44*	0.98
	Age	3.0×10^{-3}	−0.063	0.21	0.61

[a] Multinomial logistic regression included malnutrition as the reference category thus, parameter estimates represent the relative likelihood of dying from a particular cause compared with malnutrition.
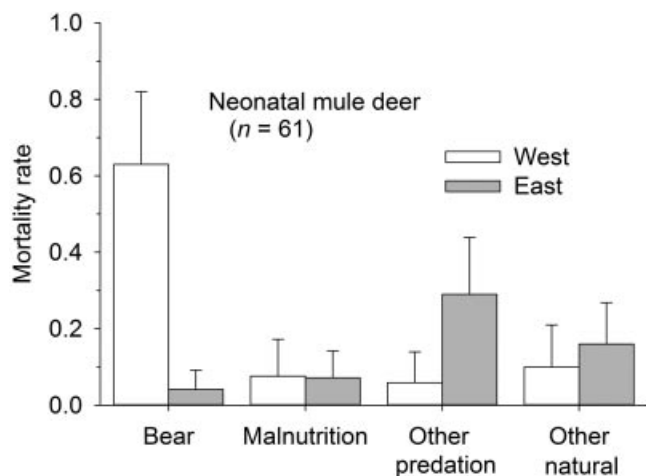
Figure 8. Estimated probability (±95% CI) of mortality caused by black bear, malnutrition, other forms of predation (canid and felid), and other natural causes (e.g., physical injury, potential disease, drowning) for neonatal mule deer ≤20 weeks of age as a function of the side of the Sierra crest occupied in the Sierra Nevada, California, USA, 2006–2008. Results are based on the best model at the population level, which included summer residency as the only influential predictor variable.

predation (mostly canids or felids) increased from birth to 140 days-of-age relative to other causes (Fig. 9b).

Mean estimated birth mass was 2.8 kg (SE = 0.061), and ranged from 1.0 kg to 4.1 kg; mass at birth was influenced primarily by litter size (Table 5), and was not influenced strongly by sex (Table 5). From a maternal standpoint, larger litters had lower individual birth mass (Fig. 10a), but greater total litter mass (Fig. 10a). Date of parturition was highly synchronous (based on SD) during 2006 (SD = 8.0 days), 2007 (SD = 8.1 days), and 2008 (SD = 6.5 days), and was 6 days earlier for east-side females (178.6, SE = 1.18 days; 28 June) than for females on the west side (184.7, SE = 1.62 days; 4 July; Fig. 10). In addition, females with

larger litters gave birth later than those with smaller litters (Fig. 10b; Table 5), and females of larger body mass gave birth earlier than smaller-bodied females (Fig. 11).

Recruitment and Ratios of Young-to-Adult Females

At the population level, autumn recruitment of young mule deer was influenced by summer residency and nutritional condition of adult females in March (Table 6). Recruitment of young was consistently higher for females that summered on the east side ($\bar{x}$ = 0.70, SE = 0.043) of the Sierra crest than for females on the west side ($\bar{x}$ = 0.42, SE 0.034; Fig. 12a). Annual variation in recruitment was influenced positively by mean IFBFat (%) of adult females in March (Fig. 12b). IFBFat (Fig. 13a) and litter size (Fig. 13b) of individual females positively affected autumn recruitment of young (Table 6), indicating that females in better nutritional condition with larger litter sizes yielded more recruits (Table 6). After accounting for the influence of nutritional condition on recruitment, effects of summer residency remained (Table 6), with lower recruitment for west-side compared with east-side females (Fig. 13).

Ratios of young-to-adult females collected in January surveys from 1985 to 2009 were highly variable (CV = 30.2%), averaged 37.9 (SE = 2.31), and ranged from 19.3 to 63.0 (Fig. 14a). Percent IFBFat of females in the current March and that of the preceding March were positively related to age ratios at the end of the calendar year (Fig. 14b). Mean IFBFat of females in current March (β = 3.2) had a stronger positive effect than mean IFBFat from the preceding year (β = 2.3), although their parameter estimates were not significantly different (Table 6). Predicted ratios of young-to-adult females dropped below the 24-year average of 37.9 when mean IFBFat of females in March was <5.7% (95% CI: 3.5–6.5%), and mean March IFBFat of the preceding year was held constant at the long-term average. Notably, correlation of mean March IFBFat between successive years was low (r = 0.29).
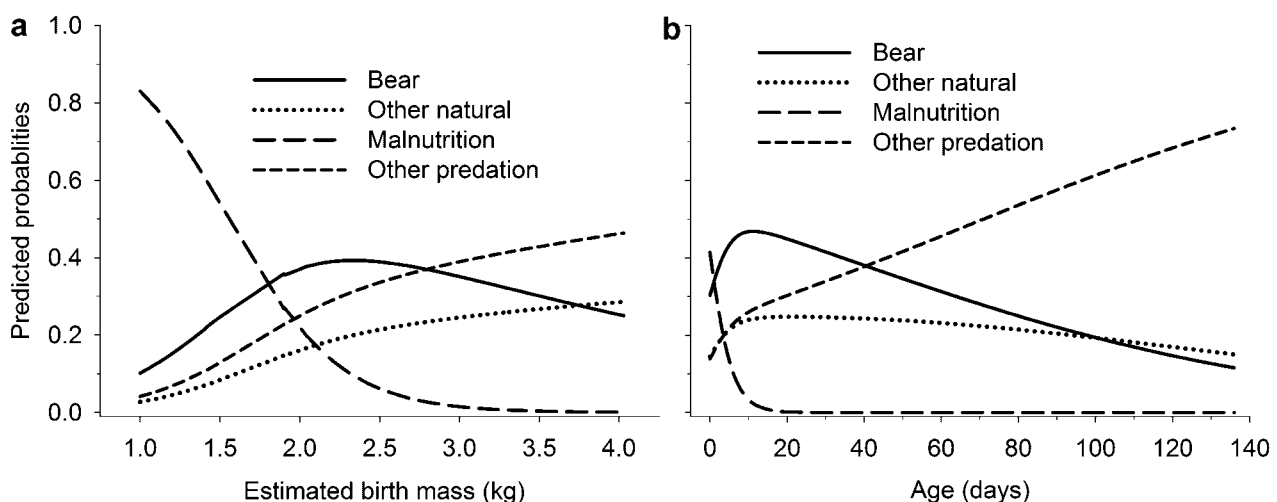
Figure 9. Estimated probability of mortality caused by black bear, malnutrition, other forms of predation (canid and felid), and other natural causes (e.g., physical injury, potential disease, drowning) for neonatal mule deer ≤20 weeks of age as a function of estimated birth weight (a) and age (b) in the Sierra Nevada, California, USA, 2006–2008. Predicted probabilities of mortality represent the relative likelihood of a neonate dying from a particular cause given that the deer dies. Results are based on the best model at the individual level, which included summer residency, age at death, and birth weight. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean. We removed confidence intervals for ease of interpretation.

Table 5. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced birth characteristics of adult (>1 yr) female mule deer at the population and maternal levels, Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices C and D.

| Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Birth mass	Individual	Litter size	−0.21*	−0.37	−0.055	0.82
	Maternal	Litter size	−0.37*	−0.60	−0.14	0.93
		Mar IFBFat	−0.051	−0.01	6.0×10^{-4}	0.56
Julian birth	Population	Summer residency	−4.08*	−7.22	−0.94	0.98
		Mean Mar IFBFat	−0.82	−2.27	0.63	0.51
		Litter size	2.93*	0.74	5.12	0.97
	Maternal	Summer residency	−5.48*	−8.45	−2.52	1.00
		Mean Mar IFBFat	−1.53	−3.83	0.77	0.88
		Litter size	5.86*	3.10	8.63	1.00
		Age	0.20	−0.15	0.56	0.58
		Mar IFBFat	−0.13	−0.56	0.30	0.56
		Mar body mass	−0.36*	−0.65	−0.073	0.99

IFBFat, ingesta-free body fat.

Pregnancy and Fetal Rate

Thirty-two percent of yearling females (1.5-yr-old) that we monitored failed to attain pregnancy at 1.5 years of age, but all that survived became pregnant the following autumn. Although our sample size for yearling females was small ($n = 22$), probability of primiparity as a yearling was influenced positively by per capita snowpack during their second summer of growth before rut in autumn (Table 7, Fig. 15a). Unfortunately, logistical constraints precluded us from directly assessing the effect of body mass during November when young females potentially were bred. For adult females (≥2-yr-old), body mass in March was related ($r^2 = 0.35$, $F_{1,252} = 136.0$, $P < 0.001$) to November body mass; body mass of yearling females in March likely provided a surrogate for their body mass in November. At the individual level, March body mass was the most parsimonious explanation for probability of pregnancy for yearling females (Table 7). Yearling females that were >41 kg in March had a >0.90 (95% CL: 0.50–0.99) probability of having conceived the previous autumn (Fig. 15b).
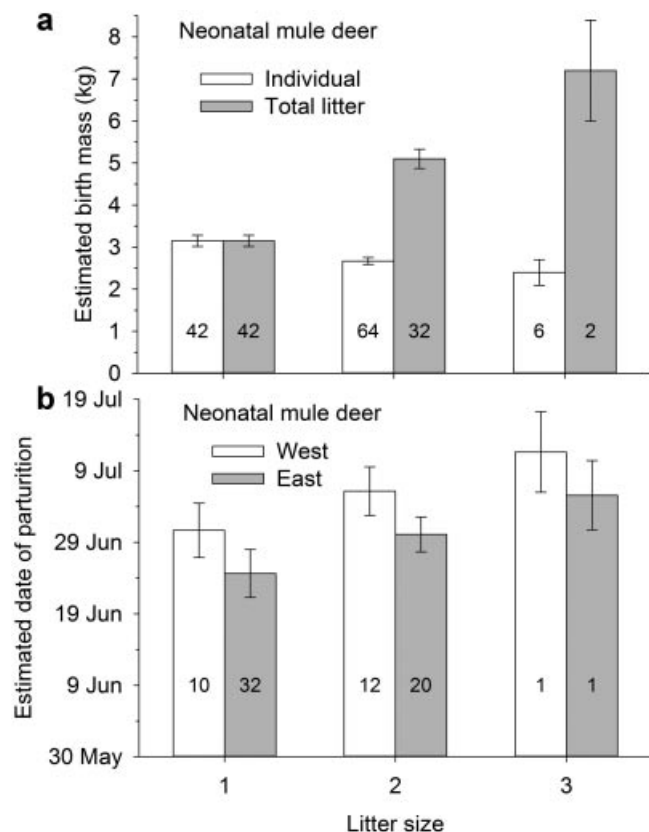
Figure 10. Average individual birth mass and total litter mass relative to litter size (a) and estimated effect (±95% CI) of litter size on estimated date of parturition (b) for adult (>1 yr) female mule deer, Sierra Nevada, California, USA, 2006–2009. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, mean March ingesta-free body fat (IFBFat), and litter size for date of parturition (b). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean. Numbers within bars represent sample sizes for each group.
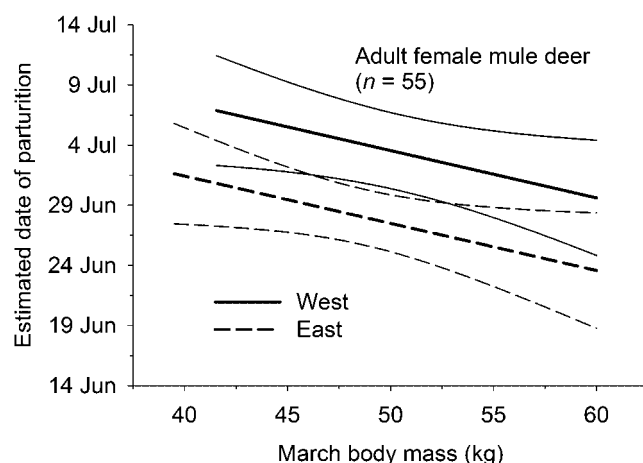
Figure 11. Estimated effect (±95% CI) of March body mass of adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer on estimated date of parturition, Sierra Nevada, California, USA, 2006–2009. Results are based on the best model at the maternal level, which included summer residency, mean March ingesta-free body fat (IFBFat), litter size, age, March IFBFat, and March body mass. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

Table 6. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced age ratios and individual recruitment of young for mule deer, Sierra Nevada, California, USA, 1991–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices E and F.

| Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Recruitment	Population	Summer residency	0.27*	0.18	0.36	1.00
		Per capita snowpack	5.44	−1.22	12.10	0.96
		Mean Mar IFBFat	0.090*	0.032	0.15	0.84
	Individual	Summer residency	0.35*	0.25	0.45	1.00
		Per capita snowpack	2.30	−3.66	8.27	0.88
		Mar IFBFat	0.025*	3.9×10^{-3}	0.046	0.83
		Litter size	0.12*	9.3×10^{-3}	0.23	0.94
		Mar weight	7.3×10^{-3}	-3.3×10^{-3}	0.018	0.92
Age ratio	Population	Mean Mar IFBFat$_{t-1}$	2.28*	1.12	3.53	0.99
		Mean Mar IFBFat$_t$	3.21*	1.89	4.50	1.00
		Mean Mar body mass	−0.41	−1.52	0.70	0.72
		Mean litter size	2.89	−27.43	33.22	0.99
		Per capita snowpack	44.61	−132.33	221.58	0.78
		Summer precipitation	0.29	−1.20	1.78	0.75
		Summer temperature	−5.58	−11.41	0.24	0.97

IFBFat, ingesta-free body fat.

Fetal rate of females ≥2.5 years old during 1997–2009 was 1.69 (SE = 0.027), and ranged from 1.57 (SE = 0.065) in 2001 to 1.91 (SE = 0.053) in 1999 (Fig. 16). In addition, litter size varied as a function of per capita snowpack and summer temperature (Table 7). Per capita snowpack had a positive effect on litter size (Fig. 17), whereas summer temperature had a negative influence. At the individual level, litter size was not related to age, November body mass, or nutritional condition (Appendix H). Nonetheless, females residing on the west side (1.72, SE = 0.026) had larger litter sizes than females that summered on the east side of the Sierra crest (1.59, SE = 0.031; Table 7). Notably, inclusion of yearlings in the sample for litter size resulted in a significant effect of age and November body mass, which were not influential when only females ≥2.5 years old were considered.

Pregnancy of females ≥2.5 years old during 1997–2009 was relatively constant at 0.98 (SE = 0.006; Fig. 16), despite substantial variation in nutritional condition during those years (Fig. 5). Initial models that included yearlings indicated pregnancy varied as a curvilinear function of age; however, that pattern was dictated by variable pregnancy among yearlings. After removing yearlings from the analysis we considered summer residency, per capita snowpack, summer precipitation, summer temperature, mean November IFBFat, and year at the population level, and age, age^2, November IFBFat, and November body mass at the individual level. No single variable at the population or individual levels influenced probability of pregnancy for females ≥2.5 years old, despite an adequate sample size (n = 803; Table 7).

Seasonal Survival of Adult Females

We conducted a separate survival analysis that included only prime-aged females (2–9 yrs old) before evaluating factors that
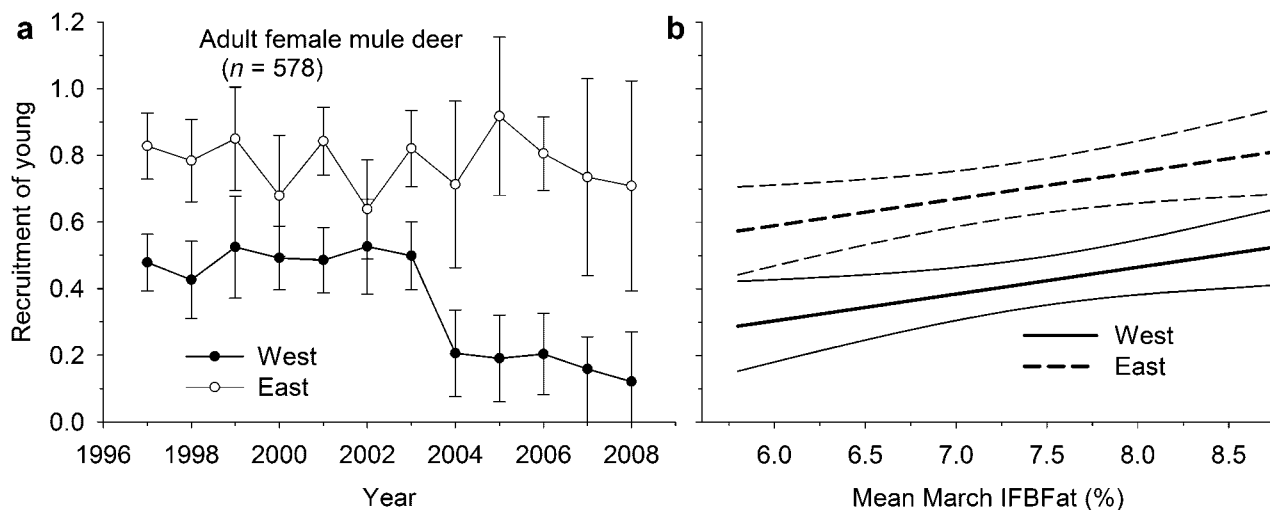
Figure 12. Annual average (±SE) recruitment of young in autumn (a) and predicted effect (±95% CI) of mean ingesta-free body fat (IFBFat) of female mule deer in March on number of young recruited in autumn (b) by adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Effect of mean IFBFat is based on the best model at the population level, which included summer residency, per capita snowpack, and mean March IFBFat.
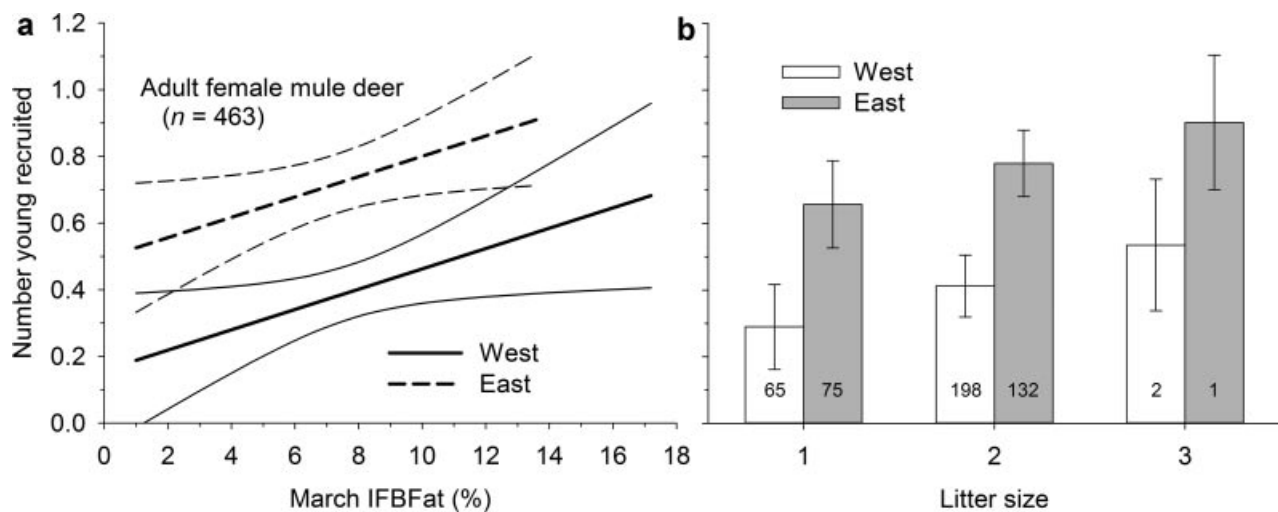
Figure 13. Estimated effect (±95% CI) of percent ingesta-free body fat (IFBFat) of individual females in March (a) and number of young in utero in March (b) on number of young recruited in autumn by adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the maternal level, which included summer residency, per capita snowpack, litter size, March body mass, and March IFBFat. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean. Numbers within bars represent sample sizes for each group.
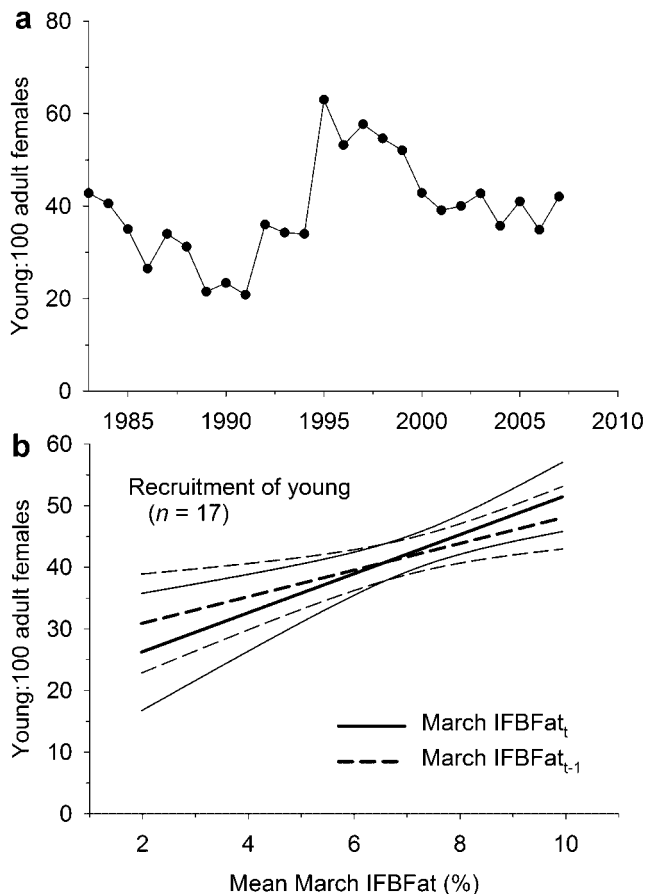
Figure 14. Annual estimates of recruitment of young from surveys conducted in January (a) and estimated effect (±95% CI) of mean ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer during the current (t) and preceding ($t-1$) March on annual herd composition of young (<1 yr):100 adult females the following January (b), Sierra Nevada, California, USA, 1991–2008. Results for recruitment of young are based on the best model, which included per capita snowpack, mean March IFBFat$_t$, mean March IFBFat$_{t-1}$, mean litter size, mean March body mass, summer precipitation, and summer temperature. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

affected seasonal survival to obtain seasonal and annual estimates of survival during 1998–2008. Estimates of summer survival for prime-age females ranged between 0.76 and 1.0, with a mean of 0.90 (SE = 0.021; Fig. 18a). Overwinter survival of prime-age females averaged 0.94 (SE = 0.012) and ranged between 0.87 and 1.0 (Fig. 18b). Mean annual survival of prime-age females was 0.87 (SE = 0.025) with minor variation among years (CV = 9.6%; Fig. 18c).

Summer survival among years for adult females was related to the previous April snowpack and the number of females estimated in the population (Table 8). Models of survival for adult females during summer that included April snowpack and estimated number of females as separate variables performed better ($\Delta AIC_c > 2$) than combining the 2 variables into per capita snowpack; the relationships, however, remained in the expected direction (Fig. 19). Estimated number of females in the population had a stronger negative effect on summer survival, compared with the positive effect of winter snowpack (Fig. 19). Mean IFBFat of adult females in March was positively related to annual patterns of survival in summer for adult females, and was significant for analyses at the individual level (Table 8). In contrast, summer residency had no effect on summer survival of adult females (Appendix I).

Winter survival of adult females varied by month, and interannual patterns varied as a function of per capita snowpack (Table 8). Probability of overwinter survival increased with per capita snowpack (Fig. 20a), but was not affected by previous summer residency (Appendix J). At the individual level, body mass in November had a positive effect on overwinter survival, with heavier females having a greater probability of surviving winter than lighter ones (Fig. 20b). Levels of IFBFat for individual females in March or November did not influence survival in summer or winter significantly (Appendices I and J).

Probability of survival during summer and winter declined with age (Table 8). Adult females were progressively less likely to survive winter as they grew older (Fig. 21b). Probability of

Table 7. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced reproduction of yearling (1.5 yr) and adult female (≥2.5 yr) mule deer at the population and individual levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices G, and H.

Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Yearling primiparity	Population	Per capita snowpack	92.86*	3.58	182.12	0.64
	Individual	Mar body mass$_{t-1}$[a]	0.51*	0.044	0.98	0.91
Litter size	Population	Summer residency	−0.11*	−0.17	−0.043	0.88
		Per capita snowpack	2.95*	0.96	4.95	1.00
		Summer temperature	−0.042	−0.058	$−8.1 \times 10^{-3}$	0.68
	Individual	Summer residency	−0.11*	−0.18	−0.050	0.92
		Per capita snowpack	4.12*	1.98	6.13	0.93
		Summer temperature	−0.031*	−0.062	$−1.2 \times 10^{-4}$	0.63
Pregnancy		None				

[a] We used March body mass of the previous year ($t-1$) because sample size ($n = 7$) was insufficient for November body mass.

surviving an average winter for females 9.5 years old was 0.89 (Fig. 21b), declining to approximately 0.60 at 15.5 years of age. Although survival of females during summer also declined with age, the parameter estimate for age^2 was positive, indicating the additional mortality with each year of age declined as females grew older (Fig. 21a). On an annual basis, probability of survival declined as a curvilinear function of age (Fig. 21c).

For adult females during summer, mortalities for which we could determine cause of death included cougar predation ($n = 13$), canid or ursid predation ($n = 11$), accidents ($n = 15$; comprised of deer-vehicle collisions, illegal harvest, dystocia, and drowning), and malnutrition ($n = 3$). During winter, causes of mortality included cougar predation ($n = 32$), coyote predation ($n = 12$), malnutrition ($n = 7$), and accidents ($n = 7$; comprised of deer-vehicle collisions and poaching). Small sample sizes and a large proportion of undetermined causes of death precluded a rigorous analysis of cause-specific mortality; however, during summer the most common cause of mortality for females on the east side of the Sierra crest was accidents (0.52; mostly deer vehicle collisions) compared with cougar predation (0.45) for west-side females. During winter, the most common source of

mortality for both east-side (0.53) and west-side (0.43) females was cougar predation, followed by malnutrition (east = 0.27, west = 0.21).

Nutritional Condition, Body Mass, and Life-History Characteristics

Mean IFBFat of adult female mule deer in March during 1997–2009 was 7.22% (SE = 0.077), and ranged from 4.98% (SE = 0.27) in 2009 to 8.74% (SE = 0.27) in 1999 (Fig. 5). For individual females, IFBFat ranged from 1.0% to 17.1%. At the population level, March IFBFat varied as a function of summer residency, per capita snowpack, mean IFBFat the previous March, and winter precipitation (Table 9). Per capita snowpack had a positive influence on IFBFat of adult females in March (Fig. 22a). Females that summered on the west side of the Sierra crest (7.46%, SE = 0.10) maintained higher levels of IFBFat through winter compared with females that summered on the east side (6.92%, SE = 0.11). Mean IFBFat of adult females during March of the previous year exhibited a strong, positive relationship with IFBFat of females the following year (Fig. 22b). In contrast, at the individual level, IFBFat of a female
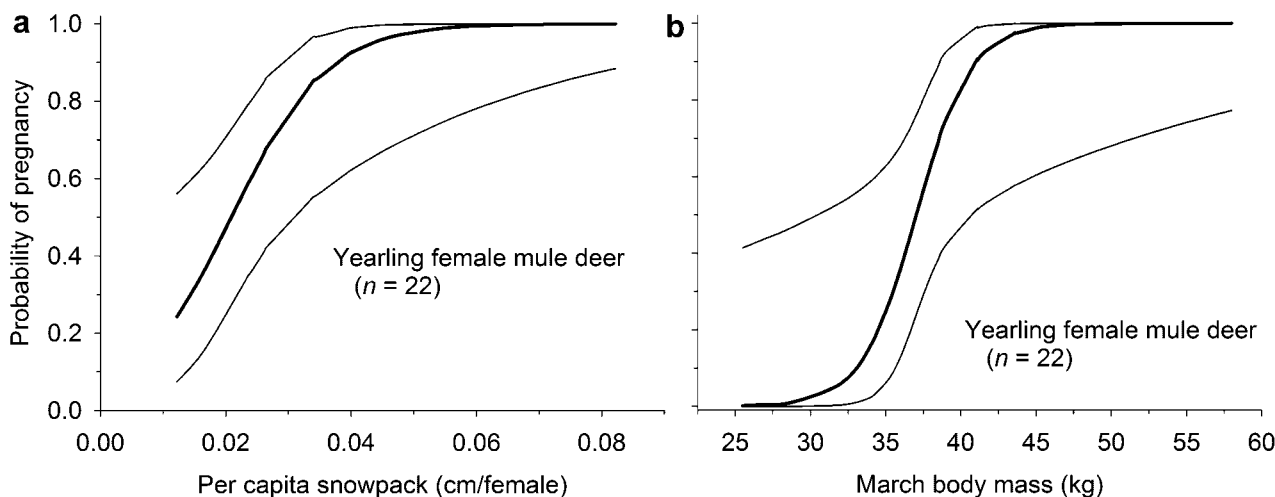

Figure 15. Estimated probability (±95% CI) of pregnancy for yearling (1.5 yr) female mule deer as a function of per capita snowpack (a) and March body mass (b) in the Sierra Nevada, California, USA, 1997–2009. Results are based on the best model, which included per capita snowpack at the population level (a), and body mass at the individual level (b).
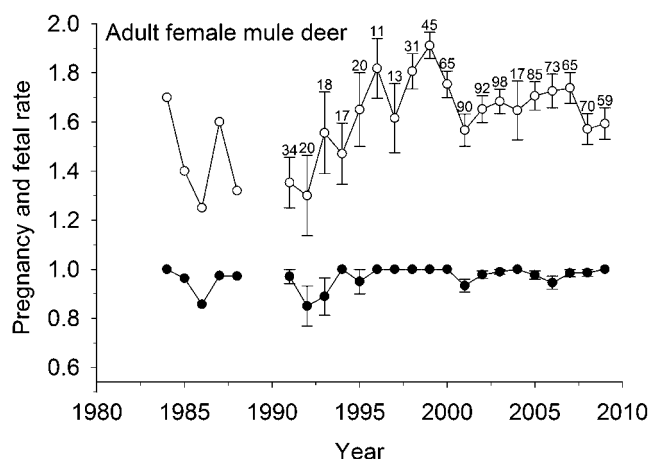
Figure 16. Annual pregnancy (solid circles ± SE) and fetal rate (hollow circles ± SE) of adult female mule deer in March on a winter range in Round Valley, Inyo County, California, USA. We determined reproductive variables by deer collections before 1997 and ultrasonography thereafter. We obtained point estimates before 1997 from Kucera 1992 and Pierce et al. (2012), and those following 1997 were from adult females (≥2.5 yr) monitored in this study. Sample sizes for fetal rates are displayed above means.

in March had little effect on her IFBFat in March the following year (Appendix K). Percent IFBFat of an individual female in November, however, carried over winter and had a positive effect on her IFBFat in March (Fig. 23a). Litter size was positively related to IFBFat of individual female deer in March (Table 9), indicating that females with larger litters had higher fat levels. In addition, March IFBFat declined linearly with age (Fig. 23b).

Annual variation in body mass of adult female deer (CV = 2.97%) was markedly less than for IFBFat (CV = 15.03%) during March 1997–2009. Body mass during March averaged 48.5 kg (SE = 0.18) and ranged from 47.1 kg (SE = 0.51) in 2000
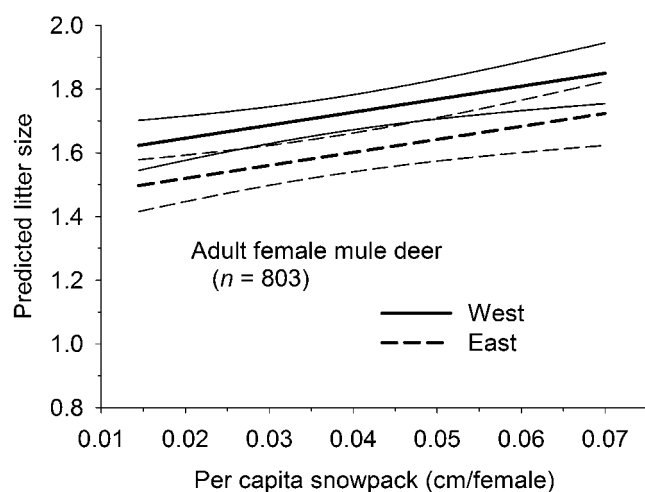
Figure 17. Estimated litter size (±95% CI) for adult (≥2.5 yrs) female mule deer as a function of per capita snowpack relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model, which included summer residency (east or west), per capita snowpack, and summer temperature at the population level. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.
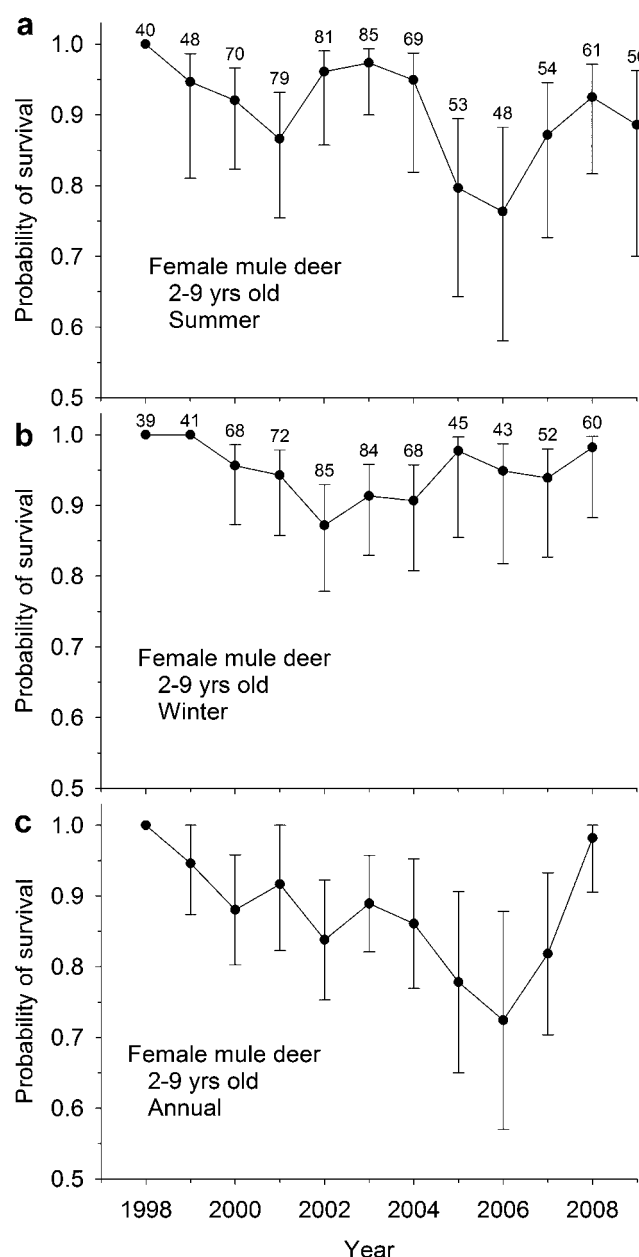
Figure 18. Estimates (±95% CI) of summer (a; May–Oct), winter (b; Nov–Apr), and annual (c; May–Apr) survival of prime-aged (2–9 yr) female mule deer in the Sierra Nevada, California, USA. Seasonal sample sizes are displayed above estimates.

to 50.4 kg (SE = 0.61) in 2006. Among individual adult females, body mass in March ranged from 25.5 kg to 68.9 kg. At the population level, body mass of adult females varied as a function of summer residency and positively with winter temperature (Table 9). On average, females that summered on the west side (49.0 kg, SE = 0.23) of the Sierra crest during summer were heavier than east-side females (47.9 kg, SE = 0.21 kg). Individual females exhibited a curvilinear pattern of body mass with respect to age in March (Table 9), with middle-aged (6- to 12-yr) females being heaviest (Fig. 24b). In addition, IFBFat of individual female deer in March had a positive effect on body mass (Table 9), indicating that after accounting for effects of

Table 8. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced summer (Apr–Oct) and winter (Nov–Mar) survival of adult (>1 yr) female mule deer at the population ($n = 944$ and 1037, respectively) and individual ($n = 830$ and 574, respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices I and J.

| Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Adult summer	Population	Snowpack	0.011*	1.2×10^{-3}	0.020	0.72
		Number female	$-2.7 \times 10^{-3*}$	-3.9×10^{-3}	-1.5×10^{-3}	0.94
		Mean Mar IFBFat	0.18	-6.9×10^{-4}	0.361	0.66
	Individual	Snowpack	0.014*	2.4×10^{-3}	0.025	0.80
		Number female	$-2.3 \times 10^{-3*}$	-3.7×10^{-3}	-8.5×10^{-4}	0.98
		Mean Mar IFBFat	0.26*	0.036	0.49	0.79
		Age	−0.60*	−1.10	−0.11	1.00
		Age²	0.023	-4.7×10^{-3}	0.052	1.00
Adult winter	Population	Per capita snowpack	50.72*	21.37	80.12	1.00
		Month				0.97
	Individual	Per capita snowpack	31.54*	1.89	61.08	0.74
		Month				1.00
		Age	−0.24*	−0.345	−0.15	1.00
		Nov body mass[a]	0.064*	0.015	0.11	0.86

IFBFat, ingesta-free body fat.

[a] Results obtained from a separate set of models using a subset of data ($n = 334$) during 2002–2008.

summer residency and age on body mass, females in better nutritional condition were generally heavier (Fig. 24a).

Mean IFBFat of adult female mule deer in November during 2002–2008 was 9.7% (SE = 0.23), and ranged from 8.4% (SE = 0.57) in 2007 to 11.0% (SE = 0.68) in 2005, whereas IFBFat of individual females in November ranged from 1.0% to 24.3%. At the population level, November IFBFat varied as a function of summer residency, per capita snowpack, and summer precipitation (Table 10). West-side females (11.10%, SE = 0.30) had greater IFBFat in autumn (Table 10, Fig. 25a) compared with east-side females (8.32%, SE = 0.30). Total summer precipitation and per capita snowpack had similar, positive influences on IFBFat of adult females in November (Fig. 25). Mean IFBFat the preceding March had a positive influence on IFBFat in November at the individual level after we accounted

for variation of IFBFat in November explained by other individual covariates (Table 10). Percent IFBFat of individual females in March was less influential than mean IFBFat (Table 10), likely because individual recruitment status in November had an overriding influence on nutritional condition of females in autumn (Table 10). Number of young recruited had a strong negative effect on IFBFat of adult females in November (Fig. 26); however, the effect of summer residency remained significant (Table 10). Adult females summering on the east side of the Sierra crest had lower IFBFat in November with respect to number of young recruited compared with females summering on the west side of the Sierra crest (Fig. 26a).

Mean body mass of adult females in November was 52.2 kg (SE = 0.36), and ranged from 49.2 kg (SE = 0.93) in 2007 to 55.7 kg (SE = 0.89) in 2005, whereas body mass of individual
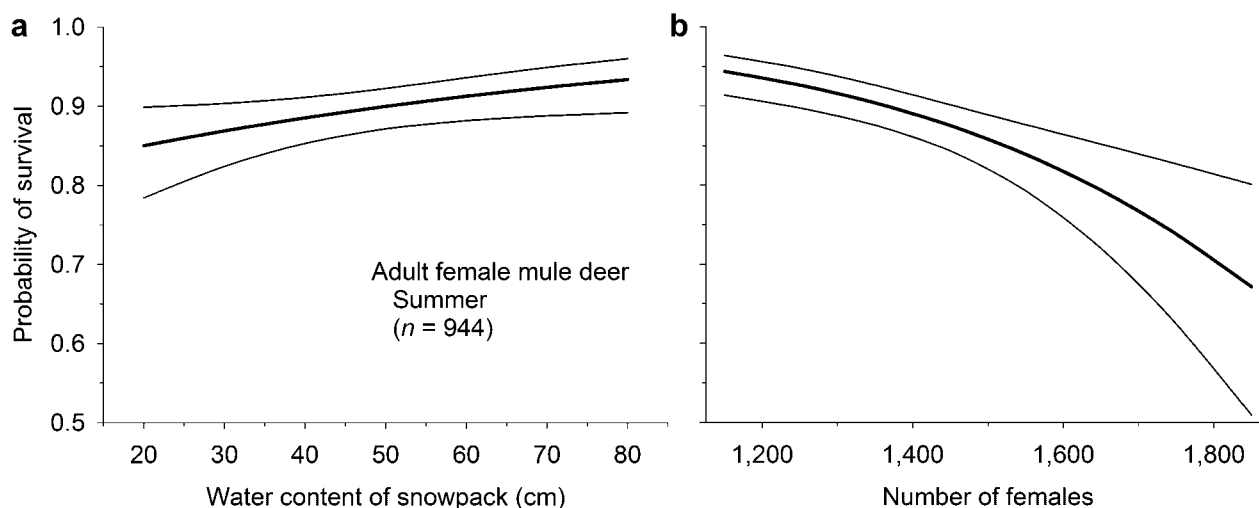
Figure 19. Estimated probability (±95% CI) of summer survival of adult (>1 yr) female mule deer as a function of the water content of the April snowpack (a), and the estimated number of adult females in the population during January (b), Sierra Nevada, California, USA. Results are based on the best model at the population level, which included April snowpack, number females, and mean March ingesta-free body fat (IFBFat).
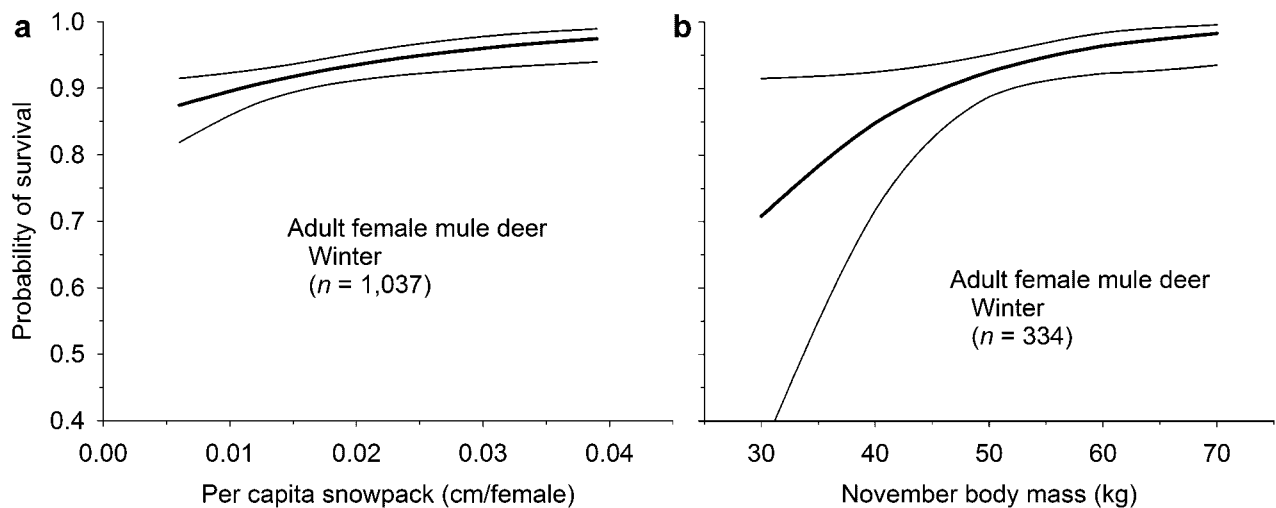
Figure 20. Estimated probability (±95% CI) of winter survival of adult (>1 yr) female mule deer as a function of per capita snowpack at the population level (a), and November body mass at the individual level (b), 1998–2008, Round Valley, Inyo County, California, USA. Results are based on the best model at the population level, which included per capita snowpack, monthly temperature, and Month (a), and at the individual level, which included per capita snowpack, month, age, and November body mass (b). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

adult (>1 yr old) females ranged from 20.8 kg to 70.2 kg. Females that resided on the west side of the crest during summer (54.2 kg, SE = 0.40) were heavier than east-side females (50.0 kg, SE = 0.52; Table 10). Summer precipitation had a positive effect on November body mass, whereas summer temperature had a negative effect on November mass (Table 10). At the individual level, November body mass of adult females varied as a function of age, IFBFat, and recruitment status. Females that had higher levels of IFBFat in November were generally heavier than those with lower IFBFat after accounting for age-specific patterns (Fig. 24c). Similar to March body mass, November body mass exhibited a curvilinear relationship with age (Fig. 24d); however, the senescent pattern of declining body mass was not as pronounced in autumn compared with late winter (Fig. 24b). In addition, albeit not significant, recruitment status was related negatively (importance weight = 1.0) to body mass of females in November (Table 10).

Finite Rate of Increase

The most parsimonious explanation for annual population growth of mule deer (λ) was a single variable that represented nutritional condition of adult females in March of the current year (importance weight = 0.79). Therefore, we conducted an additional analysis using simple linear regression, which supported a positive relationship between March IFBFat and lambda ($\lambda = 0.63 + 0.055 \times$ IFBFat; $r^2 = 0.32$, $P = 0.018$). Increasing mean IFBFat of adult females in March above 6.7% (95% CI: 3.6–8.6%) resulted in a predicted increase in total population size of mule deer in Round Valley during the following year (Fig. 27). Predicted λ ranged from 0.74 (95% CI: 0.49–0.99) at 2.0% IFBFat, to 1.18 (95% CI: 1.04–1.31) at 9.4% IFBFat, based on the range in IFBFat that we observed during 1991–2009. One data point in 1993, when the population had low IFBFat and experienced a decline ($\lambda = 0.84$; Fig. 27), potentially had a strong influence on those results (leverage = 0.59). Removing that datapoint, however, had little influence

on the relationship ($\lambda = 0.51 + 0.07 \times$ IFBFat; $r^2 = 0.26$, $n = 16$, $P = 0.045$) or the point at which $\lambda = 1$ (IFBFat = 7.0%). Because our post-1991 dataset was somewhat sparse with IFBFat values <7% (Fig. 27), we also included data on IFBFat and λ during the population crash (1985–1991) to further examine this relationship. The relationship remained positive and significant ($\lambda = 0.62 + 0.052 \times$ IFBFat; $r^2 = 0.30$, $n = 21$, $P = 0.011$), with a slight adjustment in the IFBFat level when $\lambda = 1.0$ (IFBFat = 7.3%); both analyses support the robustness of the relationship.

Nutritional Potential for Recruitment

To estimate the nutritional potential for recruitment (Fig. 4), we included mean March IFBFat during the current and preceding year, mean litter size, per capita snowpack, summer precipitation, and summer temperature for age ratios, because those variables potentially reflected the nutritional capacity to support allocation of resources to provisioning offspring (Table 6). For individual recruitment models, we included mean March IFBFat and summer residency; however, we removed the effects of summer residency ($\beta = -0.28$) on females residing on the west side of the Sierra crest (by subtracting out its effect), because that variable largely reflected increased predation (i.e., a negative effect) on young born on the west side rather than a positive effect from better nutrition available to west-side females.

Annual variation in patterns of ratios of young-to-adult females was similar to that predicted based on the nutritional state of the population. Residuals indicated that during 1992–2009, overall mortality of young at the level of the population was largely compensatory (Fig. 28), except during the early 2000s, when mortality of young was likely beginning to have an additive effect on population growth, as evidenced by young-to-female ratios that were less than the predicted nutritional capacity for females to recruit young (Fig. 28). A slightly different pattern emerged when we considered the influence of migratory tactic on patterns of recruitment. Observed recruitment for females summering on the east side was similar to that predicted based on nutritional
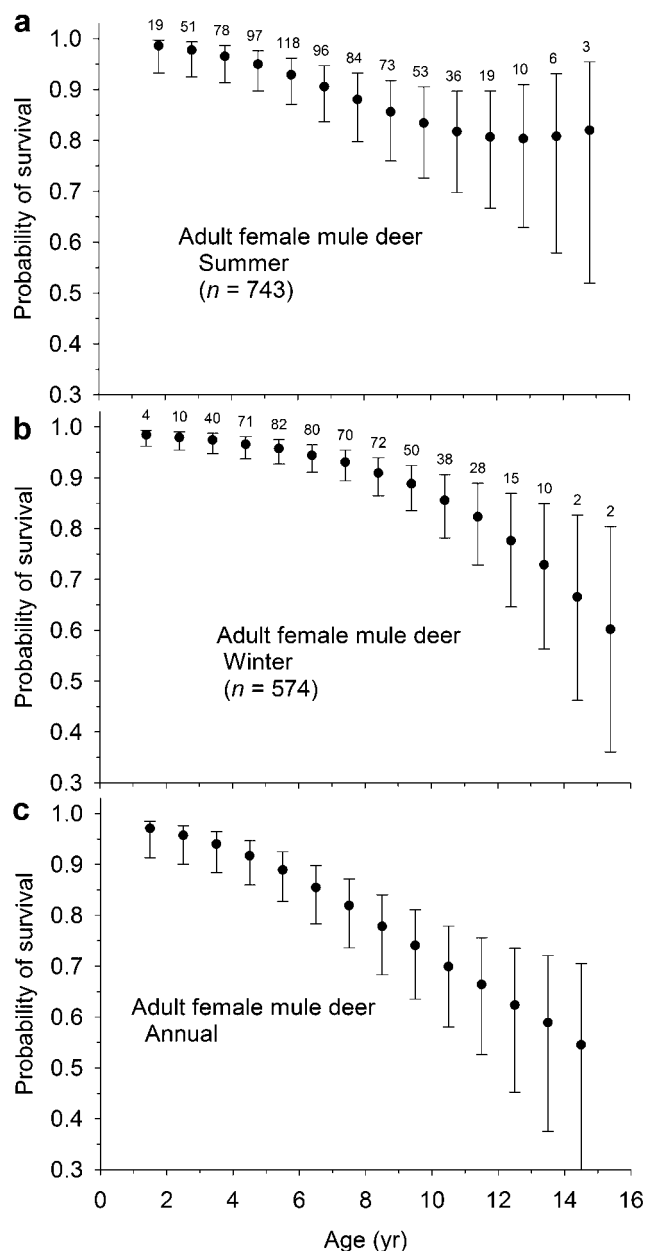
Figure 21. Estimated probability (±95% CI) of summer (a), winter (b), and annual (c) survival of adult (>1 yr) female mule deer as a function of age in the Sierra Nevada, California, USA. Results are based on the best model at the individual level, which included snowpack, number females, mean March ingesta-free body fat (IFBFat), age, and age^2 for summer (a); per capita snowpack, age, month, and November body mass for winter (b); and the product of summer and winter survival within age classes using the delta method for annual survival (c). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean. Sample sizes are indicated above error bars.

capacity; thus, mortality was largely compensatory (Fig. 29a). Conversely, for west-side females, recruitment residuals often were lower than nutritionally based predictions, indicating that at least some mortality was additive (Fig. 29b). The difference between the nutritional potential and realized recruitment for west-side females (Fig. 29b) indicated that average amount of additive mortality during 1997–2008 was 0.30 young per female per year.

DISCUSSION

Our long-term, longitudinal investigation of individual mule deer in the central Sierra Nevada revealed that nutritional condition at the population, individual, and maternal levels provided the necessary framework for understanding factors regulating population growth. Nutritional condition of female mule deer was sensitive to environmental stochasticity and density-dependent processes. The influence of nutritional condition on fitness components of mule deer mostly supported the paradigm of sensitivity to resource limitation expected for large herbivores (Fig. 1; Table 11), indicating that nutrition serves as an underlying foundation for life-history characteristics in large herbivores.

The carryover of nutritional relationships from previous seasons and years, which also may interact with migratory status, presents a difficult obstacle to overcome for research and monitoring programs that focus solely on demography and mortality factors to address population status. Demographic relationships, even when accompanied with information on cause-specific mortality, can be deceptive when nutritional status is unknown, because observed patterns may reflect previous, rather than current, environmental conditions (Testa 2004, Monteith et al. 2009). Nutritional condition at the level of the population provided a metric for assessing habitat adequacy relative to population density, and was related to finite rate of population growth. At the individual level, nutritional condition had implications for fitness and tradeoffs in life-history strategies that, in turn, determined the nutritional state of an individual transitioning between seasons. Along with a growing body of literature (Franzmann 1985; Cook et al. 2004, 2013; Bowyer et al. 2005; Parker et al. 2009; Pierce et al. 2012), our results provide additional support for the notion that nutritional condition, when considered in concert with other life-history and population characteristics, is an ecological indicator of critical importance for research, conservation, and management of large herbivores.

Long-term studies are essential to understanding natural processes that develop slowly and are highly variable and complex, and for evaluating ecological concepts and theoretical hypotheses, especially for long-lived, iteroparous mammals (Lindström 1999, Gaillard et al. 2000, Bleich et al. 2006, Clutton-Brock and Sheldon 2010). Short-term studies can be misleading and yield entirely different conclusions compared with more lengthy research (McCullough 1990, Kie et al. 2003, Monteith et al. 2009, Pierce et al. 2012). Long-term study (>20 yr) of a population of mule deer in the Sierra Nevada allowed us to capture variation in fitness components during disparate trajectories of population growth and intensities of predation (Kucera 1991, 1997; Bowyer et al. 2005; Pierce et al. 2012).

Conducting long-term research presents other challenges including the integration of new technology and improved techniques with older methodologies. In our study area before 1997, data on nutritional condition of adult females were obtained via culling and estimating body fat from kidney-fat indices. Beginning in 1997, we employed ultrasonography, which allowed in vivo estimation of IFBFat, and longitudinal monitoring of individual deer. We estimated IFBFat from

Table 9. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced ingesta-free body fat (IFBFat) and body mass of adult (>1 yr) female mule deer in March at the population ($n = 842$ and 828, respectively) and individual ($n = 531$ and 517, respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices K and L.

| Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Mar IFBFat	Population	Summer residency	−0.50*	−0.73	−0.26	1.00
		Per capita snowpack	45.23*	30.69	59.77	1.00
		Mean Mar IFBFat$_{t-1}$	0.51*	0.36	0.66	1.00
		Winter precipitation	−0.28*	−0.35	−0.21	1.00
	Individual	Mean Mar IFBFat$_{t-1}$	33.07	−2.54	68.67	0.99
		Per capita snowpack	0.74*	0.26	1.26	0.95
		Winter precipitation	−0.15*	−0.27	−0.018	0.71
		Age	−0.16*	−0.24	−0.079	0.96
		Litter size	0.56*	0.17	0.96	1.00
		Nov IFBFat$_{t-1}$[a]	0.14*	0.088	0.20	1.00
Mar body mass	Population	Summer residency	−1.00*	−1.81	−0.19	0.92
		Winter temperature	0.67*	0.37	0.96	0.99
	Individual	Summer residency	−1.11*	−1.87	−0.35	0.96
		Winter temperature	0.24*	0.018	0.47	0.74
		Age	2.70*	2.22	3.19	1.00
		Age^2	−0.15*	−0.18	−0.11	1.00
		Mar IFBFat	0.30*	0.19	0.40	1.00

[a] Results obtained from a separate set of models using a subset of data ($n = 215$) during 2002–2008.

kidney-fat indices for all deer before 1997 to provide a comparable estimate; however, kidney-fat indices are less sensitive to IFBFat at high levels of nutritional condition (Stephenson et al. 1998, Cook et al. 2007, Pierce et al. 2012). The bulk of our detailed analyses included only those data collected since 1997, which we collected with consistent methodology using ultrasonography. Nonetheless, we incorporated data from 1991 to 1996 for analyses of population-level metrics to increase sample size and obtain a wider range of population densities. Although those analyses may have been biased slightly because we calculated IFBFat from kidney fat or from smaller sample sizes during that time (Fig. 5), we weighted each sample by the inverse of the variance, which apportioned less weight to estimates with greater uncertainty. Sample size (often >100) was adequate for most analyses, but logistical challenges resulted in reduced sample size for neonatal survival, pregnancy of yearlings, and for characterizing cause-specific mortality of both neonates and adults. Consequently, evaluation of some covariates was not possible.

Effects of Nutritional Condition on Vital Rates

Survival and recruitment of young.—Because of the influence of survival and recruitment of young on the population dynamics of large ungulates (Gaillard et al. 1998, 2000; Raithel et al. 2007),
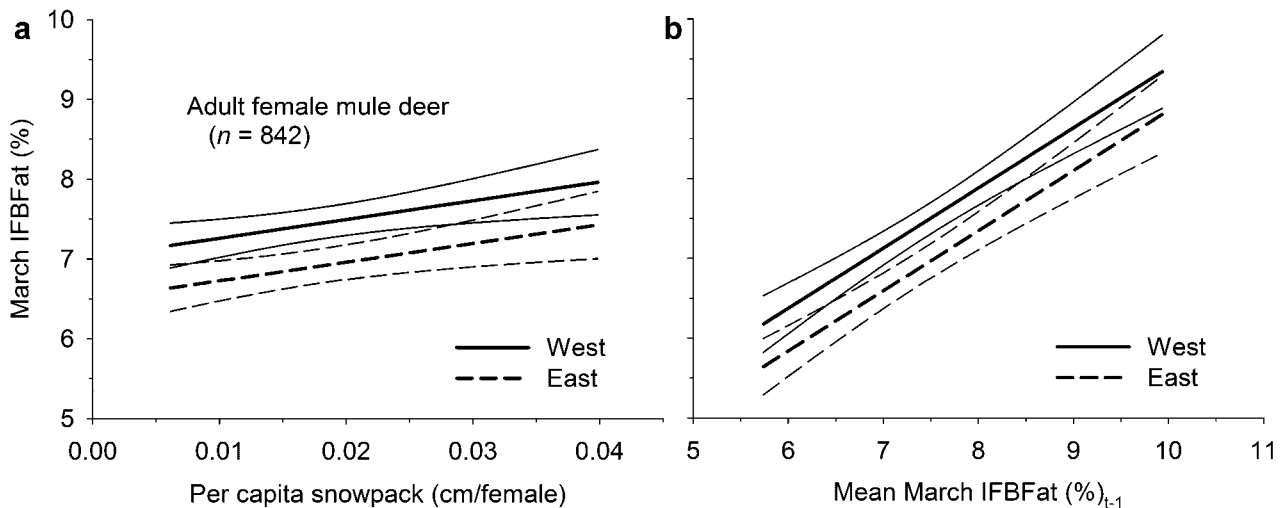
Figure 22. Estimated population-level effects (±95% CI) of per capita snowpack (a) and mean March ingesta-free body fat (IFBFat; b) on IFBFat of individual adult (>1 yr) female mule deer the subsequent March relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, winter precipitation, and mean March IFBFat the previous year ($t - 1$). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.
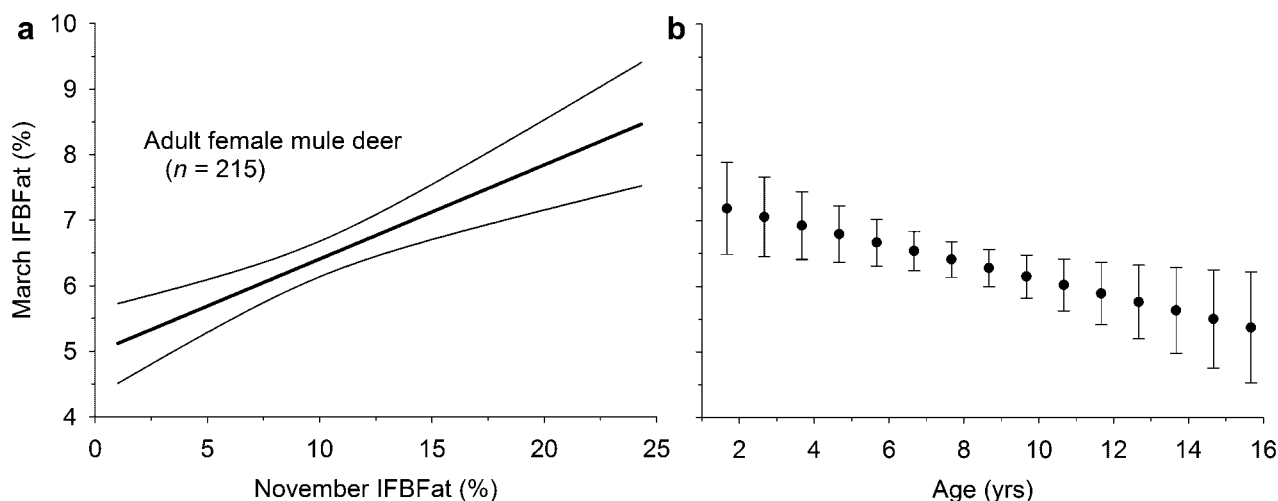
Figure 23. Estimated effect (±95% CI) of percent ingesta-free body fat (IFBFat) of individual females in November (a) and age (b) on IFBFat of adult (>1 yr) female mule deer in March, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the individual level, which included per capita snowpack, mean March IFBFat the previous year ($t-1$), winter precipitation, age, litter size, and November IFBFat$_{t-1}$. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.
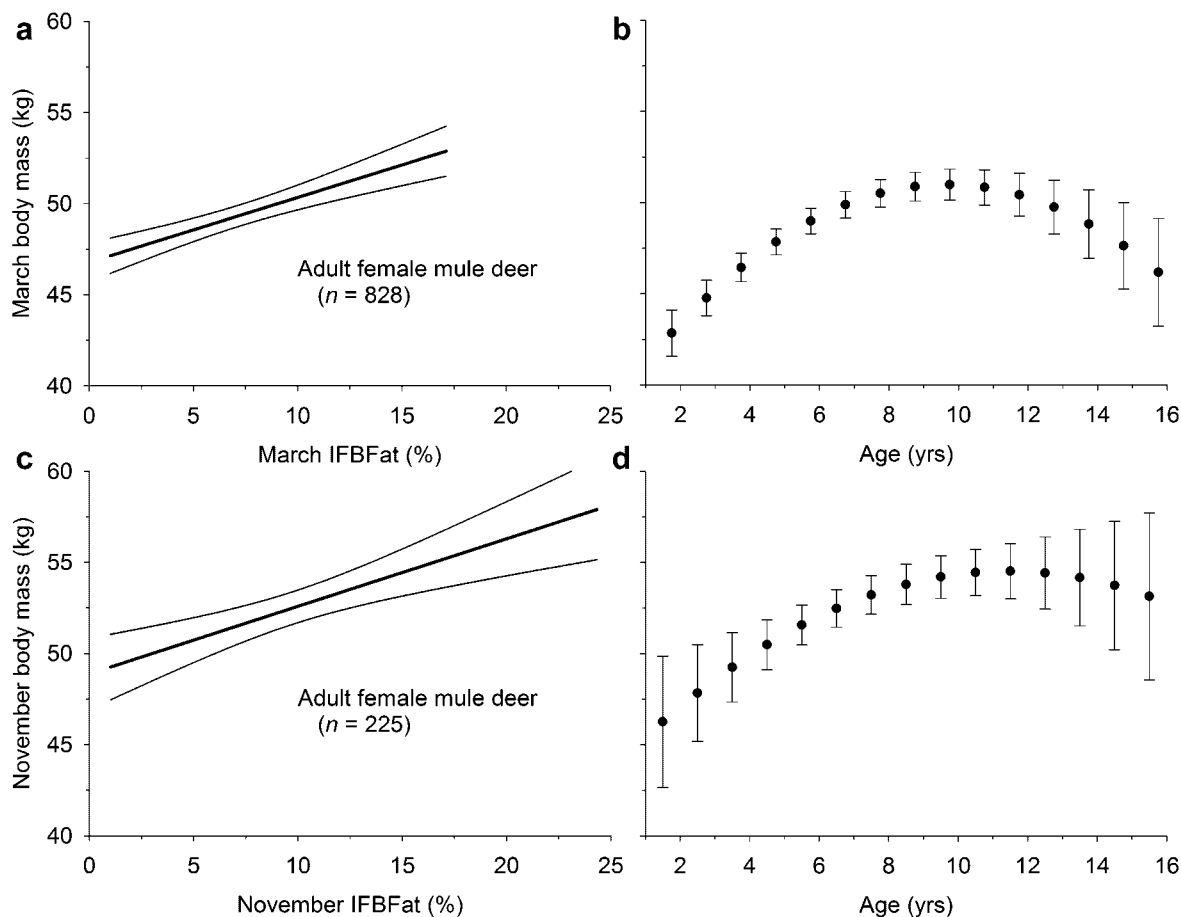
Figure 24. Estimated effect (±95% CI) of percent ingesta-free body fat (IFBFat) of individual females in March (a) and November (c), and age (b and d) on body mass of adult (>1 yr) female mule deer in March and November, respectively, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model at the individual level, which included summer residency (east or west), winter temperature, age, age^2, and March IFBFat for March body mass (a and b), and included summer residency, summer precipitation, summer temperature, mean March IFBFat, age, age^2, November IFBFat, and recruitment status for November body mass (c and d). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

Table 10. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced ingesta-free body fat (IFBFat) and body mass of adult (>1 yr) female mule deer in November at the population (n = 359 and 330, respectively) and individual (n = 249 and 253, respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices M and N.

Response	Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Nov IFBFat	Population	Summer residency	−2.35*	−3.22	−1.48	1.00
		Per capita snowpack	78.53*	14.16	142.89	1.00
		Summer precipitation	0.087*	0.012	0.16	0.69
		Mean Mar IFBFat	0.27	−0.12	0.65	0.64
	Individual	Summer residency	−1.97*	−2.84	−1.11	1.00
		Per capita snowpack	132.38*	71.54	193.22	1.00
		Mean Mar IFBFat	0.89*	0.28	1.50	0.94
		Age	−0.030	−0.18	0.13	1.00
		Mar IFBFat	0.10	−0.027	0.23	0.51
		Litter size	−0.24	−0.93	0.45	1.00
		Recruitment status	−2.81*	−3.43	−2.20	1.00
Nov body mass	Population	Summer residency	−2.75*	−4.15	−1.33	1.00
		Summer precipitation	0.37*	0.27	0.47	1.00
		Summer temperature	−0.61*	−1.11	−0.12	0.88
		Mean Mar IFBFat	−0.55	−1.13	0.039	0.79
	Individual	Summer residency	−2.72*	−4.27	−1.16	1.00
		Summer precipitation	0.27*	0.15	0.39	0.99
		Summer temperature	−0.36	−0.86	0.14	0.69
		Mean Mar IFBFat	0.13	−0.11	0.37	1.00
		Age	1.93*	0.80	3.06	1.00
		Age^2	−0.084*	−0.15	−0.016	1.00
		Nov IFBFat	0.37*	0.22	0.52	1.00
		Recruitment status	−0.81	−1.71	0.079	1.00

identifying factors that limit those life-history components is critically important. Survival of neonatal mule deer up to 20 weeks of age in the Sierra Nevada was relatively low compared with other populations of mule deer (Hamlin et al. 1984, Pojar and Bowden 2004, Bishop et al. 2009, Johnstone-Yellin et al. 2009), but similar to those experiencing nutritional limitation (Lomas and Bender 2007) or other large herbivores experiencing high predation (Barber-Meyer et al. 2008). Al-

though comparing mortality rates is common among studies of neonatal survival, a simple comparison of rates of survival among populations reveals little information as to the underlying consequences of mortality, and their effect on population dynamics. Indeed, we observed distinct differences in factors affecting mortality of neonates within a single population during 2006–2008. Nutrition was the dominant factor affecting survival of young on the east side of the Sierra crest (Fig. 7), whereas
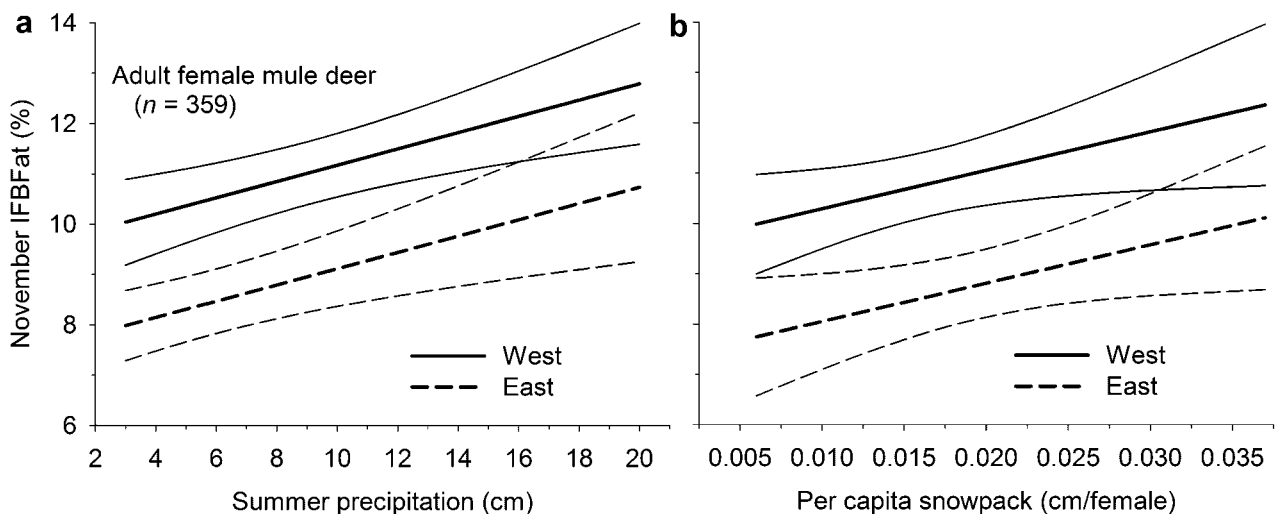
Figure 25. Estimated effect (±95% CI) of total summer precipitation (a) and per capita snowpack (b) on percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, mean March IFBFat, and summer precipitation. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.
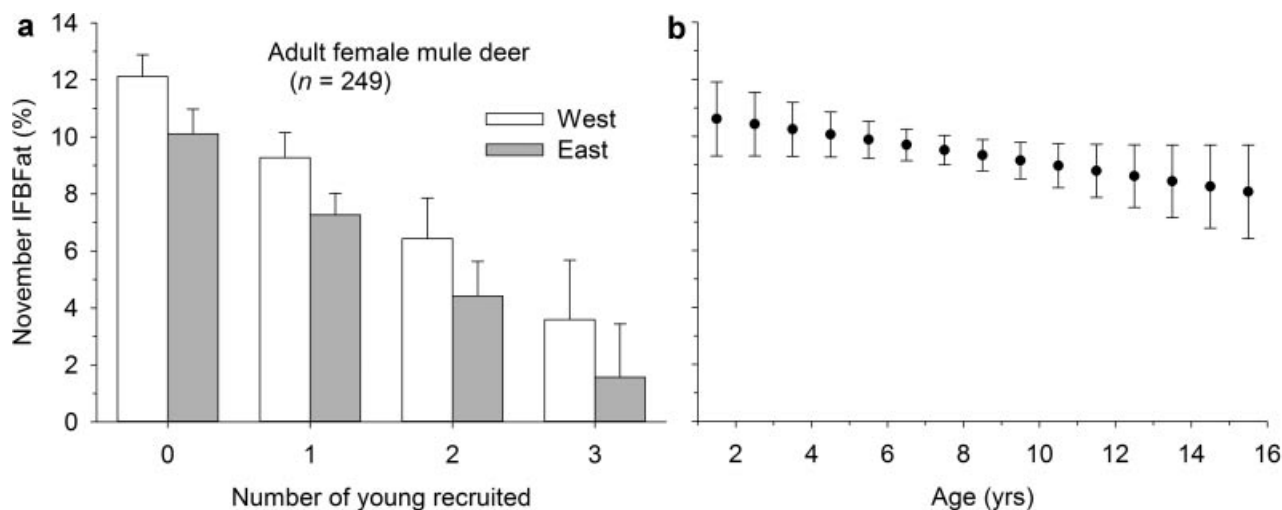
Figure 26. Estimated effect (±95% CI) of number of young recruited in autumn (a) and age (b) on percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the individual level, which included summer residency, per capita snowpack, mean March IFBFat, age, March IFBFat, litter size, and recruitment status. Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

survival of young born on the west side was affected mostly by predation (Fig. 8).

Birth mass of young is a widely recognized life-history trait that can have life-lasting consequences (Albon et al. 1987, Monteith et al. 2009), and often has a marked influence on survival of neonatal ungulates (Clutton-Brock et al. 1987, Keech et al. 2000, Tveraa et al. 2003, Lomas and Bender 2007, Carstensen et al. 2009, Johnstone-Yellin et al. 2009). Nevertheless, when predation is high and has an additive effect on mortality rates, effects of birth mass on viability and survival of young can be negligible and washed out by condition-independent predation (Fig. 7a; Barber-Meyer et al. 2008). On the east side of the Sierra crest, smaller neonates had a lower probability of survival (Fig. 7a), with those <2.0 kg at birth having <35% chance of survival and being most likely to succumb to malnutrition

(Fig. 9a), which is in accordance with poor survival of neonatal white-tailed deer ≤1.9 kg (*Odocoileus virginianus*; Verme 1962). Neonates dying of malnutrition are likely to die immediately after birth (Ozoga and Clute 1988, Carstensen et al. 2009), which also was evident in our study (Fig. 9b). Low birth mass is often attributed to poor maternal nutrition (Verme 1965, 1969; Robinette et al. 1973; Cook et al. 2004; Adams 2005; Lomas and Bender 2007), but birth mass in our study was not influenced strongly by any maternal characteristic that we measured
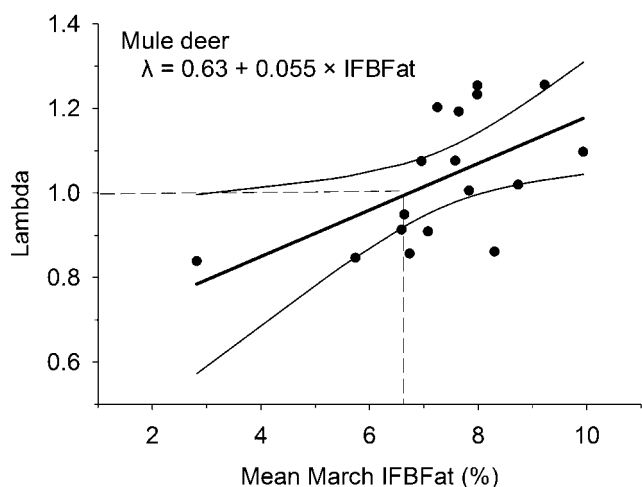
Figure 27. Estimated effect (±95% CI) of mean ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in March on population growth (lambda) during the current year, Sierra Nevada, California, USA, 1991–2008. Results are based on the best model, which included only mean March IFBFat.
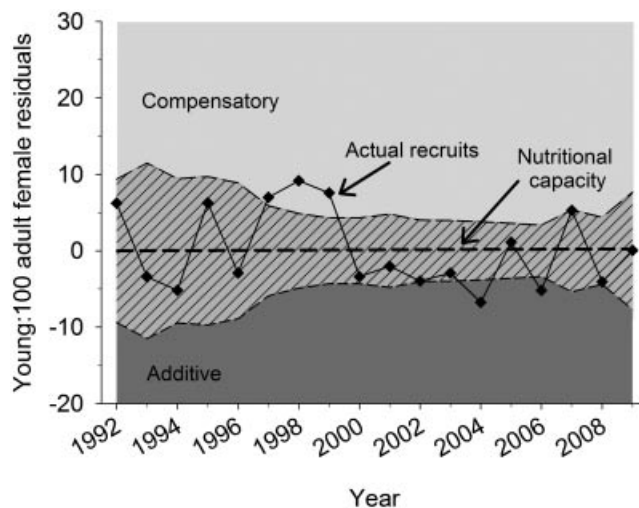
Figure 28. Residuals of the model used to predict the nutritional capacity of female mule deer to recruit young, relative to that attempted (based on fetal rates) and observed (based on ratios of young-to-adult females). Residuals in ratios of young-to-adult females above that predicted (dashed line) indicate the level of mortality that was compensatory (light gray), whereas ratios below that expected dictate the amount of mortality that was additive (dark gray) with respect to the nutritional capacity for recruitment of young. Hashed area around model predictions are 95% confidence intervals. The population level model included mean March ingesta-free body fat (IFBFat) of the current year (*t*), mean March IFBFat of the previous year (*t* − 1), mean March body mass, mean litter size, per capita snowpack, summer precipitation, and summer temperature.
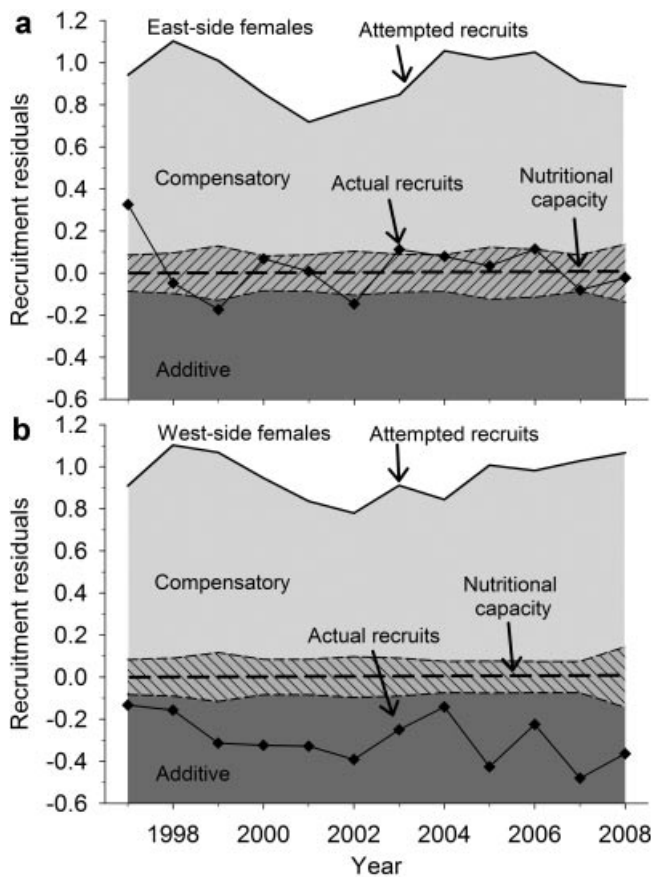
Figure 29. Residuals of the model used to predict the nutritional capacity of adult (>1 yr) female mule deer to recruit young (dashed line), relative to that attempted (based on fetal rates) and observed (based on recruitment rates) for east-side (a) and west-side (b) females. Residuals in recruitment above that predicted (dashed line) indicate the level of mortality that was compensatory (light gray), whereas recruitment below that expected dictate the amount of mortality that was additive (dark gray) with respect to the nutritional capacity for recruitment of young. Hashed area around model predictions are 95% confidence intervals. Model included summer residency and mean March ingesta-free body fat (IFBFat), with the effects of summer residency removed because it largely reflected increased predation pressure for west-side females.

(Appendix C). Birth mass of mule deer was related primarily to litter size, with larger litters resulting in lower birth mass among littermates (Fig. 10a). In contrast, timing of birth was related to maternal characteristics, which may have reflected an attempt by females to compensate for poor maternal nutrition,

thereby enhancing growth and survival of young (Monteith et al. 2009).

Gestation length is a plastic life-history trait that may be lengthened to compensate for retarded fetal development caused by nutritional deprivation (Verme 1965, Rachlow and Bowyer 1991, Berger 1992, Flydal and Reimers 2002, Clements et al. 2011), or shortened to coincide with resource availability if females are nutritionally capable (Berger 1992, Mysterud et al. 2009, Rowell and Shipka 2009). Heavier females in good nutritional condition may have conceived earlier in the autumn, resulting in earlier parturition dates (Robinette et al. 1973, Garel et al. 2009, Mysterud et al. 2009, Clements et al. 2011); however, conception date is often related negatively to gestation length (Scott et al. 2008, Mysterud et al. 2009, Clements et al. 2011). We postulate that females with larger litter sizes, or possibly low body mass, lengthened gestation to boost fetal growth and enhance birth mass of young, because larger litter size resulted in delayed birth dates (Fig. 10a) and low birth mass was selected against (Fig. 7a). Females also may have increased allocation of maternal resources to compensate for late birth dates and enhance neonatal growth (Rachlow and Bowyer 1994, Andersen and Linnell 1997), although this may not always occur (Asher et al. 2005, Whiting et al. 2009). Red deer (*Cervus elaphus*) maintained on varying levels of nutrition gave birth to similar-sized young; gestation length varied widely, however, with females on poor-quality diets lengthening gestation (Asher et al. 2005). In contrast, large-bodied females may have the potential to enhance fetal growth and give birth earlier than smaller females (Fig. 11). Timing of birth occurred earlier for caribou (*Rangifer tarandus*) that were heavier in summer (Cameron et al. 1993), Alaskan moose (*Alces alces*) with greater rump fat (Keech et al. 2000), and during years of lower population density for North American elk (*Cervus elaphus*; Singer et al. 1997). Similarly, date of parturition occurred earlier, and offspring were heavier at birth, following a mild winter compared with a harsh winter for reindeer (*Rangifer tarandus*) in Norway (Tveraa et al. 2003).

Varying gestation length to compensate for poor fetal growth may be possible only under moderate levels of nutrition (Albon et al. 1983*a*, Asher et al. 2005). Although limited peritoneal space probably constrained birth mass potential for females with larger litters (Fig. 10; Robinette et al. 1973), selective pressures likely favored reproductive strategies to maximize birth mass of young within morphological limits, because birth mass is one of the

Table 11. Relative magnitude of the influence of density-dependent (DD) availability of forage, mean nutritional condition (population level), individual nutritional condition, and migratory tactic on life history of mule deer in the central Sierra Nevada, California, USA, 1997–2009.

| Life-history component | Population level | | Individual level | |
	DD forage availability	Nutritional status	Nutritional status	Migratory tactic
Neonate survival	Minimal	Minimal	Strong	Strong
Recruitment of young	Minimal	Moderate	Strong	Strong
Young:adult female	Moderate	Strong		
Age at first reproduction	Strong	Minor	Strong	None
Litter size	Strong	Minimal	None	Strong
Pregnancy	None	None	None	None
Adult summer survival	Moderate	Moderate	Minimal	None
Adult winter survival	Strong	Minimal	Strong	None
Population growth	None	Strong		

most influential factors affecting survival of young. Strategies of extending gestation may not be favorable, however, for species that depend on parturition to coincide with a flush of nutrients in spring to support lactational costs (Côté and Festa-Bianchet 2001, Post et al. 2008) and provide sufficient time for growth and accruing body reserves to survive winter (Rachlow and Bowyer 1991, Bowyer et al. 1998b, Cook et al. 2004, Bishop et al. 2005, Hurley et al. 2011).

Date of birth often influences survival, with neonates born early or during the peak of birthing enjoying greater survival rates (Testa 2002, Landete-Castillejos et al. 2003, Whiting et al. 2011). Timing of nutritional needs to support late-born young may be mismatched with peak resource availability in spring, with young being underweight and experiencing poor survival (Clutton-Brock et al. 1987, Rachlow and Bowyer 1994). Other studies have shown that young born outside the peak of parturition may be subjected to increased predation pressure (Testa 2002, Barber-Meyer et al. 2008). Conversely, timing of parturition had no effect on survival in other studies (Bowyer et al. 1998b, Feder et al. 2008, Musante et al. 2010) or for neonates in the Sierra Nevada (Appendix A). Despite substantial predation experienced by young within the first few weeks of life, no effect of timing of birth on probability of survival led us to reject the potential for a dilution effect on predation.

Lactation is the most energetically demanding event (up to 4× baseline metabolism) in the life-history of an ungulate (Moen 1978, Monteith et al. 2014), and forage demands increase from 130% of summer maintenance when supporting 1 young during peak lactation to 170% for 2 young during peak lactation (Sadleir 1982). Provisioning of young following birth was influenced positively by the nutritional condition of the dam, but that effect was most evident with the onset of peak lactation (4 weeks post-parturition; Monteith et al. 2014), and was diluted by high predation pressure on young born on the west side of the Sierra crest (Fig. 7b). During early life, growth and development of young depend on the amount and quality of milk produced by the dam (Robbins and Robbins 1979; Cook et al. 2004; Tollefson et al. 2010, 2011), which may be dependent upon her nutritional state or foraging conditions (Sadleir 1982, Landete-Castillejos et al. 2003, Tollefson et al. 2011).

Ungulates are generally thought to be capital breeders because they rely on stored energy for reproduction (Jönsson 1997); however, small ungulates such as mule deer and European roe deer (*Capreolus capreolus*) may function more like an income breeder, because they rely on energy acquired during reproduction to support provisioning of young (Andersen et al. 2000, Tollefson et al. 2010). The relationship between nutritional condition and probability of survival of young for females summering on the east side of the Sierra crest, and the evident costs of reproduction on nutritional condition in autumn, indicate that mule deer also are reliant on current capital to support reproductive allocation (Stearns 1992, Jönsson 1997, Stephens et al. 2009). Similar relationships between nutritional capital, as measured by body mass or fat reserves, and survival of young have been reported for numerous large herbivores including North American elk (Cook et al. 2004), red deer (Landete-Castillejos et al. 2003), moose (Keech et al. 2000), bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1998, Festa-Bianchet and Jorgenson 1998), caribou

(Bårdsen et al. 2010), and mule deer (Lomas and Bender 2007, Johnstone-Yellin et al. 2009, this study).

The young-to-adult female ratio is a composite measure of several demographic processes including survival of adult females, fertility, fecundity, and survival of young (Bonenfant et al. 2005). Although the use of ratio data for inferring population dynamics has been criticized (Caughley 1974, McCullough 1994), others have used these data for characterizing demographics of ungulate populations (Raithel et al. 2007; Harris et al. 2008; Hegel et al. 2010a, b). If reproductive rates and survival of adult females remain high with little variation, age ratios can provide a reliable index to relative changes in λ, because variation in survival of young drives interannual changes in that metric (Gaillard et al. 1998, 2000; Raithel et al. 2007; Harris et al. 2008).

The young-to-female ratio for mule deer in the Sierra Nevada was highly variable (Fig. 14a), and was influenced primarily by nutritional condition of adult females in March. Density-dependent effects on age ratios were evident in a number of studies reviewed by Bonenfant et al. (2009). Nutritional condition in March provided an integrative measure of range conditions as affected by precipitation and density-dependent processes; nutritional condition reflected reproductive potential for females the following summer, and was a reference of carryover of range conditions and nutritional limitation from the previous year (Fig. 14b).

Age at first reproduction.—The age at which young females first reproduce is of considerable theoretical interest for understanding life-history strategies (Stearns 1992, Proaktor et al. 2008), and can have a profound effect on population dynamics (Cole 1954). Age at first reproduction is expected to follow recruitment of young in sensitivity to resource limitation (Eberhardt 2002). In support of that prediction, probability of pregnancy for yearling female mule deer in the Sierra Nevada was determined mostly by an index of density-dependent availability of forage, which likely influenced growth of young females before the mating season (Fig. 15).

Age of primiparity for most species of large ungulates is associated with attaining a threshold in body mass before mating (Langvatn et al. 1996, Sand and Cederlund 1996, Adams and Dale 1998, Swihart et al. 1998, DelGiudice et al. 2007), which is sensitive to resource limitation and may delay age at first reproduction for 1–3 years depending on the severity of such limitation (Jorgenson et al. 1993, Festa-Bianchet et al. 1995, Bonenfant et al. 2002, Strickland et al. 2008). Although our data on body mass were collected during March, the threshold of ≥41 kg for a high (0.90) probability of pregnancy among yearling mule deer was comparable to that reported previously for 6-month-old and yearling mule deer (41–45 kg; Robinette et al. 1973) and white-tailed deer (55.1 kg; DelGiudice et al. 2007). In contrast, probability of pregnancy for females ≥2.5 years old was unrelated to age, nutritional condition, or body mass, even though body mass of pregnant females ranged as low as 34 kg in November and 30 kg in March—body-mass levels that represented a probability of pregnancy of almost zero for yearlings (Fig. 15b). Likewise, young female moose required greater body mass to ovulate compared with older females (Schwartz and Hundertmark 1993, Garel et al. 2009). We hypothesize that the strong effect of body mass on age of

primiparity when compared with the absence of such a relationship in older females may represent a tradeoff between early maturation and future growth (Green and Rothstein 1991, Stearns 1992, Sand 1996). Furthermore, nutrition experienced by dams during the year of birth holds the potential to influence age of primiparity (Pettorelli et al. 2003, McLoughlin et al. 2008), which may be manifested through its influence on birth mass and growth of offspring (Monteith et al. 2009).

Fetal rate.—Mean litter size during 1997–2009 (1.69 young/ adult female) was comparable to that reported for other populations of mule deer in California (1.72; Salwasser et al. 1978) and Colorado (1.70; Andelt et al. 2004), was less than in a captive herd in Colorado (1.82; Robinette et al. 1973), and a free-ranging population in Colorado (1.81; Bishop et al. 2009), but was greater than that observed (1.40) during the population crash in Round Valley in the late 1980s (Kucera 1988). Litter size of female mule deer ≥2.5 years old was sensitive to summer climate, per capita snowpack, and summer residency. We hypothesize that summers with warmer temperatures resulted in accelerated drying and senescence of forage, thereby reducing its nutritional quality (Marshal et al. 2005a, b). Winters with greater snowpack relative to population density, however, probably helped sustain forage quality further into the summer, which may moderate effects of summer weather (Table 7).

Effects of nutritional condition on fertility rates have been reported for numerous species of ungulates (Adamczewski et al. 1997, Cook et al. 2004, Stewart et al. 2005), including mule deer (Johnstone-Yellin et al. 2009, Tollefson et al. 2010). Our results, however, indicated that age, nutritional condition, and body mass did not influence fertility patterns for female mule deer ≥2.5 years old. In other studies, patterns of fertility were related either to body mass or nutritional condition (Cameron et al. 1993, Adams and Dale 1998, Stewart et al. 2005, Tollefson et al. 2010); however, forage resources available immediately before or during estrus have the potential to override effects of current nutritional state (Verme 1969, Bowyer 1991, Tollefson et al. 2010).

Maintaining high fertility may be possible for migratory ungulates that are capable of following phenological gradients (Monteith et al. 2011, Sawyer and Kauffman 2011) and relocating to ranges that have experienced negligible browsing pressure during the preceding season (Skogland 1985, Andelt et al. 2004). Mule deer in the Sierra Nevada migrate to winter range before rut in autumn, where browsing intensity has been relaxed during the entire growing season (Monteith et al. 2011), which may offer a diet sufficient in digestible energy and protein to enhance probability of pregnancy and litter size, and may partially explain the absence of an effect of nutritional condition on those reproductive parameters. Large litter size among females that summer on the west side of the Sierra crest, however, may be explained partially by their longer residence on summer ranges supporting greater plant diversity and quality of forage than females summering on the east side (Monteith et al. 2011).

Reproductive senescence in fertility or fecundity did not occur for mule deer up to 15.5 years old in the Sierra Nevada despite lower body mass (Fig. 24d) and nutritional condition (Fig. 26b) of old-aged females in autumn. Pregnancy and litter size remained largely unaffected by age for females ≥2.5 years old. These data are consistent with the absence of a strong relationship between fertility and body mass or nutritional condition. Verme and Ullrey (1984) suggested that reproductive senescence occurs in white-tailed deer >7 years old; however, most empirical evidence indicates an absence of senescence in fertility or fecundity for *Odocoileus* (McCullough 1979, Nelson and Mech 1990, Strickland et al. 2008), including up to 15.5 years old in white-tailed deer in midwestern North America (DelGiudice et al. 2007). Despite actuarial senescence for mule deer occurring at about 10 years old (Fig. 21), particularly during winter, reproductive senescence was not evident.

Increases in occurrence of reproductive pauses and declines in fecundity have been reported for other female ungulates at advanced ages (generally >12 yr), or within a few years of actuarial senescence (Festa-Bianchet et al. 1994, Adams and Dale 1998, Bérubé et al. 1999, Ericsson et al. 2001, Festa-Bianchet and King 2007). We suspect reproductive senescence is unlikely to be evident in deer populations experiencing hunter harvest or predation by large carnivores, especially when senescence in survival begins as early as 10 years of age. Litter sizes remained high and were inconsistent with individual nutritional status, which limits their value for evaluating interannual variation in degree of resource limitation for populations of *Odocoileus*.

Pregnancy in adults.—Patterns of pregnancy for large herbivores vary markedly among species and populations, with reproductive pauses commonly occurring in some taxa (Julander et al. 1961, Testa and Adams 1998, Cook et al. 2004, Stewart et al. 2005), compared with high and consistent patterns of pregnancy that appear insensitive to resource limitation in others (Skogland 1985, DelGiudice et al. 2007, Bishop et al. 2009). Although low rates have been documented under extreme levels of population density and range deterioration (Julander et al. 1961, Bowyer 1991), high levels of pregnancy across a wide range of environmental variation, and nutritional limitation seems to be the norm for *Odocoileus* (Andelt et al. 2004, DelGiudice et al. 2007, Strickland et al. 2008). Those patterns support pregnancy of adult females as being one of the last factors to be influenced by inadequate nutrition (Fig. 1; Eberhardt 2002), and indicate that monitoring of pregnancy rates will provide limited insight into variation of nutritional limitation within or among populations (Andelt et al. 2004), except under extreme nutritional deprivation. In contrast, patterns of pregnancy in moose are sensitive to nutritional condition with 9% and 13% IFBFat in autumn equating to 50% and 100% pregnancy rates, respectively (Testa and Adams 1998).

Reproductive pauses and variable pregnancy rates do occur in polytocous species (Julander et al. 1961, Hamel et al. 2010, Pierce et al. 2012), but are much more common in species that typically give birth to a single offspring such as red deer and North American elk (Albon et al. 1983b, Cook et al. 2004, Stewart et al. 2005), and caribou (Cameron 1994, Adams and Dale 1998), where an adjustment from 1 to 0 young is normally the only possibility. High rates of pregnancy and litter sizes >1 are typical for *Odocoileus*, which are more likely to adjust resource allocation to reproduction according to nutritional conditions during gestation or at onset of post-natal care, rather than during

ovulation (Johnstone-Yellin et al. 2009, Monteith et al. 2009). Prenatal mortality among *Odocoileus* has been documented, but mostly occurs early in gestation and is rare (Robinette and Gashwiler 1950, Kie and White 1985, Bishop et al. 2008).

Adult female survival.—Survival of adult female ungulates generally exhibits a consistent pattern of high (>85%) survival with a strong resilience to climatic or density-dependent factors (Barrett 1982; van Vuren and Bray 1986; Gaillard et al. 1993, 2000; Loison and Langvatn 1998; Unsworth et al. 1999; Hamel et al. 2010). We documented positive effects of snowpack relative to animal density on both summer and winter survival of adult females, after accounting for age structure (Festa-Bianchet et al. 2003). Despite those interannual relationships with density and forage growth, mean annual survival was 0.87 and seasonal survival was almost always >0.90, albeit with some variation among years. High adult survival (Fig. 18) within a variable environment supports the stability in survival of adult females for large herbivores (Fig. 1), especially when compared with the variation in weather, predation, and nutrition we observed. Adult survival may be strongly influenced, however, in overshoots of K coupled with extreme drought (Pierce et al. 2012).

Besides age, the only individual characteristic that was related to seasonal survival of adult female mule deer was November body mass, which increased the probability of overwinter survival (Fig. 20b). Diets of mule deer in Round Valley progressively shift from bitterbrush to sagebrush as winter browsing depletes the availability of bitterbrush (Pierce et al. 2004). Sagebrush is high in protein, but can contain an abundance of toxic phenolics (Bray et al. 1991), and is consumed primarily when alternative forage sources are unavailable in Round Valley (Kucera 1997; Pierce et al. 2004, 2012). Overwinter survival may have been related to body mass rather than IFBFat, because body mass integrates both body protein and fat, and may represent total endogenous reserves available to buffer against depletion in forage protein and digestible energy as winter progresses (Barboza and Parker 2008). Loss of body mass over winter is substantial for most ungulates and, as fat reserves are depleted, mobilization of muscle mass accelerates to satisfy energy and nitrogen requirements for maintenance (Torbit et al. 1985, Parker et al. 1993, Monteith et al. 2013). Therefore, maintaining sufficient muscle mass for individuals experiencing poor range conditions may be critical to their survival (Torbit et al. 1985, Bender et al. 2008).

Nutritional condition of adult females can influence their survival (Lawrence et al. 2004, Bender et al. 2007), but rare events of extreme weather or nutritional deprivation may be necessary for relationships between nutrition and adult survival to become evident (sensu Gaillard et al. 2000, Bishop et al. 2005). During a 3-year study coincident with a drought in north-central New Mexico, nutritional condition of individuals had a significant influence on survival of female mule deer (Bender et al. 2007). Likewise, the population of mule deer in Round Valley crashed from roughly 6,000 animals in 1985 to <1,000 by 1991 in response to severe drought conditions with declines in adult survival caused by nutritional deprivation (Kucera 1988, Pierce et al. 2012). Alternatively, nutritional enhancement of winter range increased annual adult survival by 0.05 (Bishop et al. 2009). Although our study overlapped a 12-year period with highly variable precipitation, deer were not subjected to extremes in climatic conditions or density that would be expected to dramatically affect a life-history characteristic that can be buffered against moderate environmental variation (Gaillard et al. 1998, 2000). The resistance in adult survival to nutritional limitation may be accounted for by the number of behavioral and reproductive strategies available to females to preserve their own survival in light of other decisions that increase risk of mortality (Festa-Bianchet and Jorgenson 1998; Bårdsen et al. 2010; Monteith et al. 2011, 2013).

Actuarial senescence (Nussey et al. 2008), or suppressed survival with increasing age, occurred during both winter and summer, but is likely to be most apparent during seasons or years of nutritional limitation (Gaillard et al. 1993, Garrott et al. 2003, Nussey et al. 2008). Although survival declined as females progressed in age during summer, predicted survival of females >10 years old declined at a reduced rate and remained >80% in older age classes (Fig. 21a). This moderate decline contrasted with the increasing rate of mortality with age for females during winter (Fig. 21b), as is typical for large ungulates (Loison et al. 1999; Nussey et al. 2007, 2008). Summer, for many temperate ungulates, represents the season of forage abundance (Parker et al. 2009), which may have lowered the nutritional suppression associated with old age and tooth wear (Loe et al. 2006, Nussey et al. 2008). In contrast, the nutritional bottleneck of winter offers aged females fewer options to reduce energy expenditure or increase forage gain (Monteith et al. 2013), especially when they are generally in poorer nutritional condition by March than are prime-aged females (Fig. 23b).

Sensitivity of Nutritional Condition

Our results were in general accordance with the hypothesized sensitivity of life-history traits to nutritional limitation (Gaillard et al. 2000, Eberhardt 2002) with the exception of pregnancy rates, which were less variable and also affected to a lesser extent by nutritional limitation than was survival of adult females (Fig. 1). We hypothesized that nutritional condition would offer the most sensitive and direct measure of resource limitation. In support of that hypothesis, nutritional condition was more variable than other life-history traits and the influence of nutritional condition on life-history characteristics followed those same predictions (Fig. 1).

Numerous life-history traits, including nutritional condition, reflected a lag of population-level (mean) nutritional condition from previous years. Nutritional condition at the population level, particularly post-winter, likely reflected a metric of habitat condition from the previous year that would carry over between seasons (McCullough 1979, Fryxell 1991, Singer et al. 1997, Cook et al. 2013, Monteith et al. 2013). Direct and lagged effects of density dependence have been documented in numerous populations of large mammals across an array of habitats (Singer et al. 1997, Beckerman et al. 2002, Pettorelli et al. 2002, Månsson et al. 2007), which likely caused lagged effects of age structure, delayed effects of nutritional carryover at the individual level, and residual effects of habitat conditions relative to density from the previous season. If nutritional condition represents the relative position of the population with respect to K (Piasecke and Bender 2009), then that position would be expected to be partially reflected in the following year. Time lags and carryover

effects in response to resource limitation are becoming increasingly recognized as influential factors in the regulation of ungulate populations (Fryxell 1991, Gilbert and Raedeke 2004, Keyser et al. 2005, Monteith et al. 2009, Harrison et al. 2011), and stress the importance of not considering a particular season or year in isolation (Kie et al. 2003, Monteith et al. 2013).

Nutritional condition represents a direct measure of energy acquisition and debt experienced by an individual; hence, nutritional condition is sensitive to minor changes in resource quality and availability (Cook et al. 2004, Parker et al. 2009). Accordingly, changes in habitat quality and animal density will be reflected by nutritional condition before demographic effects are observed, because demographic effects are mediated largely through nutrition (Bender et al. 2008, Parker et al. 2009). Moreover, because long-lived, iteroparous ungulates favor a conservative life-history strategy (Gaillard and Yoccoz 2003), some vital rates are insensitive to habitat changes or are only affected once a threshold is reached, thereby offering incomplete information across a wide range of resource limitation.

Nutritional condition (i.e., percent body fat) is more sensitive to habitat factors experienced by an individual than is body mass. Patterns of body mass can reflect resource limitation and environmental variation, but interpreting patterns of body mass as a reference to nutritional limitation can be plagued by long-term cohort and maternal effects (Albon et al. 1987, Post et al. 1997, Sams et al. 1998, Hamel et al. 2009, Monteith et al. 2009). For example, individuals may be in good nutritional condition after habitat conditions have improved, yet body mass remains low because of intergenerational and cohort effects acting through maternal nutrition (Monteith et al. 2009). Furthermore, fat reserves provide a different form of energetic currency compared with protein reserves, which is what body mass primarily reflects (Monteith et al. 2013). Protein reserves, and thus body mass, function mostly as insurance against winter malnutrition, whereas fat reserves provide a universal source of energy for both survival and reproduction (Monteith et al. 2013). Despite marked changes in nutritional condition for mule deer in Round Valley during 1997–2009, patterns of body mass were nearly invariable (CV = 3%) and were influenced primarily by age and summer residency, with females residing on the west side of the crest being larger than east-side females. The higher plane of nutrition on the west side of the Sierra crest, and greater potential for pre- and post-natal allocation by mothers summering on the west side likely explains the disparity in body mass between females occupying opposite sides of the Sierra crest. We hypothesize that nutritional limitation on the east side has resulted in life-long negative effects on adult body mass for young born to mothers on the east side, because body mass can reflect maternal condition from previous generations (Mech et al. 1991, Monteith et al. 2009), rather than current habitat conditions.

Variation in access to resources and how individuals allocate those resources during a particular season has implications for inclusive fitness, particularly for animals that partially rely on current capital for survival and reproduction (Stearns 1992, Jönsson 1997, Stephens et al. 2009). Such residual effects from previous seasons are defined as carryover effects, wherein life-history events and ecological processes evident in one season result in individuals transitioning between seasons having different nutritional states, and thereby affecting individual performance in the subsequent season (Harrison et al. 2011, Monteith et al. 2013). Downstream consequences of current nutritional and reproductive state on future fitness have important implications for the evolution of life-history strategies and the dynamics of populations when individual effects are scaled up to the population level (Testa and Adams 1998, Norris 2005). Despite their importance, carryover effects are difficult to document, because they occur at the individual level and, thus, require longitudinal data on individuals throughout the annual cycle (Clutton-Brock and Sheldon 2010, Harrison et al. 2011).

The relative magnitude of the effect of current nutritional state of individual mule deer on life-history components during the following season were in accordance with life-history theory for large herbivores (Stearns 1992, Eberhardt 2002). Furthermore, individuals made transitions between seasons at different nutritional states depending upon previous forage availability, migratory status, and reproductive output. The most evident carryover effect on reproductive success was mediated through the winter environment, where foraging opportunities on winter range along with nutritional condition during November determined late-winter nutritional condition (Figs. 22 and 23), which in turn influenced survival and recruitment of young the following summer (Figs. 7b, 13a, and 14b). Similarly, nutritional state of individuals transitioning from summer to winter was largely determined by migratory tactic and reproductive expenditure (Figs. 25 and 26). Substantial carryover of nutritional condition reinforces the notion that K is a year-round phenomenon (Kie et al. 2003), and nutritional contributions from seasonal ranges are not independent (Monteith et al. 2013).

Nutritional Cost of Reproduction

A central question in life-history theory is the degree to which individuals allocate resources to support current reproduction versus securing their own survival (Stearns 1992). Species with long life spans that have the opportunity to reproduce repeatedly are expected to employ a conservative strategy regarding reproductive allocation that favors maternal survival over reproductive output (Martin and Festa-Bianchet 2010). This bet-hedging strategy has been termed risk-sensitive reproductive allocation (Bårdsen et al. 2008), and is the primary reason why survival of young is more variable and more sensitive to resource limitation than adult survival (Gaillard et al. 1998, 2000). Indeed, individual females may rely on body reserves to fuel periods of low energy intake or high reproductive output (Monteith et al. 2013). Although spring and summer represent the season of forage abundance in many ecosystems, mothers incur substantial energetic costs to support late gestation and lactation (Moen 1978, Pekins et al. 1998, Monteith et al. 2014), which may result in a tradeoff if current reproductive allocation affects nutritional reserves that are insurance against nutritional deprivation during winter (Bender et al. 2007).

Nutritional condition in late winter had a positive effect on reproductive success of female mule deer the following summer; however, reproductive effort, in turn, influenced autumn

nutritional condition (Fig. 26a). The lactational costs incurred by mothers during the summer, along with their summer residency, were the most influential factors determining nutritional reserves of females before the onset of winter (Fig. 26a). Although IFBFat of individual females did not affect probability of overwinter survival, heavier females were more likely to survive winter (Table 8). Body mass for adult females in autumn was positively influenced by their fat reserves, which was determined primarily by their reproductive status in autumn (Table 10). Furthermore, nutritional condition of females in autumn had a positive influence on nutritional condition in March, which in turn, affected reproductive success the following summer (Fig. 13a). Therefore, mule deer incurred a fitness cost by trading-off current reproductive allocation against accumulation of somatic reserves to survive winter and support reproduction the following summer.

Large herbivores undergo seasonal rhythms in nutritional condition, with poor condition often occurring following winter, and summer forage offering support for reproduction and fat accretion (Parker et al. 2009). In accordance with that pattern, mean nutritional condition of females in autumn (9.7% IFBFat) was greater than in late winter (7.2%). Nonetheless, for reproductive individuals, seasonal dynamics of body mass and nutritional condition did not follow the expected pattern, because of the considerable somatic costs incurred from successful reproduction. For example, we observed a measurable cost of reproduction on nutritional condition for female mule deer during autumn based on the number of young recruited, which likely reflected a reduction in the autumn threshold of nutritional condition among females that successfully recruited young (Monteith et al. 2013). Negative effects of reproduction on fat stores was moderated by per capita snowpack and summer precipitation (Fig. 25), which likely influenced forage quality and availability on seasonal ranges (Sinclair et al. 1985; Marshal et al. 2005a, b). Regardless of summer residency or climatic variation, females that recruited 1 young were still in poorer condition in autumn than those that failed to recruit young.

The substantial immediate cost of reproduction to nutritional condition and the influence of range quality in summer indicated that mule deer rely on nutritional reserves (i.e., capital) and available forage (i.e., income) to subsidize reproductive allocation (Stephens et al. 2009). Although other investigators have suggested that mule deer might function like other small ungulates (Andersen et al. 2000) by relying on nutritional income (Johnstone-Yellin et al. 2009, Tollefson et al. 2010), our results indicate that they reside somewhere in the middle of the capital-income continuum. Furthermore, that current capital is used to finance reproductive allocation attests to the value of nutritional condition for interpreting or predicting population dynamics.

Selective Pressures on Migratory Tactics

Patterns of migration within populations affect subsequent life-history characteristics and, thus, selective pressures that determine the balance between migratory segments of a population (Kaitala et al. 1993). Coexistence of divergent migratory tactics within a single population indicates that animals are following a mixed evolutionary stable strategy, wherein various strategies may occur at some relatively equal benefit, but at different times

(Sinclair 1983). Differential mortality among migratory segments may permit the coexistence of the 2 tactics, but advantages of each will be sensitive to changes in reproductive success and survival (Kaitala et al. 1993). Poor recruitment and survival resulting from a particular migratory tactic, given natal and adult fidelity to a particular seasonal range, will inherently reduce the proportion of individuals in the population employing the more costly tactic. Indeed, we documented differences in litter size, survival and recruitment of young, and seasonal fat levels between females that shared a common winter range but exhibited divergent migratory tactics relative to occupancy of summer ranges on opposite sides of the Sierra crest (Fig. 3).

Migration to the west side of the Sierra crest was the most common migratory tactic for mule deer wintering in Round Valley before 1985, because deer migrating to the west side of the Sierra crest composed most (87%) of the population (Kucera 1988); by 2005, however, that proportion had declined to <50% and continued to decline through the remainder of our study (Appendix P). During 1997–2009, we documented high fidelity to summer range, with an absence of switching summer residency between sides of the Sierra crest for adult females ($n = 251$) and young ($n = 26$). Given high fidelity to seasonal range, which is common among mule deer (McClure et al. 2005), dispersal was not responsible for the shifting trends in migratory segments of the population.

Habitats and annual moisture regimes differed considerably between sides of the Sierra crest (Storer et al. 2004, Bleich et al. 2006). The more mesic environment and lower deer densities on the west side of the Sierra crest probably resulted in better foraging conditions for mule deer (Monteith et al. 2013). Accordingly, females that summered on the west side of the Sierra crest were larger than east-side females, which likely represents long-term differences in summer nutrition and growth of young (Monteith et al. 2009). Similar relationships with body size were documented for caribou occupying disparate summer ranges (Crête and Huot 1993). Furthermore, females that summered on the west side of the Sierra crest were consistently in better nutritional condition in autumn after controlling for lactational costs (Fig. 26a), and remained in better nutritional condition through March (Fig. 22). Despite those nutritional benefits, survival of young on the west side of the Sierra crest during 2006–2008 was <30% that of young born on the east side. In addition, autumn recruitment of young during 1997–2008 for west-side females was only 60% that of east-side females. Long-term suppression in recruitment of young in the absence of a difference in adult survival between females occupying summer ranges on opposite sides of the Sierra crest, in conjunction with high fidelity to their summer ranges, indicates that disparity in recruitment of young was the life-history component responsible for the shift in migratory segments of the population. Examples of natural selection bringing about demographic changes in large mammals are rare.

Selective pressures for mule deer overwintering in Round Valley have shifted during the most recent decades to favor animals that reside on the east side of the Sierra crest during summer, ostensibly the result of greater predation on the west side. Populations of black bears throughout California and other western states have increased dramatically in recent decades

(Brown et al. 2009). Abundance estimates of black bears in California have increased nearly 5-fold in the last 3 decades (California Department of Fish and Game 2010), the same period that the proportion of deer migrating to the west side of the Sierra crest declined from nearly >80% to <50%. The proliferation of black bears in the Sierra Nevada may have resulted from expansion of the urban–wildlife interface (Beckmann and Berger 2003) or competitive release associated with elimination of the California grizzly bear in 1922 (Storer and Tevis 1955, Brown et al. 2009). The poor recruitment of young despite greater nutritional potential on the west side of the Sierra crest indicates that high mortality of young caused by bear predation is limiting that migratory segment of the population.

Although migration generally is presumed to be a favorable strategy (Fryxell et al. 1988), the interplay between intensity of predation and nutritional gain can determine trajectories for different migratory segments of a population (Kaitala et al. 1993, McClure et al. 2005, Middleton et al. 2013a). For example, North American elk obtained forage of 6.5% greater digestibility by migrating to higher elevation during summer than resident elk (Hebblewhite et al. 2008), which resulted in greater pregnancy rates and increased body mass of offspring during midwinter (Hebblewhite and Merrill 2011). Despite the increase in forage quality obtained by migrants, predation risk from gray wolves (*Canis lupus*) during migration was 1.7 times higher than that observed for resident elk. Lower survival of adult females and reduced recruitment of young by migratory elk resulted in a decline in the migratory segment of the population (Hebblewhite and Merrill 2007, 2009). High rates of predation for particular migratory segments of populations that have a greater nutritional potential imply that some mortality is additive if their migratory counterpart is capable of successfully recruiting disproportionately more young while on an inferior nutritional plane.

Carrying Capacity

Carrying capacity (K) in wildlife management is usually defined by the number of animals a range supports at equilibrium (i.e., long-term mean of population abundance; McCullough 1979, Macnab 1985, Kie et al. 2003). In stochastic environments, herbivore populations may rarely, if ever, be at equilibrium with their highly variable food supply (McCullough 1999), which may undermine density-related estimates of K (Macnab 1985, McLeod 1997, Kie et al. 2003), and complicate detection and interpretation of density dependence (Marshal et al. 2009). The absence of a relationship with density does not always imply an absence of density dependence, but may merely be a consequence of a fluctuating food supply. In arid environments, quality and abundance of forage is sensitive to precipitation (Sinclair et al. 1985; Marshal et al. 2005a, b; Pierce et al. 2012) and annual food supply varies markedly relative to the density of the population. Consequently, the position of the population with respect to their food supply varies not by animal density alone, but by the interaction between forage production (a consequence of environmental conditions) and population density (Sinclair et al. 1985, McCullough 1999).

Although many methods have been proposed to estimate K (or other derivations thereof) for large herbivore populations, including Ricker-like models (McCullough 1979), food-based models (Hobbs et al. 1982, Hobbs and Swift 1985, DeYoung et al. 2000, Beck et al. 2006), and time-series models (Boyce 1989, Sæther et al. 2002, Forsyth and Caley 2006, Kaeuffer et al. 2009), all have experienced only limited application to research or management scenarios (Macnab 1985). For most approaches, data collection can be difficult and labor intensive (DeYoung et al. 2000), models are sensitive to precision of population estimates and require long-term estimates of population size (Freckleton et al. 2006, Clark et al. 2010, Knape and de Valpine 2011), and generally perform poorly in variable environments. A method of determining the capacity of habitat to support large herbivores that integrates both animal density and variation in food availability caused by environmental variation, and that is logistically feasible and tangible, is warranted. Such an approach would further our understanding of the interaction between density dependence and environmental variation (Caughley and Gunn 1993), and would be more likely to be applied in research and management of large herbivores.

Piasecke and Bender (2009) presented a new approach for estimating K for North American elk, based on the difference in autumn nutritional condition of lactating versus nonlactating elk, whereby the relative difference indicates the proximity of the population to K. Application of this technique may be limited to some monotocous species, such as elk, in which lactating females can acquire similar fat levels by autumn compared with nonreproductive females when under an adequate nutritional regime (Cook et al. 2004). For polytocous species, reproductive costs can be markedly greater (Sadleir 1982, Tollefson et al. 2010), and timing of mortality of young alters reproductive costs for the nonlactating individuals, thereby affecting the baseline reference of comparisons when determining proximity to K. Nonetheless, the use of nutritional condition is an insightful advance in identifying the proximity of a population to K.

Animal-indicated nutritional carrying capacity.—Because nutritional condition is an integrated measure of previous energetic gains and expenditures experienced by individuals (Parker et al. 2009), forage quality and quantity relative to the density of the population (density dependence) for large herbivores is inherent within that metric. Nutritional condition of a population should signify the relative position of that population to its current food supply, with the food supply being representative of nutritional carrying capacity (NCC). We propose that the relative position of a population to its annual food supply is reflected by, and thus can be determined by, the seasonal patterns of nutritional condition and population performance. We term our approach animal-indicated NCC because nutritional condition is a product of an animal's environment (animal-indicator concept; Franzmann 1985), which is determined by a population's food supply (NCC). We parameterized animal-indicated NCC based upon the nutritional condition of the population when $\lambda = 1$, which is in keeping with the classic definition of K when the population is at (or near) equilibrium with its environment (Caughley 1979). Poor nutritional condition relative to that threshold implies proximity to, or above, NCC when compared with good nutritional condition, which is typical of a population below

NCC, and is indicative of habitat conditions that support population growth.

Nutritional condition during the current March explained 32% of the variation in λ for mule deer in the Sierra Nevada (Fig. 27). An absolute increase in IFBFat of 1 percentage point yielded a predicted increase in λ of 0.06 and the predicted point of animal-indicated NCC (λ = 1) occurred at 6.7% IFBFat. Because nutritional condition is sensitive to forage growth, competition for forage, and carryover from the previous year (Fig. 22), the actual number of individuals that can be supported at animal-indicated NCC during a particular year may vary. This approach does not require the herbivore population to be at equilibrium with its environment and, therefore, should be of value for estimating NCC in stochastic systems.

We admonish that animal-indicated NCC does not represent a long-term equilibrium density that may be referred to as K but, instead, represents the short-term capacity of the environment to support population growth as a function of resource availability and animal density. For example, we observed a mean IFBFat in March near 6.7% when estimated population size was 1,250 animals in 1992 and 2,281 animals in 1998. Water content of snowpack the preceding April was markedly lower for 1992 (15.7 cm), and higher for 1998 (45.7 cm) than the 24-year average (26.3 cm). Differences in habitat conditions as a function of snowpack and browsing pressure the preceding year likely were responsible for the differences in the number of animals the habitat could support at a nutritional level of 6.7% IFBFat, and determined the expected population performance the following year. Carryover effects of life history and nutrition from the previous season affect populations (Harrison et al. 2011), both of which are inherent in estimates of animal-indicated NCC (Fig. 23). Nutritional status at one point in time provides a reference point of nutritional history and nutritional carryover to the following season (Monteith et al. 2013).

Using the long-term mean or historical highs in population size to estimate K can be deceptive when true changes in K have occurred as a result of habitat alteration or changing climate. For example, in Round Valley an alfalfa ranch (approx. 0.36 km²) that was frequented by hundreds of deer on a daily basis during winter was enclosed in the late-1980s. In addition, in June 1995, a fire burned 22 km² (approx. 24%) of primary winter range in an area dominated by bitterbrush and sagebrush in Round Valley. Because of the intensity of the fire, little regrowth of bitterbrush occurred in subsequent years, and the burned area has become dominated by desert peach and cheat grass (*Bromus tectorum*), both of which offer little forage value to deer (Pierce et al. 2004). Based on the nutritional limitation and leveling of the population size that we observed between 1991 and 2009 as the population recovered from the crash in the late 1980s, habitat in Round Valley can no longer support the abundance of deer present in the 1980s (Fig. 5)—a conclusion that would have been far less certain or more speculative without data on nutritional condition. Patterns of nutritional condition were indicative of increased nutritional limitation as the population approached 3,000 animals, indicating that animal-indicated NCC was reached well below the nearly 6,000 animals in 1985 (Fig. 5), and that K has decreased to <2,500 animals. This outcome illustrates the importance of avoiding the use of historical levels of ungulates to

estimate K, and that concluding habitat is not limiting because animal densities are lower than previously documented is poorly justified. These complications reinforce the use of animal-indicated NCC, because that metric directly accounts for changes, whether by habitat alteration or climate, in the nutritional capacity of the habitat.

Predation risk may affect habitat use and foraging efficiency for large herbivores (Bleich et al. 1997, Bleich 1999, Creel and Winnie 2005, Schroeder et al. 2010); however, the links of those non-consumptive effects of predation with prey demography and how non-consumptive effects scale up to influence the ability for large herbivores to make use of available habitats remain uncertain (Lima 2002, Christianson and Creel 2008, Creel and Christianson 2008, White et al. 2011, Middleton et al. 2013b). If predation risk limits the ability of individuals to make complete use of available habitats and reduces foraging efficiency and energetic gain, then nutritional interactions between large herbivores and their habitat may be modified because of the distribution of forage and risky habitat in the presence of large carnivores (Creel and Christianson 2008) or other novel disturbances (Sawyer et al. 2009, Wasser et al. 2011). Regardless, those non-consumptive effects are inherently incorporated in estimates of animal-indicated NCC. We postulate that experiments incorporating in vivo measures of nutritional condition with changes in use of space will provide the best means to directly test risk-effect hypotheses, because the physiological costs can be quantified (White et al. 2011, Middleton et al. 2013b), and models can be developed to account for state-dependent behavior (Monteith et al. 2011, Lendrum et al. 2013) and use of habitat (Morales et al. 2010).

Despite many advantages, an approach incorporating nutritional condition to estimate animal-indicated NCC may be of less value for populations of large herbivores that are maintained at low density by predation or other sources of mortality. Nutrition in those populations is not a major limiting factor; females are in good nutritional condition and population growth is regulated by predation rather than nutrition (Gasaway et al. 1992, Bowyer et al. 2005, Boertje et al. 2007)—much like females residing on the west side of the Sierra crest that experienced heavy and additive predation by black bears (Figs. 9 and 29b). Nutritional condition, however, would reflect potential top-down forcing by predators and the lack of bottom-up forcing, indicating that habitat was not a major limiting factor (Bowyer et al. 2005).

Another potential weakness in the use of nutritional condition to calibrate animal-indicated NCC is the confounding effect of pathogens or other diseases on nutritional condition; prevalence of specific pathogens, parasites, or diseases can have a negative influence on nutritional condition. For example, tick infestations were attributed to nutritional deprivation and eventual death for moose in New Hampshire (Musante et al. 2010). Infections and nutritional status may be interactive because malnutrition can lead to immunosuppression and greater parasitism and disease, whereas pathogens cause tissue damage and have a negative effect on energy balance, resulting in greater nutritional suppression (Gulland 1992, Holmes 1995, Sams et al. 1995, Gunn and Irvine 2003). Knowledge of the nutritional status of the population or individuals relative to other mortality factors

related to disease could provide the inference necessary to disentangle pathological and nutritional limitation, or their synergistic effects, just as it can for patterns of mortality.

Consequences of Mortality

The ultimate causes and consequences of mortality are fundamental questions in population ecology, management, and evolutionary biology (Messier 1994, Metcalf and Pavard 2007, Griffin et al. 2011, Pettorelli et al. 2011, Connelly et al. 2012). In particular, the influence of predation by large carnivores on population dynamics of ungulates has been hotly debated (Ballard et al. 1991, 2001; Boutin 1992; Powell 2001), and remains a controversial topic (Bowyer et al. 2005, 2013; Griffin et al. 2011). Interpreting predator–prey relationships are difficult considering the myriad of factors that influence their dynamics including climate, diversity and abundance of predators and prey, habitat conditions, and nutrition (Van Ballenberghe and Ballard 1994, Linnell et al. 1995, Lima 2002, Sinclair et al. 2003, Griffin et al. 2011, Grovenburg et al. 2012b).

The relative influence of mortality on limiting a prey population is characterized by its additive or compensatory effects on population growth. The concepts underlying the consequences of mortality for prey populations originally were formulated by Errington (1946) based on his observations that prey populations contain a surplus of individuals that are doomed to face mortality each year, which he coined the "doomed surplus." Predation that cuts only into the doomed surplus has no net effect on prey population growth (compensatory mortality), whereas predation taking more than the doomed surplus (additive mortality) results in a prey population maintained at a lower level than would have occurred in the absence of such predation (Errington 1956). Therefore, compensatory mortality operates under the fluxes of density dependence, where a decrease in population density with respect to NCC lessens intraspecific competition for resources resulting in decreased natural mortality rates and, subsequently, the potential for increased survival and reproduction (Boyce et al. 1999). Indeed, differentiating between the proximate and ultimate causes (Mayr 1961) of mortality is necessary to understand the population dynamics of ungulate populations. The killing of an individual results in a numerical change in the population and is thus limiting (Sinclair 1991), but this alone is not very informative and its relative consequence is inextricably linked to the level of density dependence (i.e., nutritional limitation) within the population (Van Ballenberghe and Ballard 1994, Pierce et al. 2012). Nevertheless, the interaction between mortality because of predation or malnutrition is difficult to disentangle without manipulative experiments or other means of assessment (Boutin 1992).

Numerous investigators have confronted the challenge of identifying the relative effects of predation on prey populations by comparing rates of predation or malnutrition, population density, and winter severity among populations or years (Ballard et al. 2001, Barber-Meyer et al. 2008, Boertje et al. 2009, Garrott et al. 2009, White et al. 2010). In these instances, authors often were faced with the challenge of interpreting the consequences of mortality without direct knowledge of the nutritional status of the population. The conclusion that mortality is additive because mortality rates were high compared with other populations or

during another time, or because predation rates remained constant through time without sufficient evidence describing the nutritional status of the population, is potentially erroneous. Interannual variability in environmental conditions, density, carryover effects from previous seasons, and potential changes in NCC, make temporal and between-population comparisons of mortality rates and their consequences tenuous (Kie et al. 2003).

Another approach used to distinguish additive versus compensatory mortality that has experienced increased use in recent years (Griffin et al. 2011, Brodie et al. 2013, Johnson et al. 2013) is to regress rates of mortality caused by predation against overall survival rates. Predation rates that correlate negatively with survival rates are assumed to be additive (Anderson and Burnham 1976, Schaub and Lebreton 2004); but when predation is compensatory, no relationship is expected between predation and survival. Although this method is novel and seemingly intuitive, the basis for distinguishing differences in the consequences of specific mortality causes is circular, because survival rate is inherently an artifact of mortality (i.e., predation) rate and, thus, may be of value only for demonstrating which proximate mortality factors are driving survival rate. Furthermore, vulnerability to predation is influenced by individual variability in the vitality and size of prey, and prowess and size of the predator (Fitzgibbon and Fanshawe 1989, Kunkel et al. 1999, Husseman et al. 2003, Sinclair et al. 2003, Barber-Meyer et al. 2008), which may dictate the likelihood that a specific predator could have an additive effect on a prey population, but does not imply that predation was additive (Errington 1946, 1956, 1967).

Some advances have been made in elucidating the relative influence of these ecological processes (Burnham and Anderson 1984, Bowyer et al. 2005, Servanty et al. 2010), but little progress has been made regarding a quantitative approach to characterize compensatory versus additive mortality for large ungulates. Failure to recognize the underlying mechanism dictating the population-level consequences of mortality likely has hampered progress in this field, yet that underlying mechanism has been identified in experimental studies.

Bartmann et al. (1992) evaluated effects of coyote predation on survival of young mule deer by manipulating the presence of predators. The proportion of animals lost to predation simply replaced those lost to malnutrition when predators were absent. The study emphasized that the number of individuals lost to malnutrition (often used to reference compensatory mortality) was not a good reference to the consequences of mortality, which is a common fallacy in predator–prey studies. Malnutrition is an obvious consequence of nutritional limitation in the absence of predators; however, in the presence of large carnivores, losses to malnutrition can be replaced by predation, thereby clouding interpretation of the underlying effects of mortality. Tveraa et al. (2003) monitored survival of neonatal reindeer after being released at approximately 5 weeks of age from a predator-free enclosure following mild and severe winters. High losses of young to predators occurred following the severe winter when females were food limited. In contrast, after the mild winter, when females were in markedly better physical condition, no loss to predation occurred (Tveraa et al. 2003). Loss of young to predation in both studies was

conditional upon nutrition—the underlying factor dictating the consequences of mortality.

We propose that the consequences of mortality, regardless of the cause, can be determined based on an assessment of the nutritional capacity for survival and reproduction. In predation-regulated systems, the nutritional capacity for survival or recruitment is greater than what is observed (Fig. 4), compared with resource-regulated systems where nutritional capacity for survival or recruitment is similar to that observed. As populations approach NCC, females attempt to produce more young than the habitat can support (McCullough 1979); that is, the nutritional capacity to recruit young is less than what females attempt to recruit (Fig. 4). The difference between those values indicates the amount of mortality that is potentially compensatory. Mortality that reduces recruitment to the nutritional potential in any 1 year is compensatory, with greater mortality transitioning toward having an additive effect on recruitment (Fig. 4). Resource availability and density are inherently linked to determine nutritional condition, and dictate the nutritional capacity for adults to survive and for females to produce and rear young. Therefore, estimating the nutritional capacity for survival or recruitment should provide a reference for the degree to which mortality is compensatory or additive relative to observed survival and recruitment. Indeed, studies have demonstrated positive effects of predator removal for ungulate populations that were not resource-limited (i.e.,those in which predation had an additive effect; Gasaway et al. 1983, Kie and White 1985, Gasaway et al. 1992, Hegel et al. 2010b, White et al. 2010), compared with those that were resource-limited when predator removal had little effect (i.e., those in which predation was compensatory; Bartmann et al. 1992, Ballard et al. 2001, White et al. 2010, Hurley et al. 2011).

Adult survival.—Life-history theory and empirical evidence for long-lived ungulates indicate that females should favor their own survival over reproductive allocation, which results in adult survival being relatively insensitive to resource limitation (Unsworth et al. 1999, Eberhardt 2002, Bonenfant et al. 2009). Nonetheless, during rare conditions such as extreme drought (Bender et al. 2007, Pierce et al. 2012) or severe winter conditions (DelGiudice et al. 2006), adult mortality may be constrained by nutritional deprivation as a result of reductions in NCC. During the severe drought in Round Valley in the late 1980s, estimated adult survival of female mule deer was the demographic largely responsible for the population crash (Pierce et al. 2012); however, that change in vital rate was underpinned by severe nutritional deprivation likely caused by an overshoot of NCC. Therefore, mortality of adult females during the population crash was largely compensatory, because fewer animals could be supported following the reduction in food supply (Pierce et al. 2012). Following the population crash, adult survival was high and relatively consistent with modest influences of forage availability on survival (Table 8).

Survival of young.—Survival and recruitment of young are typically highly variable, and sensitive to nutritional limitation and the maternal capacity to support reproduction (Gaillard et al. 1998, 2000; Eberhardt 2002). Because female ungulates rely on nutritional capital and income to support reproductive allocation (which influences survival of young), accounting for variation attributable to nutrition while removing other external factors not related to nutrition in predictive models should yield the nutritional potential for recruitment of young. Interannual patterns in the young-to-adult female ratio in the Sierra Nevada closely mirrored that expected based on the nutritional state of the population, indicating that from 1992 to 2009, mortality of young at the level of the population was mostly compensatory (Fig. 28). Contrasting patterns of autumn recruitment of young emerged when we compared the 2 migratory segments within the mule deer population wintering in Round Valley. Observed recruitment was mostly compensatory for females that summered on the east side of the Sierra crest, whereas recruitment of young by west-side females often was less than what should have been possible based on their nutritional capacity to provision young (Fig. 29). Mortality of young that had a large additive component (0.30 young per female per year) for females that occupied the west side of the Sierra crest supports the hypothesis that changes in predation, mostly by black bears, were responsible for the shift in the proportion of migratory segments within the population of mule deer wintering in Round Valley in recent decades (Fig. 3).

The influence of bear predation on survival of neonatal ungulates has been emphasized in a number of recent studies (Linnell et al. 1995, Bowyer et al. 1998a, Zager and Beecham 2006, Barber-Meyer et al. 2008, Griffin et al. 2011, Middleton et al. 2013c). Bears specialize on neonates during the period of greatest vulnerability within the first few weeks of life (Fig. 9b; White et al. 2010, Griffin et al. 2011). Consequently, among large carnivores, bears have been proposed to have the greatest potential to affect dynamics of ungulate populations, because vulnerability of neonates may not strongly reflect nutrition at that age (Barber-Meyer et al. 2008, White et al. 2010). Although greater nutritional limitation within a population will inherently result in an increase in the proportion of prey predisposed to mortality, viewing compensatory versus additive mortality as a function of the vulnerability of individual prey—especially neonates—is misleading because the true consequences of mortality are based on the nutritional capacity of the habitat. Documenting that predation by a particular predator seems to be unaffected by the condition of prey indicates the potential for that predator to have an additive effect, but does not imply that all deaths because of predation were additive. Mortality of neonates on one side of the Sierra crest was partially additive (Fig. 29b), whereas mortality of neonates on the other side was largely compensatory (Fig. 29a).

Our approach for assessing the consequences of mortality on a population provides a simple, yet sensitive, measure for determining whether recruitment patterns of young are limited purely by nutrition (i.e., mortality is compensatory), or if other extrinsic factors such as predation are having a partially additive effect on mortality. We recognize that model predictions were determined from field data and, thus, may not reflect the true nutritional capacity to support young when predation or other extrinsic factors interact to influence the potential for survival and reproduction (Fischhoff et al. 2007, Christianson and Creel 2010, Hegel et al. 2010b). Placing individuals on an identical nutritional regime in captivity would likely yield higher recruitment, because young exhibiting poor growth and vigor may survive in captivity, but be predisposed to predation where

predators occur. Nonetheless, the interaction among nutrition, weather, and predation in a natural system should reveal the nutritional capacity to recruit young in light of other competing risks, and should provide a conservative and realistic estimate of the nutritional ability of females to recruit young.

We caution that attempts to conclude whether mortality is purely additive or purely compensatory are likely misguided. Purely additive mortality would only occur when the population is in superb nutritional condition (i.e., density well below NCC), and mortality would be purely compensatory only when nutrition is limiting and mortality rates do not exceed the nutritional potential for survival and reproduction (e.g., east-side females; Fig. 29a). Between those 2 endpoints, however, mortality up to a certain point (depending on the proximity to NCC) is compensatory, with higher levels of mortality becoming increasingly additive (Fig. 4). For mule deer in Round Valley during 1997–2008, in no single year was all mortality additive given the nutritional limitation that we observed (Fig. 29) but, instead, was compensatory to a specific level of mortality and transitioned to being additive when levels of mortality forced recruitment below what was nutritionally achievable. This pattern of compensatory versus additive mortality is in accordance with that proposed in conceptual models by others (McCullough 1979, Kie et al. 2003, Bowyer et al. 2005), and indicates that compensatory and additive mortality should be viewed as more of a continuum rather than as a dichotomy, because both processes can occur within a single year and population.

We recognize that patterns of recruitment of young may not be as sensitive to nutritional condition for all species or systems. The approach proposed herein should work well for species that rely heavily on current capital to support reproduction such as bighorn sheep (Festa-Bianchet 1998), moose (Testa and Adams 1998, Keech et al. 2000), or North American elk and red deer (Landete-Castillejos et al. 2003, Cook et al. 2004). Nevertheless, for more income-based breeders, incorporating variables that describe the nutritional capacity of females to support reproduction such as timing and rate of spring green up (Pettorelli et al. 2007, Post et al. 2008), population density (Andersen et al. 2000), spring and summer precipitation (Marshal et al. 2005a, b; Lomas and Bender 2007; Tollefson et al. 2011), or other climatic factors (Albon et al. 1983a) may provide the information necessary to explain the variation in recruitment patterns caused by nutrition. Moreover, factors such as density or winter severity could be incorporated into models for overwinter survival of young, and be used to explain variation caused by interactions of forage availability with severe weather (Bartmann et al. 1992, White and Bartmann 1998, Hurley et al. 2011). Additionally, an absence of a relationship between nutritional condition and patterns of recruitment for a capital breeder could be indicative of strong top-down forcing. Such forcing should result in ungulate populations held well below NCC. Therefore, nutritional condition would be high and not strongly related to recruitment, because high rates of predation, despite good nutrition, would limit annual recruitment.

MANAGEMENT IMPLICATIONS

Monitoring programs for large herbivores often seek to determine population trajectory, or total population size to interpret effects of harvest, predation, and other factors that might be limiting or regulating populations, because animal abundance is usually considered the minimal information necessary for management. Nonetheless, estimating population size of large herbivores that occupy broad geographic regions with reasonable precision and accuracy is difficult and often cost-prohibitive (Jachmann 2002, Morellet et al. 2007). Attempts frequently are made to interpret time-series data of population size; however, pattern-oriented analyses of those data are limited in their ability to detect factors underlying population dynamics (Coulson et al. 2000). Moreover, estimates of population density alone provide no inference about the relationship between population and habitat (i.e., proximity to NCC), yet understanding that relationship is critically important to informed management of large herbivores. Management of large herbivores may be improved if resources invested in monitoring programs are aimed at variables of greater ecological relevance than simple estimates of abundance (Morellet et al. 2007).

Empirical estimates of vital rates that underpin population trajectories provide important information regarding the dynamics of ungulate populations, but are difficult and costly to obtain, and require monitoring for multiple years (Lebreton et al. 1992, White and Lubow 2002, Johnson et al. 2010). Much like abundance estimates, data on vital rates also lack a mechanistic foundation. Morellet et al. (2007) called for the use of appropriate ecological indicators to assess the response of animals to their habitat, thereby providing a quantitative basis for management decisions. Dale and Beyeler (2001) noted that useful ecological indicators should be measured easily, be sensitive to factors affecting the system, respond in a predictable manner, be anticipatory, predict changes that can direct management actions, be integrative, and have a consistent response to system changes. We propose that nutritional condition is the most insightful ecological indicator for research, management, and understanding population dynamics of large herbivores. Nutritional condition can be accurately quantified by both in vivo and post-mortem measures (Stephenson et al. 1998, 2002; Cook et al. 2010); is sensitive to and responds in a predictable manner to density-dependent availability of forage, habitat conditions, and individual life-history traits; holds predictive value for future performance (including λ) in populations regulated by bottom-up factors; is an integrative measure of the current nutritional state of the population when viewed at the population level; and incorporates previous nutritional gains and debts relative to life history at the individual level (Table 11).

Combining data on nutritional condition with routine monitoring data such as recruitment patterns of young and occasional abundance estimates should provide greater insight to interpret factors underpinning population growth and, thus, allow for empirically driven management. Using a nutritional approach to monitor and manage populations reduces the need to estimate population abundance or set goals according to population size. Alternatively, management goals can be set according to measures of nutritional condition and the proximity of a population to animal-indicated NCC.

We recommend monitoring nutritional condition and population density over a period of years, depending upon the

fluctuations in population size and conditions, to uniquely define the relationship between λ, population size, and nutritional condition. When funds to cover such an expense are unavailable, animal condition could be determined from harvested females (as long as seasonality is recognized) or with small capture efforts each year or every few years. Implementing special antlerless hunts, with required examination of harvested animals for data acquisition, would provide valuable data on nutritional condition at minimal cost, while simultaneously allowing increased recreational opportunity and the opportunity for stakeholders to be involved with data collection. Those data could be used to understand the nutritional status of the population relative to relationships or expectations that have been established in other studies for that species and, at a minimum, should indicate the potential degree of bottom-up forcing within the population (Bowyer et al. 2005). Those few data also would yield expectations for population growth in subsequent years, and anticipated effects of management strategies.

Because nutritional condition indicates the position of a population relative to animal-indicated NCC, harvest criteria can be based on a desired nutritional level as indexed by measures of nutritional condition. For example, a realistic goal with respect to incorporating female harvest for mule deer in Round Valley could be one of reducing density to lower competition for resources and maintain a mean IFBFat level of approximately 7%, which was near animal-indicated NCC for mule deer in that population (Fig. 27). Reducing density with respect to NCC would result in improved nutritional condition and increased recruitment of young, especially for females summering on the east side of the Sierra crest. Improved nutritional condition also could result in less variable population dynamics because the population would potentially be better buffered against environmental perturbations (Kie et al. 2003).

We caution that immediately adjusting harvest in response to changing nutritional status in a stochastic environment may be problematic, because animal-indicated NCC represents the short-term capacity of the habitat and is thus, sensitive to environmental variation. An emphasis on more long-term goals of the proximity to animal-indicated NCC is a more reasonable strategy for density-dependent species, where the harvest determines the surplus because of feedbacks of enhanced nutrition and younger age structure with reduced population size relative to NCC (Leopold 1933, McCullough 1979, Boyce et al. 1999). The position of a population relative to animal-indicated NCC can fluctuate from year to year in response to environmental variation, which is beyond the control of managers unless densities are reduced in an attempt to improve nutritional condition and reduce the influence of massive fluctuations in food supply. We recommend parameterizing where the population is with respect to animal-indicated NCC, and examining how the proximity of the population to animal-indicated NCC responds to various levels of harvest.

Evidence of additive mortality often is used as a justification for predator control to increase ungulate populations (Ballard et al. 2001), which highlights the need to interpret the consequences of mortality correctly. We offer a new approach for quantifying the influence of predation on large ungulate populations by assessing the degree of compensatory or additive mortality based on the nutritional capacity to produce and provision young. From a management perspective, if nearly all mortality is compensatory, and thus is a function of interannual patterns of nutrition, then predator control would yield little change in population performance (Ballard et al. 2001, Hurley et al. 2011). In those situations, management efforts should focus on strategies to enhance nutrition, such as habitat improvements or density reductions (McCullough 1979, Bishop et al. 2009).

The combined effects of anthropogenic and climate-induced changes in habitat for mule deer may have reduced K of mule deer range throughout western North America, thereby affecting population trends through nutritionally mediated reductions in recruitment of young. We suggest that incorporating indices of nutritional condition (i.e., estimates of body fat) into current monitoring and research programs holds the greatest potential for disentangling the relative effects of habitat alteration, climate, and predation on the population dynamics of mule deer and other large herbivores. Moreover, linking habitat use and selection with change in nutritional condition and fitness among seasons will provide a means to quantify the net benefits of particular habitat assemblages or habitat treatments.

SUMMARY

- Our goal was to evaluate the nutritional basis of life-history strategies and population ecology of free-ranging mule deer to aid in the management of large herbivores.
- We obtained longitudinal data on 347 individual females in a population of mule deer in the Sierra Nevada, California, USA, during 1997–2009 as it recovered from a population crash during 1985–1991.
- Survival and recruitment of young was highly variable, and was strongly influenced by nutritional condition at the population level. Maternal nutritional condition had a strong influence on survival and recruitment of young except under intense predation, mostly by black bears, wherein nutritional relationships with probability of survival of young were diluted.
- Summer residency of females affected probability of recruiting young; females that summered on the west side of the Sierra crest recruited fewer young than females summering on the east side, despite better nutrition on the west side. Primary proximate cause of mortality for neonates on the west side was predation by black bears (cause-specific mortality = 0.63), compared with low bear predation on neonates born on the east side of the Sierra crest (0.041).
- Reproduction by yearling females was sensitive to foraging conditions during summer as a function of per capita snowpack (a density-dependent index to annual forage growth) that determined whether yearling females reached sufficient body mass (>41 kg in Mar) to conceive.
- Litter size of adult females ≥2.5 years old was less variable and less sensitive to resource limitation when compared to yearling females, but was influenced moderately by per capita snowpack and summer temperatures, which influenced forage availability.
- Pregnancy of adult females ≥2.5 years old was high and constant (0.98) throughout our study. Adult females failed to exhibit senescent effects on fecundity up to 15.5 years of age.

- Seasonal survival of adult females exhibited minor variation among years with only modest effects of resource limitation. Females exhibited actuarial senescence at >9.5 years of age, but that decline in survival with age was most prominent during winter.
- Nutritional condition of adult females during both winter and summer was sensitive to the nutritional history of individual animals, including forage growth, population density, migratory tactic, reproductive allocation, and nutritional carryover. Nutritional condition of adult females in March also was the most parsimonious predictor for λ during the forthcoming year.
- Nutritional status of a population can provide inferences about the proximity of a population to NCC (termed animal-indicated NCC), even in stochastic environments.
- Partially additive predation, mostly by black bears, was the likely explanation for shifting selective pressures on migratory tactic as individuals migrating to the west side of the Sierra crest declined from 87% of the population in 1985 to <50% by 2005.
- We offer a new approach to assess the consequences of mortality on population dynamics that is based on the nutritional capacity to recruit young. Our approach provides a mechanistic basis for gauging the effectiveness of predator-management programs.
- Our results indicate that management and conservation of large herbivores would be improved by integrating indices of nutritional condition into current monitoring and research programs.

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Appendix A. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of survival of neonatal mule deer from birth to 20 weeks of age evaluated at the population ($n = 119$), individual ($n = 113$), and maternal levels ($n = 73$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero and results were based on $\hat{c} = 1.18$.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	0.98*	0.49	1.47	1.00
	Spring precipitation	0.097	−4.09	4.29	0.28
	Spring temperature	0.023	−5.19	5.24	0.31
	Summer precipitation	−0.033	−4.89	4.82	0.33
	Summer temperature	−0.065	−4.35	4.22	0.33
	Snowpack	2.7×10^{-3}	−0.16	0.17	0.24
	Number female	9.5×10^{-5}	−0.014	0.014	0.26
	Mean March IFBFat	0.013	−2.34	2.37	0.18
	Stage[a]				1.00
	Year				0.02
Individual	Summer residency	0.33	−0.45	1.10	1.00
	Stage[a]				1.00
	Age at capture	0.035	−0.017	0.086	0.49
	Sex	0.062	−0.087	0.21	0.29
	Litter size	2.8×10^{-3}	−0.092	0.087	0.21
	Julian birth	1.7×10^{-3}	-9.1×10^{-3}	5.7×10^{-3}	0.22
	Deviation from mean birth	0.039	-2.8×10^{-3}	0.081	0.68
	Birth mass[b]	0.73*	0.19	1.27	1.00
	Summer residency × birth mass[b]	1.19*	0.61	1.78	1.00
Maternal	Summer residency	−2.19	−4.64	0.24	1.00
	Stage[a]				1.00
	Birth mass[b]	0.25	−0.34	0.85	1.00
	Summer residency × birth mass[b]	1.82*	0.84	2.80	1.00
	Deviation from mean birth	0.024	−0.013	0.061	0.46
	Mar IFBFat[c]	−0.068	−0.46	0.32	1.00
	Summer residency × Mar IFBFat[c]	0.39*	0.089	0.68	1.00
	Age	2.9×10^{-3}	−0.033	0.027	0.27
	Mar body mass	5.1×10^{-3}	−0.012	0.022	0.29

[a] Stage-specific variable that allowed survival to vary during the first 4 weeks, with constant survival the remaining 16 weeks.
[b] Age-specific effect of birth mass on survival during the first 3 weeks of life.
[c] Age-specific effect of March ingesta-free body fat (IFBFat) on survival during 4–20 weeks old.

Appendix B. Model-averaged parameter estimates and Akaike importance weights from an analysis to determine the factors that influence cause of mortality of neonatal mule deer evaluated at the population ($n = 62$), individual ($n = 57$), and maternal levels ($n = 47$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Cause of mortality[a] Bear	Other natural	Other predation	Importance weight
Population	Summer residency	−2.39*	0.50	1.47	1.00
	Per capita snowpack	−37.32	−16.67	7.29	0.47
	Mean Mar IFBFat	0.35	0.042	−0.13	0.24
	Year				0.04
Individual	Summer residency	−2.67	1.91	2.86	1.00
	Litter size	−0.15	−0.011	−0.072	0.10
	Julian birth	0.082	0.11	0.11	0.34
	Sex	0.56	1.35	1.36	0.39
	Age at death	0.26	0.25	0.25	0.64
	Birth mass	2.21*	3.16*	3.30*	1.00
Maternal	Summer residency	−0.041	3.3×10^{-3}	9.0×10^{-3}	0.02
	Age at death	0.19	0.19	0.19	0.45
	Birth mass	1.96*	2.47*	2.44*	0.98
	Age	3.0×10^{-3}	−0.063	0.21	0.61
	Mar IFBFat	−0.41	−0.19	−0.44	0.43
	Mar body mass	0.015	0.017	0.024	0.28

IFBFat, ingesta-free body fat.
[a] Multinomial logistic regression included malnutrition as the reference category thus, parameter estimates represent the relative likelihood of dying from a particular cause compared with malnutrition.

Appendix C. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence birth mass (kg) of neonatal mule deer evaluated at the population ($n = 113$), individual ($n = 113$), and maternal levels ($n = 55$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	0.066	−0.050	0.18	0.40
	Per capita snowpack	−0.13	−0.44	0.70	0.07
	Spring precipitation	1.6×10^{-4}	-8.7×10^{-4}	5.5×10^{-4}	0.01
	Spring temperature	−0.037	−0.11	0.040	0.31
	Mean Mar IFBFat	−0.010	−0.028	8.2×10^{-3}	0.05
	Year				0.00
Individual	Julian birth	1.1×10^{-4}	-4.8×10^{-4}	2.7×10^{-4}	0.02
	Sex	0.083	−0.037	0.20	0.46
	Litter size	−0.21*	−0.37	−0.055	0.82
Maternal	Litter size	−0.37*	−0.60	−0.14	0.93
	Age	-1.3×10^{-3}	-5.5×10^{-3}	2.8×10^{-3}	0.08
	Mar IFBFat	−0.051	−0.010	6.0×10^{-4}	0.56
	Mar body mass	-5.6×10^{-3}	−0.016	3.9×10^{-3}	0.27

IFBFat, ingesta-free body fat.

Appendix D. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence date of parturition of mule deer evaluated at the population ($n = 88$), and maternal levels ($n = 55$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	−4.08*	−7.22	−0.94	0.98
	Per capita snowpack	−31.71	−91.79	28.37	0.47
	Spring precipitation	−0.18	−0.51	0.16	0.35
	Spring temperature	−0.58	−1.80	0.65	0.42
	Mean Mar IFBFat	−0.82	−2.27	0.63	0.51
	Litter size	2.93*	0.74	5.12	0.97
	Year				0.10
Maternal	Summer residency	−5.48*	−8.45	−2.52	1.00
	Mean Mar IFBFat	−1.53	−3.83	0.77	0.88
	Litter size	5.86*	3.10	8.63	1.00
	Age	0.20	−0.15	0.56	0.58
	Mar IFBFat	−0.13	−0.56	0.30	0.56
	Mar body mass	−0.36*	−0.65	−0.073	0.99

IFBFat, ingesta-free body fat.

Appendix E. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence annual age ratios ($n = 17$) evaluated at the population level, Sierra Nevada, California, USA, 1991–2009. Herd composition and population estimates from 1991 to 1996 were obtained from Pierce et al. (2012). We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Mean Mar IFBFat$_{t-1}$	2.28*	1.12	3.53	0.99
Mean Mar IFBFat$_{t}$	3.21*	1.89	4.50	1.00
Mean Mar body mass	−0.41	−1.52	0.70	0.72
Mean litter size	2.89	−27.43	33.22	0.99
Per capita snowpack	44.61	−132.33	221.58	0.78
Summer precipitation	0.29	−1.20	1.78	0.75
Summer temperature	−5.58	−11.41	0.24	0.97

IFBFat, ingesta-free body fat; $t - 1$, previous year; t, current year.

Appendix F. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence autumn recruitment of young for adult (>1 yr) female mule deer evaluated at the population ($n = 578$) and individual levels ($n = 484$), Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

| Level | Parameter | Estimate | 90% CI | | Importance weight |
			Lower	Upper	
Population	Summer residency	0.27*	0.18	0.36	1.00
	Per capita snowpack	5.44	−1.22	12.1	0.96
	Summer precipitation				0.00
	Summer temperature	6.2×10^{-3}	-6.7×10^{-3}	0.019	0.15
	Mean Mar IFBFat	0.090*	0.032	0.15	0.84
	Year				0.00
Individual	Summer residency	0.35*	0.25	0.45	1.00
	Per capita snowpack	2.30	−3.66	8.27	0.88
	Mean Mar IFBFat	0.17	-8.9×10^{-3}	0.043	0.17
	Age	1.2×10^{-3}	-2.5×10^{-3}	4.8×10^{-3}	0.15
	Mar IFBFat	0.025*	3.9×10^{-3}	0.046	0.83
	Litter size	0.12*	9.3×10^{-3}	0.23	0.94
	Mar body mass	7.3×10^{-3}	-3.3×10^{-3}	0.018	0.92

IFBFat, ingesta-free body fat.

Appendix G. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence primiparity of yearling (1.5 yr) female mule deer evaluated at the population ($n = 22$) and individual ($n = 22$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

| Level | Parameter | Estimate | 90% CI | | Importance weight |
			Lower	Upper	
Population	Summer residency	−0.54	−6.85	5.77	0.47
	Per capita snowpack	92.86*	3.58	182.12	0.64
	Summer precipitation	0.86	−3.32	5.05	0.32
	Summer temperature	−0.77	−1.99	0.45	0.43
	Mean Mar IFBFat$_{t-1}$[a]	−1.76	−13.86	10.34	0.19
	Mean Mar IFBFat$_{t-2}$[a]	1.31	−8.33	10.95	0.22
	Year				0.00
Individual	Per capita snowpack	11.96	−7.98	31.90	0.09
	Mar IFBFat$_{t-1}$[a]	3.9×10^{-2}	−0.26	0.18	0.30
	Mar body mass$_{t-1}$[a]	0.51*	0.044	0.98	0.91

[a] We used March ingesta-free body fat (IFBFat) and body mass because sample size ($n = 7$) for November was insufficient; $t-1$, previous year; $t-2$, 2 years prior.

Appendix H. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence litter size of adult (≥2 yr) female mule deer evaluated at the population ($n = 803$) and individual ($n = 803$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

| Level | Parameter | Estimate | 90% CI | | Importance weight |
			Lower	Upper	
Population	Summer residency	−0.11*	−0.17	−0.043	0.88
	Per capita snowpack	2.95*	0.96	4.95	1.00
	Summer precipitation	2.6×10^{-5}	-5.8×10^{-5}	1.0×10^{-4}	0.02
	Summer temperature	−0.042	−0.058	-8.1×10^{-3}	0.68
	Mean Nov IFBFat[a]	1.5×10^{-3}	-1.2×10^{-3}	4.3×10^{-3}	0.02
	Year				0.05
Individual	Summer residency	−0.11*	−0.18	-5.0×10^{-2}	0.92
	Per capita snowpack	4.12*	1.98	6.13	0.93
	Summer temperature	−0.031*	−0.062	-1.2×10^{-4}	0.63
	Age	-1.9×10^{-4}	-3.3×10^{-4}	7.1×10^{-4}	0.02
	Age^2	-1.0×10^{-5}	-2.9×10^{-5}	8.8×10^{-5}	0.02
	Nov IFBFat[a]	1.0×10^{-4}	-5.1×10^{-4}	7.2×10^{-4}	0.05
	Nov body mass[a]	1.5×10^{-4}	-3.1×10^{-4}	6.1×10^{-4}	0.04

[a] We obtained results for November ingesta-free body fat (IFBFat) and body mass from a separate set of models using a subset of data ($n = 268$) during 2002–2008.

Appendix I. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of summer (Apr–Oct) survival of adult (>1 yr) female mule deer evaluated at the population ($n = 944$) and individual ($n = 830$) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	0.070	−0.086	0.23	0.33
	Montly precipitation	-6.6×10^{-3}	−0.028	0.014	0.19
	Monthly temperature	−0.30	−0.65	.060	0.44
	Snowpack	0.011^*	1.2×10^{-3}	0.020	0.72
	Number female	$-2.7 \times 10^{-3*}$	-3.9×10^{-3}	-1.5×10^{-3}	0.94
	Mean Mar IFBFat	0.18	-6.9×10^{-4}	0.36	0.66
	Month				0.42
	Year				0.06
Individual	Snowpack	0.014^*	2.4×10^{-3}	0.025	0.80
	Number female	$-2.3 \times 10^{-3*}$	-3.7×10^{-3}	-8.5×10^{-4}	0.98
	Mean Mar IFBFat	0.26^*	0.036	0.49	0.79
	Age	-0.60^*	−1.10	−0.11	1.00
	Age^2	0.023	-4.7×10^{-3}	0.052	1.00
	Mar IFBFat	9.7×10^{-3}	−0.025	0.045	0.29
	Mar body mass	0.043	−0.099	0.19	0.28
	Litter size	−0.046	−0.18	0.092	0.29

IFBFat, ingesta-free body fat.

Appendix J. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of winter (Nov–Mar) survival of adult (>1 yr) female mule deer evaluated at the population ($n = 1,037$) and individual level ($n = 574$), Sierra Nevada, California, USA, 1998–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	5.4×10^{-3}	−0.10	0.12	0.27
	Monthly precipitation	0.031	−0.025	0.087	0.43
	Monthly temperature	0.10	−0.011	0.21	0.47
	Per capita snowpack	50.72^*	21.37	80.12	1.00
	Mean Nov IFBFat[a]	0.083	−0.080	0.25	0.41
	Month				0.97
	Year				0.01
Individual	Per capita snowpack	31.54^*	1.89	61.08	0.74
	Age	-0.24^*	−0.34	−0.15	1.00
	Nov IFBFat[a]	3.4×10^{-3}	−0.016	0.022	0.19
	Nov body mass[a]	0.064^*	0.015	0.11	0.86
	Recruitment status[a]	−0.041	−0.16	0.077	0.31
	Month				1.00

[a] We obtained results for November ingesta-free body fat (IFBFat), November body mass, and recruitment status from a separate set of models using a subset of data ($n = 334$) during 2002–2008.

Appendix K. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in March evaluated at the population ($n = 842$) and individual ($n = 531$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	−0.50*	−0.73	−0.26	1.00
	Per capita snowpack	45.23*	30.69	59.77	1.00
	Winter temperature	0.050	−0.013	0.030	0.29
	Mean Mar IFBFat$_{t-1}$	0.51*	0.36	0.66	1.00
	Winter precipitation	−0.28*	−0.35	−0.21	1.00
	Year				0.00
Individual	Summer residency	−0.018	−0.24	0.20	0.43
	Per capita snowpack	33.07	−2.54	68.67	0.99
	Mean Mar IFBFat$_{t-1}$	0.74*	0.26	1.26	0.95
	Winter precipitation	−0.15*	−0.27	−0.018	0.71
	Age	−0.16*	−0.24	−0.079	0.96
	Litter size	0.56*	0.17	0.96	1.00
	Mar IFBFat$_{t-1}$	0.033	−0.017	0.081	0.28
	Nov IFBFat$_{t-1}$[a]	0.14*	0.088	0.20	1.00

[a] We obtained results for November IFBFat of the previous year from a separate set of models using a subset of data ($n = 215$) during 2002–2008.

Appendix L. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence body mass (kg) of adult (>1 yr) female mule deer in March evaluated at the population ($n = 828$) and individual ($n = 517$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	−1.00*	−1.81	−0.19	0.92
	Per capita snowpack	2.19	−7.48	11.87	0.32
	Winter temperature	0.67*	0.37	0.96	0.99
	Mean Mar IFBFat$_{t-1}$	0.011	−0.094	0.12	0.33
	Year				0.00
Individual	Summer residency	−1.11*	−1.87	−0.35	0.96
	Winter temperature	0.24*	0.018	0.47	0.74
	Age	2.70*	2.22	3.19	1.00
	Age^2	−0.15*	−0.18	−0.11	1.00
	Mar IFBFat	0.30*	0.19	0.40	1.00

IFBFat, ingesta-free body fat, $t-1$, previous year.

Appendix M. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November evaluated at the population ($n = 359$) and individual ($n = 249$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	−2.35*	−3.22	−1.48	1.00
	Per capita snowpack	78.53*	14.16	142.89	1.00
	Summer precipitation	0.087*	0.012	0.16	0.69
	Summer temperature	−0.030	−0.23	0.16	0.42
	Mean Mar IFBFat	0.27	−0.12	0.65	0.64
	Year				0.00
Individual	Summer residency	−1.97*	−2.84	−1.11	1.00
	Per capita snowpack	132.38*	71.54	193.22	1.00
	Summer precipitation	0.037	−0.016	0.092	0.37
	Mean Mar IFBFat	0.89*	0.28	1.5	0.94
	Age	−0.030	−0.18	0.13	1.00
	Mar IFBFat	0.10	−0.027	0.23	0.51
	Litter size	−0.24	−0.93	0.45	1.00
	Recruitment status	−2.81*	−3.43	−2.20	1.00

Appendix N. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence body mass (kg) of adult (>1 yr) female mule deer in November evaluated at the population ($n = 330$) and individual ($n = 253$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Population	Summer residency	−2.75*	−4.15	−1.33	1.00
	Per capita snowpack	6.98	−30.61	44.57	0.49
	Summer precipitation	0.37*	0.27	0.47	1.00
	Summer temperature	−0.61*	−1.11	−0.12	0.88
	Mean Mar IFBFat	−0.55	−1.13	0.039	0.79
	Year				0.00
Individual	Summer residency	−2.72*	−4.27	−1.16	1.00
	Summer precipitation	0.27*	0.15	0.39	0.99
	Summer temperature	−0.36	−0.86	0.14	0.69
	Mean Mar IFBFat	0.13	−0.11	0.37	1.00
	Age	1.93*	0.80	3.06	1.00
	Age^2	−0.084*	−0.15	−0.016	1.00
	Nov IFBFat	0.37*	0.22	0.52	1.00
	Recruitment status	−0.81	−1.71	0.079	1.00

IFBFat, ingesta-free body fat.

Appendix O. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence population growth (lambda; $n = 17$) evaluated at the population level, Sierra Nevada, California, USA, 1991–2009. Herd composition and population estimates from 1991 to 1996 were obtained from Pierce et al. (2012). We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Response	Parameter	Estimate	90% CI Lower	90% CI Upper	Importance weight
Lambda	Mean Mar IFBFat$_{t-1}$	1.4×10^{-4}	-2.0×10^{-4}	2.2×10^{-3}	0.07
	Mean Mar IFBFat$_t$	0.043*	0.013	0.075	0.79
	Mean Mar mass	5.5×10^{-4}	-1.7×10^{-3}	2.8×10^{-3}	0.07
	Per capita snowpack				0.00
	Summer precipitation	1.3×10^{-3}	-2.9×10^{-3}	5.6×10^{-3}	0.10
	Summer temperature	-5.9×10^{-4}	−0.016	0.015	0.18
	Young ratio	1.7×10^{-4}	-1.9×10^{-4}	5.3×10^{-4}	0.03

IFBFat, ingesta-free body fat; $t-1$, previous year; t, current year.

Photograph looking south on winter range for mule deer (*Odocoileus hemionus*) in Round Valley with Mount Tom in the distance demarking the western edge of Round Valley and the eastern edge of the Sierra Nevada, California, USA, where the Great Basin Desert begins. Note the fire lines evident at the base of Mount Tom from a fire that burned approximately 24% of the winter range in June 1995. Photo by Kevin L. Monteith.

A biologist processes twin mule deer (*Odocoileus hemionus*) recently born to a radiocollared adult female in the Sierra Nevada, California, USA. Photo by Ryan A. Long.

Biologists conduct aerial telemetry for radiocollared mule deer (*Odocoileus hemionus*) along the east side of the Sierra crest in November 2008 after a recent snowstorm. Note the Sierra crest at the horizon line and the notable rainshadow caused by the Sierra Nevada. Photo by Kevin L. Monteith.

Female mule deer (*Odocoileus hemionus*) being transported to a central staging area for processing in Round Valley, California, USA. Photo by Tim Glenner.

Mule deer (*Odocoileus hemionus*) on winter range in Round Valley, California, USA. Photo by Thomas R. Stephenson.