

Effects of predation and forage availability on the survival of black-tailed deer (*Odocoileus hemionus columbianus*) in the Mendocino National Forest, California

By

TAVIS DONAHUE FORRESTER

B.S. (Oregon State University) 1999

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Heiko U. Wittmer, Assistant Adjunct Professor, Wildlife, Fish, and Conservation Biology

Douglas A. Kelt, Professor, Wildlife, Fish, and Conservation Biology

Andy Sih, Professor, Professor, Environmental Science and Policy

Andrew M. Latimer, Associate Professor, Plant Sciences

Committee in Charge

2014

I. Title Page

**EFFECTS OF PREDATION AND FORAGE AVAILABILITY ON THE SURVIVAL OF
BLACK-TAILED DEER (*ODOCOILEUS HEMIONUS COLUMBIANUS*) IN THE
MENDOCINO NATIONAL FOREST, CALIFORNIA**



Tavis Forrester, 2014

Graduate Group in Ecology

Department of Wildlife, Fish, and Conservation Biology

University of California, Davis

One Shields Ave, Davis, CA 95616

Table of Contents

II. Acknowledgements	v
Thesis dedication	vii
III. Abstract.....	viii
IV. Introduction.....	xi
V. Chapter 1: A review of the population dynamics of mule deer and black-tailed deer (<i>Odocoileus hemionus</i>) in North America	1
Table 1.1	37
Table 1.2	39
Table 1.3	40
Table 1.4	41
Figure 1.1	42
Figure 1.2	43
Figure 1.3	44
Figure 1.4	45
VI. Chapter 2: Forage availability modifies predation risk of black-tailed deer fawns..	46
Table 2.1	78
Table 2.2	79
Table 2.3	80
Table 2.4	81
Figure 2.1	82
Figure 2.2	83
Figure 2.3	84

Appendix 2.1	85
Table A2.1.....	87
Table A2.2.....	88
Table A2.3.....	89
VII. Chapter 3: Home sweet home: Fitness consequences of site familiarity in black-tailed deer	90
Table 3.1	116
Table 3.2	117
Table 3.3	118
Figure 3.1	119
Figure 3.2	120
Appendix 3.1	121
Table A3.1.....	123
VIII. Summary	124

II. Acknowledgements

Thanks to my advisor Dr. Heiko Wittmer for working with me all these years. We had our ups and downs, but we came out the other end with a damn fine deer study and a professional working relationship. I am sure I caused him many gray hairs as I dragged myself into camp late in the evening after long mortality retrievals and as I dragged myself through the writing of this thesis. I would also like to thank the faculty who took the time to make sure I succeeded during my time at UC Davis, since the world of academia was not a natural fit for me. Thanks to Debbie Elliot-Fisk for getting me into graduate school, for sharing her passion for teaching and mentoring undergraduates, and for understanding when I switched projects. Thanks to Mark Schwartz for the Conservation Management Program and for actively encouraging me to work in conservation after academia. Thank you to John Eadie, Malcolm North, Doug Kelt, and Sharon Lawler for your encouragement and support over the years.

Thank you to David Casady at the California Department of Fish and Game (now the California Department of Fish and Wildlife) for getting this study off the ground, for capturing most of the adult deer in the study, and for mentoring me in field biology. Another round of thanks to everyone else at CDFW who helped us with deer capture and other logistics of field work. A special thanks to my field crews, especially Bryn Evans, Carlos Figuera, Clara Laursen, Ryan Carrothers, Lukas Rinnhofer, Irvin Huang, Sophie Quisquater, and Brian Williams. Field camp would not have been the same without you, and I look back fondly on our time in the Mendo wilderness.

A large thank you to my friends who supported me during my time at UC Davis, particularly Jeremiah Mann. Without his support, friendship, and unwavering ability to see the silver lining in all things I would have not made it through this process. Thank you to my fellow

graduate students in the 2008 ecology cohort; from the Odyssey through the end it was great to share this journey with you all. A heaping round of thanks to the men of the Mankind Project of Northern California for keeping me out of my head and connected with my heart while all my training in graduate school was pulling me in the opposite direction.

Funding for this project was generously provided by the California Department of Fish and Game (now the California Department of Fish and Wildlife), the California Deer Association, the UC Davis Graduate Group in Ecology, the Jastro Shields Research Award, the Stockton Sportsman's Club, and the Robert and Patricia Switzer Foundation. Thank you for your support.

This thesis is dedicated to my family, and particularly to my wife Jennifer Forrester. She dealt with my long absences for field work with grace and love, kept the family together in my absence, and helped keep me sane as I finished this thesis while being a father and working full-time. This Ph.D. would not have occurred without her, and it is as much her success as mine. I dedicate this thesis to her, and to Zea, Bodie, and little Milo. I hope that at the end of it all I will look back and know that I have saved a few of the wild places that I have known and loved for my children.

III. Abstract

Mule (*Odocoileus hemionus*) and black-tailed deer (*O. h. columbianus*) have exhibited marked population fluctuations throughout their range over the past century. The relative contributions of predation, forage availability, and weather to observed population changes remain unclear and controversial. I evaluated the effects of both predation and forage on the survival of mule and black-tailed deer through a literature review and extensive field research in the Mendocino National Forest from 2009-2013. I reviewed 48 studies on mule deer survival and predation from the past 30 years and quantified age-specific vital rates, population growth rates (λ) and causes of mortality. I also evaluated the effect of environmental variables on variation in vital rates and the contribution of age-specific survival to population growth. Age-specific survival (ϕ) was the most frequently studied population parameter. Mule deer have lower and more variable fawn survival than other ungulate species ($\phi_{\text{summer}}=0.44$, $CV=0.42$; $\phi_{\text{annual}}=0.29$, $CV=0.67$). Adult female survival conversely appeared to be high and stable throughout the geographical range of the species ($\phi_{\text{annual}}=0.84$, $CV=0.06$). Observed low fawn survival appears to be compensated for by high fecundity rates. Predation was the primary proximate cause of mortality for all age classes, and was an important source of summer fawn mortality and of mortality in multi-prey, multi-predator systems. However, predator removal studies suggest that predation is compensatory, particularly at high deer densities, and that nutrition and weather shape population dynamics. I propose three models to explain local population dynamics of mule deer: a) populations are limited by forage availability and weather; b) adult females are limited by forage availability, fawns are limited by forage availability and predation, and population growth is constrained by fecundity and fawn predation; and c) large changes in the abundance of predators or alternative prey change predation risk and destabilize population dynamics. From 2009 to

2013, I led field crews that captured and monitored 135 black-tailed deer fawns in coastal California to study possible interactions between forage and predation on survival. I estimated seasonal and annual survival rates, assessed the cause of all mortalities ($n=95$), measured available forage, estimated relative abundances of predators on summer range (i.e., fawning areas) each year, and used remote sensing to quantify habitat on winter range. I then used cumulative incidence and proportional hazards functions to evaluate how environmental covariates were related to fawn survival. Summer survival rates averaged 0.40 across all years ($SE=0.05$) and the mean annual survival rate was 0.25 ($SE=0.04$). I found that most fawn mortality resulted from predation during summer, mainly by black bears (*Ursus americanus*) and coyotes (*Canis latrans*), and spatial differences in summer survival persisted until recruitment. Black bear predation, the single largest cause of mortality, was unrelated to forage availability. Observed spatial variation in mortality risk due to other causes was linked to the availability of oak forage but not predator abundance. Additionally, characteristics of deer including adult female condition and fawn birthweight, did not provide evidence for purely bottom-up limitation. Rather my results provided evidence that both bottom-up and top-down effects were influencing fawn survival in this declining population, and that predator identity and the timing of mortality affected these interactions. I also tracked 57 adult female black-tailed deer using GPS collars and radio-telemetry to determine seasonal movements and home ranges and monitor survival and cause of mortality. I used the seasonal home range as a measure of site familiarity and modeled how mortality risk varied with use of familiar areas, forage availability, age class, and elevational overlap with simultaneously collared pumas using Cox proportional hazards models. Adult female survival was low in our study area (0.70 vs. 0.84 species average), and predation was the largest cause of mortality. The use of familiar areas was the best predictor of mortality

risk, and deer that had a 40% chance of leaving the home range in a given week were 4 times more likely to die. Puma predation was the largest cause of mortality and deer whose average weekly elevation was farther from the average elevation of pumas were less likely to die. While forage availability was not related to mortality risk, adult females with lower forage availability were more likely to leave their home range in both summer and winter. I found fitness benefits of using familiar areas and bottom-up effects on the use of familiar areas as a refuge from predation. The benefits of site familiarity are likely widespread in ungulates, especially when there are stable home ranges, complex habitats, and unclear cues of predation risk. My results provide evidence that both bottom-up and top-down effects were influencing black-tailed deer survival in this declining population, and that predator identity, the timing of mortality, and individual behavior affected these interactions.

IV. Introduction

It may seem strange that in the 21st century graduate theses are still being written about the shy and graceful black-tailed deer (*Odocoileus hemionus columbianus*). We know most of what is to be known about the natural history of the species (Wallmo 1981), yet state wildlife agencies and private foundations continue to demand and fund more research on the species. The continuing demand is both a testament to the mysteries that remain in even well-studied species (e.g. unexplained population fluctuations) (Ballard et al. 2001, Conover and deVos 2003), and to the rich and storied history of people and deer in North America.

That history is almost as old as the history of people on this continent. The first people that crossed from Asia into North America found a rich and diverse community of mammals that included the ancestral form of the black-tailed deer, at the time quietly living in obscurity as an uncommon herbivore in an ecosystem dominated by mega fauna (Geist 1998). The arrival of humans either caused or coincided with extinctions of most of the large mammals through a combination of climate change, overhunting, and the use of large-scale fires by the newly arrived hunter-gatherers (Martin 1967, Grayson and Meltzer 2003). The ancestral *Odocoileus* species took advantage of the new ecological landscape and rapidly expanded to become one of the most important game animals for indigenous people, rivaled only by the large salmon runs that filled the coastal streams and rivers (Wallmo 1981, Geist 1998).

The importance of black-tailed deer, and the newly evolved mule deer (*Odocoileus hemionus hemionus*) (Geist 1998), as game animals had a profound effect on the landscapes of the western USA. Indigenous people burned large areas to create ideal forage for deer, elk (*Cervus canadensis*), and other game, as well as to maintain preferred plant species and to facilitate easy travel (Williams 2000, Kimmerer and Lake 2001, Anderson 2005). Many of the

open habitats that colonizing Europeans saw as wilderness naturally teeming with game were in fact created and maintained by indigenous fire (Williams 2000), particularly in what would become the state of California (Anderson 2005).

The strong relationship between people and deer continued with the European colonists that arrived in North America and hunted the abundant deer for subsistence (Wallmo 1981). Unfortunately, by the 1800's the establishment of cities with a large demand for meat and hides gave rise to the widespread practice of market hunting, or killing wild game to sell. Market hunters decimated deer populations across the country (as well as bison and passenger pigeons) to feed the burgeoning urban populations (Hornaday 1913), including deer in California (Longhurst et al. 1952). The shocking decline of wildlife led to the passage of several laws that underpin the North American model of wildlife management (Hornaday 1913, Geist 1988), and catalyzed the beginning of a scientific approach to wildlife management. By the middle of the 20th century deer populations had expanded and a new science was born (Leopold 1933, Leopold et al. 1947).

The science of wildlife management owes much to the relationship between people and deer, but the relationship with predators was very different. Early wildlife managers advocated the widespread eradication of predators in order to enhance game populations (Hornaday 1913), although this view was quickly challenged (Elton 1927, Leopold 1933). The controversy about the role of predation in ungulate ecology ran deep and endures today (Ballard et al. 2001, Ripple et al. 2014). The intensity of this debate can only be understood in the context of the long-standing relationship between people and deer, and what deer and deer hunting represent to the public (Nelson 1998). It is my hope that my research is of some use in this debate and for

understanding the role, and possible importance, of predators in the tangled web of ungulate ecology.

A Brief History of Ungulate Ecology

The debate around the role of predators and food in the population fluctuations of ungulates is mainly focused on what factors ultimately set the size of an ungulate population (Sinclair and Pech 1996, Sinclair 2003). The terms limiting and regulating have been used in this debate in many different ways, and here I follow Sinclair and Pech (1996) and refer to the factors that set the equilibrium density of animals as limiting factors and the processes that return a population to the equilibrium point as regulation. Limiting factors can be both density dependent and density independent while regulating processes are always density dependent (Sinclair and Pech 1996).

The father of animal ecology, Charles Elton, speculated that removing wolves would unleash large herds of deer that would decimate the vegetation of their range (Elton 1927), an idea formalized and promoted by Aldo Leopold (Leopold 1943). Elton and Leopold did not necessarily think that deer were held far below the populations that forage could support, but that once predators were removed density dependent feedbacks would be insufficient to reduce the deer population before they had over browsed the area (Elton 1927, Leopold 1943). The famous “the world is green” hypothesis followed that posited that since the world around us was filled with vegetation, predators must be holding herbivores in check (Hairston et al. 1960). Evidence for and against this theory accumulated, and through vigorous debate a tentative consensus emerged that interactions between both bottom-up and top-down forces shape the dynamics of a given herbivore population (Hunter and Price 1992, Sinclair et al. 2003, Hopcraft et al. 2010).

Long-term research in ungulates has shown that the effects of predation and forage change depending on ungulate body size, the diversity of the predator community, and how underlying environmental gradients (e.g. soil nutrients and rainfall) affect forage quality and quantity (McNaughton et al. 1989, Radloff and Du Toit 2004, Hopcraft et al. 2010). Body size is one of the most important variables in the interactions of forage and predation (Sinclair et al. 2003, Hopcraft et al. 2010). Smaller ungulates require higher quality forage because of their smaller digestive systems (Clauss and Hummel 2005) and are vulnerable to more predators than larger ungulates (Radloff and Du Toit 2004). Predation pressure on small-bodied prey is also higher in communities where large predators select all sizes of prey (size-nested predation) versus communities where predators select only a certain size class (size-partitioned predation) (Radloff and Du Toit 2004). Finally, differences in soil nutrients and rainfall affect both the quantity and quality of forage (Hopcraft et al. 2010).

Predation and forage also affect ungulates differently depending on their age class. Ungulates are characterized by high and constant adult survival and variable fawn survival (Gaillard et al. 1998). Adult survival has a higher elasticity than fawn survival, but because adult survival is typically stable the variability in fawn survival has more influence on ungulate dynamics (Gaillard et al. 1998, 2000). Fawns are also vulnerable to a larger number of predators than adults (Linnell et al. 1995) while forage availability has strong effects on fawns through both maternal nutrition and fawn body growth during their first summer (Parker et al. 2009).

Understanding ungulate ecology requires placing top-down and bottom-up effects and interactions in the context of age-specific survival. Predation, forage availability, and weather affect separate age-classes of ungulates differently and may interact to produce synergistic effects (Pierce et al. 2012, Monteith et al. 2014). This thesis is an attempt to examine the effects

of both predation and forage availability in the context of age-structured survival for the black-tailed deer population of the Mendocino National Forest.

Study Area and Species Assemblage

The Mendocino National Forest lies within the California coastal mountains north of Clear Lake and south of the Trinity River, and is characterized by rugged terrain, sharp elevation gradients, and a diversity of habitat types. Plant communities change from oak savannah (*Quercus* spp.) and dense chaparral at low elevations, to pine (*Pinus* spp.) forests at mid-elevations, and a mix of true fir forests (*Abies* spp.) and scattered dry and wet meadows on the ridge tops. Each habitat type is a mosaic of open areas and dense young forests created by past grazing, logging, or wildfire.

The area supports a large population of black-tailed deer and has been one of the premier public access hunting areas in the state of California. This population is also one of the oldest and least interbred populations of black-tailed deer, likely because the area was a glacial refugia and is isolated from mule deer populations (Latch et al. 2009). Black-tailed deer are the only resident ungulate, although there are nearby populations of tule elk (*Cervus canadensis nannodes*). The area supports a diversity of predators, including mountain lions (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), and fishers (*Martes pennanti*). There were also abundant populations of other prey species including black-tailed jackrabbits (*Lepus californicus*), California ground squirrels (*Otospermophilus beecheyi*), and *Microtus* and *Peromyscus* rodent species.

Hunters and wildlife managers are concerned that this population of black-tailed deer has been declining for decades, pointing to declining harvest rates since the 1980's (Booth et al.

1982). The black-tailed deer population has been historically high in the area, and was identified as an overpopulated deer range in the 1940's (Leopold et al. 1947) and the 1970's (Longhurst et al. 1976) before the current decline. The latest population decline is unexplained by managers but has triggered another round of controversy over the role of predators, specifically mountain lions, in limiting deer populations (Ballard et al. 2001).

Chapter Summaries

Chapter 1 summarizes what is known about mule and black-tailed deer survival and population dynamics, including the effects of predation and forage availability. I summarize information on age-specific vital rates, cause of mortality, and population growth. My primary objectives in this chapter are to place mule and black-tailed deer vital rates and the effects of predation within the general patterns of ungulate population dynamics. In chapter 2, I analyze the effects of predator abundance and forage availability on the temporal and spatial patterns of fawn survival. I also compare the fawn survival patterns with characteristics of the deer population that typically indicate predation or forage limitation. Lastly, in chapter 3 I explore the effects of site familiarity on the survival of adult females, including how use of familiar areas affected predation risk and how forage availability affected the probability of deer leaving their seasonal home range and using higher risk areas.

Literature Cited

- Anderson, M. K. 2005. *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources*. University of California Press.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos. 2001. Deer-predator relationships: A review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99–115.

- Booth, J., P. Yull, and L. Murray. 1982. Mendocino Deer Herd Management Plan. California Department of Fish and Game.
- Clauss, M., and J. Hummel. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. *Mammal Review* 35:174–187.
- Conover, M. R., and J. C. deVos, editors. 2003. Mule Deer Conservation: Issues and Management Strategies. Jack H. Berryman Institute, Logan, Utah.
- Elton, C. S. 1927. *Animal Ecology*. University Of Chicago Press, Chicago.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Geist, V. 1988. How Markets in Wildlife Meat and Parts, and the Sale of Hunting Privileges, Jeopardize Wildlife Conservation. *Conservation Biology* 2:15–26.
- Geist, V. 1998. *Deer of the World: Their Evolution, Behaviour, and Ecology*. Stackpole Books.
- Grayson, D. K., and D. J. Meltzer. 2003. A requiem for North American overkill. *Journal of Archaeological Science* 30:585–593.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. *The American Naturalist* 94:421–425.
- Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25:119–128.

- Hornaday, W. T. 1913. *Our Vanishing Wild Life: Its Extermination and Preservation*. C. Scribner's sons.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders : heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Kimmerer, R. W., and F. K. Lake. 2001. The Role of Indigenous Burning in Land Management. *Journal of Forestry* 99:36–41.
- Latch, E. K., J. R. Heffelfinger, J. A. Fike, and O. E. RHODES Jr. 2009. Species-wide phylogeography of North American mule deer (*Odocoileus hemionus*): cryptic glacial refugia and postglacial recolonization. *Molecular Ecology* 18:1730–1745.
- Leopold, A. 1933. *Game Management*. University of Wisconsin Press, Madison, Wis.
- Leopold, A. 1943. Deer Irruptions. *Publ. Wis. Conserv. Dep.* 351–366.
- Leopold, A., L. K. Sowls, and D. L. Spencer. 1947. A Survey of Over-Populated Deer Ranges in the United States. *The Journal of Wildlife Management* 11:162–177.
- Linnell, J. D., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1:209–223.
- Longhurst, W. M., E. O. Garton, H. F. Heady, and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. *Transactions of the Western Section of the Wildlife Society* 12:1–41.
- Longhurst, W. M., A. S. Leopold, and R. F. Dasmann. 1952. A survey of California Deer Herds : their ranges and management problems. *Game bulletin;no. 6, State of California, Dept. of Fish and Game, [Sacramento]*.
- Martin, P. S. 1967. Pleistocene overkill. *Natural History* 76:32–38.

- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Nelson, R. 1998. *Heart and Blood: Living with Deer in America*. First Vintage Departures Edition edition. Vintage.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57–69.
- Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *Journal of Mammalogy* 93:977–988.
- Radloff, F. G. T., and J. T. Du Toit. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* 73:410–423.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Sinclair, A. R. E. 2003. Mammal Population Regulation, Keystone Processes and Ecosystem Dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358:1729–1740.

- Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425:288–290.
- Sinclair, A. R. E., and R. P. Pech. 1996. Density Dependence, Stochasticity, Compensation and Predator Regulation. *Oikos* 75:164–173.
- Wallmo, O. C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.
- Williams, G. W. 2000. Introduction to aboriginal fire use in North America. *Fire Management Today* 60:8–11.

V. Chapter 1: A review of the population dynamics of mule deer and black-tailed deer (*Odocoileus hemionus*) in North America

Tavis D. FORRESTER *Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, California 95616, USA.*

Heiko U. WITTMER *Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, California 95616, USA. (Currently School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand)*

ABSTRACT

- 1 Mule deer and black-tailed deer *Odocoileus hemionus* have exhibited marked population fluctuations throughout their range over the past century. The relative contributions of predation, forage availability, and weather to observed population changes remain unclear and controversial.
- 2 We reviewed 48 studies on *Odocoileus hemionus* survival and predation from the past 30 years and quantified age-specific vital rates, population growth rates (λ) and causes of mortality. We also evaluated the effect of environmental variables on variation in vital rates and the contribution of age-specific survival to population growth.
- 3 Age-specific survival (ϕ) was the most frequently studied population parameter. *Odocoileus hemionus* have lower and more variable fawn survival than other ungulate species ($\phi_{\text{summer}}=0.44$, CV=0.42; $\phi_{\text{annual}}=0.29$, CV=0.67). Adult female survival conversely appeared to be high and stable throughout the geographical range of the species ($\phi_{\text{annual}}=0.84$, CV=0.06). Observed low fawn survival appears to be compensated for by

high fecundity rates.

- 4 Predation was the primary proximate cause of mortality for all age classes, and was an important source of summer fawn mortality and of mortality in multi-prey, multi-predator systems. However, predator removal studies suggest that predation is compensatory, particularly at high deer densities, and that nutrition and weather shape population dynamics.
- 5 We propose three models to explain local population dynamics of *Odocoileus hemionus*: a) populations are limited by forage availability and weather; b) adult females are limited by forage availability, fawns are limited by forage availability and predation, and population growth is constrained by fecundity and fawn predation; and c) large changes in the abundance of predators or alternative prey change predation risk and destabilize population dynamics.
- 6 Future research should be focused on: the effects of age-specific survival on population growth; possible interactions between predation, forage availability, and weather; and the importance of multiple predator and prey species in shaping the population dynamics of *Odocoileus hemionus*.

Key words: bottom-up top-down, predation-forage interactions, weather effects, alternate prey, carrying capacity

INTRODUCTION

Population dynamics of ungulates are complex, and how predation and resource

availability affect observed growth rates has long been a focus of much debate (Peek 1980, Gaillard et al. 2000, Sinclair & Krebs 2002). The effect of predation on ungulate dynamics is particularly controversial (Gaillard et al. 1998, 2000), especially in North America where ungulates are important game animals still coexisting with native predators, and where managers face demands to maintain high population densities (Connolly 1978). While early studies of ungulate populations were based on competing hypotheses of bottom-up effects caused by food limitation versus top-down effects from predation (Connolly 1978, Peek 1980), it is now acknowledged that both bottom-up and top-down mechanisms simultaneously affect ungulate dynamics and often interact (Sinclair & Krebs 2002, Sinclair 2003). The interactions between forage and predation are also likely to be mediated by environmental conditions such as weather (Hopcraft et al. 2010). Finally, ungulate body size and the diversity of both predator and prey communities are also critical factors. For example, ungulate size simultaneously affects predation risk and nutritional demands (Hopcraft et al. 2010), and small-bodied ungulates in Africa tend to have more predators and higher predation rates than do larger ungulates (Sinclair et al. 2003).

To understand mechanisms underlying observed demographic variation caused by predation, resources, and environmental conditions requires identifying temporal changes in age-specific vital rates caused by these factors, as well as the relative contributions of vital rates to population growth (Gaillard et al. 1998, 2000, 2010). Ungulate populations typically are characterized by high and stable survival rates of prime aged females, moderately variable fecundity rates, widely variable fawn survival, and lower survival and fecundity in senescent adults (Gaillard et al. 1998, 2000). In addition, population models have shown that population growth is affected by both variability and elasticity of vital

rates, and variable fawn survival typically has a larger effect on population change than stable adult survival (Gaillard et al. 1998). However, because of the high elasticity of adult survival, small changes in adult survival can have large effects on population growth. Senescent adults generally have lower survival and fecundity, but the degree of variation in and causes of the reductions are poorly understood (Loison et al. 1999) although declines in body mass with age are the most likely explanation for observed reductions (Nussey et al. 2011).

Despite these recent theoretical advances, observed temporal variations in many ungulate populations remain unpredictable and poorly understood. For example, mule deer *Odocoileus hemionus*, including Columbian black-tailed deer *Odocoileus hemionus columbianus* and Sitka black-tailed deer *Odocoileus hemionus sitkensis* (hereafter referred to together as mule deer, or as black-tailed deer if referring to individual subspecies commonly called black-tailed deer), have exhibited large population fluctuations throughout their range in the last century (Connolly 1978, Wallmo 1981, Unsworth et al. 1999). These mid-sized members of the deer family indigenous to western North America occur in ecosystems ranging from deserts to coastal rain forests. Efforts to explain observed population fluctuations have focused on habitat conditions, although the effect of predation has received considerable attention and generated the most controversy (Connolly 1978, Ballard et al. 2001). The focus on habitat and predation across a range of environmental variables has resulted in a large array of differing explanations for observed population fluctuations, including habitat changes caused by changing weather and land use, as well as suspected high predation rates (Connolly 1978, 1981, Ballard et al. 2001).

Uncertainty concerning the relative contributions of predation, forage, and

environmental conditions to mule deer population fluctuations has caused challenges for the management of the species (Heffelfinger & Messmer 2003). We reviewed studies on mule deer survival and predation published in the past 30 years, and quantified age-specific vital rates, population growth rates (λ) and causes of mortality. We highlight data needed to predict mule deer population dynamics more accurately and thus improve both management and conservation. We used this information to test the following hypotheses: 1) age-specific vital rates for mule deer, specifically high and stable adult survival and low and variable fawn survival, are similar to those reported for other ungulates; 2) predation is the dominant cause of mule deer fawn mortality in summer but is replaced by poor nutrition in winter; 3) predation and poor nutrition are equal causes of mortality in adult females; 4) age-specific interactions between predation and nutrition drive mule deer dynamics.

METHODS

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

We used Web of Knowledge and Google Scholar to search all major wildlife and ecological journals using the search terms 'mule deer', 'black-tailed deer' and '*Odocoileus*

hemionus' combined with the keywords 'predation' and 'survival', in both topics and titles. We also searched references of published articles to find additional publications, including government reports and unpublished theses. We included all studies in which survival rates (ϕ), fecundity, cause-specific mortality, population growth rate, kill rates or prey nutritional condition were reported (Figure 1, Table 1). Following earlier authors (Ballard et al. 2001) we excluded predator diet studies, as these do not provide sufficient data to evaluate the effect of predation on prey populations.

Definitions

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

Following Sinclair (1989) and Messier (1991) we refer to regulation as the density-dependent processes that move a population toward equilibrium, and limitation as any factor that causes a reduction in population growth rate. We define fecundity as the average number of young per female per year; high snowfall as occurring in a winter with snowfall greater than the upper tail of the 99% confidence interval of a 15-year mean; and summer drought as occurring in a summer with rainfall lower than the 99% confidence

interval of the 15-year mean. We chose the 15-year timeframe due to data availability.

Survival

We searched the literature for age-specific survival estimates. We included studies in which survival rates were reported from marked animals as well as those in which estimates were based on herd composition surveys. We included results from observational studies and from non-manipulated populations in experimental studies for summaries of survival estimates. We did not include male survival since mule deer have a polygynous mating system and fluctuations in male survival do not affect population dynamics nearly as much as fluctuations in female survival (Wallmo 1981, Gaillard et al. 1998). Furthermore, mule deer sexes segregate outside the mating season (Bowyer 2004). Thus winter and summer competition for food and ensuing changes to female body condition are primarily results of intraspecific competition among females.

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

We summarized fawn survival independent of sex in three different categories: summer survival (0-6 months of age), winter survival (6-12 months), and first year survival (0-12 months). These categories allowed us to evaluate proximate causes of mortality during biologically critical periods (Wallmo 1981, Gaillard et al. 2000). Most researchers reported survival in one or more of these categories. When average monthly survival rates

were reported instead, we used a Kaplan-Meier estimator (Pollock et al 1989) to adjust these rates to match the most appropriate of our three fawn survival categories. We only included first year survival rates from studies in which fawns were followed for their entire first year of life. We report weighted means and SE for each category using the same methods as for adult survival. If rates were reported in a single study from more than one category (e.g. summer and first year survival) we used both for summary purposes.

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

Ecoregional variation in survival

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

Other vital rates

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

Factors affecting survival

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

predation and malnutrition/disease while accounting for variation due to other and unknown causes of mortality.

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

We evaluated the potential effect of weather on survival by testing both regional and local weather effects. The mean value of the southern oscillation index is correlated with regional weather patterns in the western United States (Stenseth et al. 2003). We used simple linear regression to compare the summer (June-September), winter (December-March), and annual mean southern oscillation index values with all reported fawn summer, winter and annual adult female survival, and to evaluate the relationship between regional weather and mule deer survival. We also compared annual adult female and fawn overwinter survival during winters with high snowfall to survival during normal winters in the same study areas using local weather data. We obtained weather data, for all studies in which extreme weather was reported, from National Oceanic and Atmospheric Administration weather stations. We did not examine the effects of summer drought, because survival during drought years was quantified in few studies. We report the effect size of winter weather on survival, the reduction in survival during high snowfall winters $E_{h\phi}$ as: $E_{h\phi} = \bar{f}_i - \bar{f}_{avg}$ where ϕ_i is the study-specific survival for high snowfall winters, and ϕ_{avg} is the mean survival during normal weather in that study. We then calculated the

weighted mean effect size for each category using study sample size as the weighting variable. We determined confidence intervals of effect size, after confirming survival data were normally distributed, using the mean SE of survival estimates from each study. We tested if the effect size of high snowfall winters was different from zero using a one-sample mean comparison test. To examine any potential lag effects of high snowfall, we also tested the difference between survival the year after a high snowfall winter and average survival. We examined effect size for bias across studies by regressing calculated effect size against sample size and the length of the study in years (Cooper et al. 2009). If periodic high snowfall winters have a biological effect, then longer and larger sample sizes should show increased effects, but if winter weather effects are due to sampling error, then longer and larger sample studies should show a reduced effect size. All statistical tests were conducted in Stata (Statcorp 2011).

Population growth rates

We report population growth rates from studies in which it was estimated. For studies in which changes in deer densities over multiple years were reported, we estimated λ in two ways: as the slope of the regression of the log transformed counts, and as the t^{th} root of the

ratio of the initial and the final count, $\lambda = \sqrt[t]{\frac{N_t}{N_0}}$ where N_t equals population size in the last

year of the study, N_0 equals population size in the first year of the study and t is the duration of the study in years (Largo et al. 2008). When these estimates were different we took the average of the two values. We also report results from studies in which the contribution of adult and fawn survival to λ was calculated.

RESULTS

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

Survival and factors affecting survival

Fawn survival was the most frequently studied parameter of mule deer ecology ($n=22$, Table 1). However, not all data were based on encounter histories of individuals fitted with telemetry devices (summer: $n=10$ of 11 studies; winter: $n=12$ of 12; first year: $n=5$ of 7). The weighted mean summer fawn survival was 0.44 (CV=0.42), winter survival was 0.61 (CV=0.31), and first year survival was 0.29 (CV=0.67; Table 2).

Sample size did not explain a large proportion of variance in reported summer or winter fawn survival ($R^2=0.06$ and $R^2=0.08$, respectively). However, a large proportion of variance in first year fawn survival was explained by sample size ($R^2=0.85$): first year survival was low in studies with large sample sizes. Estimates of first year fawn survival may have been biased low due to the small number of studies from which data were available.

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

Adult female survival was the second most frequently studied parameter of mule deer ecology in the studies we reviewed ($n=21$, Table 1); the weighted mean adult female annual survival was 0.84 ($CV=0.06$). Adult female survival estimates were remarkably constant throughout the entire mule deer range and over the 30 plus years of mule deer research we summarized. Sample sizes and study durations explained little of the reported

variation in adult female survival ($R^2=0.09$ and $R^2=0.01$, respectively) and did not appear to bias reported survival estimates.

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

Weather effects on mule deer survival depended on age class. High winter snowfall effect sizes for adult females were heavily correlated with sample size and study length ($R^2=0.42$ and $R^2=0.33$, respectively): larger studies that ran for more years showed reduced effect sizes. Consequently we did not report adult effect sizes since it is highly likely that results are biased. Effect sizes of winter fawn survival showed no relationship with sample size ($R^2<0.01$) or study length ($R^2=0.11$). Regional weather patterns, as indicated by southern oscillation index values, were not related to summer ($R^2<0.01$) or winter fawn survival ($R^2=0.07$). However, local snowfall had a large impact on overwinter fawn survival. The weighted mean effect size of high snowfall on winter fawn survival was -0.29 ($SE=0.06$) and was significantly different from 0 (one sample $t_7=-11.33$, $p<0.001$). Fawn survival was reduced by up to 42% during high snowfall winters (Figure 4). To evaluate whether high snowfall enhanced subsequent summer forage, we compared fawn winter survival the year after high snowfall winters with average winter survival for the same area.

We found that the weighted mean effect size was not significantly different from zero (one sample $t_7=1.17$, $p=0.28$).

Other vital rates and senescence

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

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

Population growth

Population growth rates were reported in only eight studies, and the weighted mean value of λ was 0.99 (SE=0.04). In five of these studies, effects of variation in age-specific survival on λ were also estimated. In four studies, fawn survival and recruitment were the largest contributors to changes in λ (Hatter & Janz 1994, White & Bartmann 1998, Lomas & Bender 2007, Bishop et al. 2009); in one study, adult survival had the largest effect on λ (Robinson et al. 2002). Hatter and Janz (1994) and Bishop et al. (2009) also found that adult survival was an important secondary factor in changes in population growth.

Experimental studies

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

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

Supplemental feeding during winter over large areas resulted in decreased mortality due to all causes, including predation, even though there was no evidence that

predators were preying on mule deer in poor condition in control areas (Bishop et al. 2009).

DISCUSSION

Mule deer population dynamics match the general pattern of variable fawn survival and recruitment together with high and stable adult survival reported for other ungulates (Gaillard et al. 1998, 2000). However, results from our review indicate that mule deer may experience comparatively lower (mule deer=0.44 vs. other ungulates=0.64) and more variable (mule deer CV=0.42 vs. other ungulates CV=0.27) summer fawn survival (Gaillard et al. 2000). Higher observed fecundity rates (1.70 in mule deer vs. 0.82 for all ungulates) apparently enable mule deer to compensate for reduced summer fawn survival over longer time scales. As expected, observed variation in adult female survival (CV=0.06) is considerably lower than variation in fawn survival, and is close to the mean variation in adult survival for all ungulates (CV=0.09). Thus our results indicate that mule deer may depend more than other ungulates on high fecundity and on high and stable survival of adult females to prevent long-term population declines.

The contribution of environmental variables to vital rates is affected by population density (Kie et al. 2003), and it is important to note that most studies we reviewed seemingly occurred at high density relative to nutritional carrying capacity (K). This assessment is supported by general poor or average body condition of adults, an increase in survival after density reduction (i.e. Bartmann et al. 1992a), compensatory predation (Table 4), and low reporting of high litter sizes (Kie et al. 2003). Therefore, our conclusions predominantly

relate to high-density populations, since both predation and nutrition have different effects at different populations densities. In particular, predation at low ungulate densities can be density dependent or even inversely density dependent. At higher densities, predation is often limited by handling time and predator territoriality, and so becomes density independent (e.g. Messier 1991, Bartmann et al. 1992a, Sinclair 2003, McLellan et al. 2010).

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

Nutrition further influences mule deer dynamics since fecundity and fawn birth weight are driven by nutritional status (Parker et al. 2009). Mule deer seem to depend on higher fecundity to stabilize populations, and populations are likely to be sensitive to changes in

available nutrition and have a higher intrinsic growth rate than populations of most other ungulates in good nutritional condition, because of the ability of mule deer to give birth to twins and triplets (Anderson 1981). Mule deer are highly selective feeders that depend on forage quality more than quantity (Wallmo 1981), and so annual weather effects on vegetation quality should affect year-to-year mule deer dynamics (Parker et al. 2009).

However, while we found evidence of high winter snowfall lowering winter fawn survival, we found no evidence of precipitation affecting survival in the following year, indicating that increases in forage in summers following high snowfall years did not compensate for lower survival in high snowfall winters. We also found that high snowfall only had a small effect on adult female survival, contrary to predictions for high-density populations of deer with relatively poor body condition (Kie et al. 2003). Fecundity was too sparsely reported to examine nutritional effects on birth rates in non-captive populations.

The two notable exceptions to the pattern of compensatory predation mortality were summer fawn mortality and predation in multi-predator, multi-prey systems. Predation is the largest proximate cause of summer fawn mortality, and it is unlikely that early fawn predation is linked to maternal or fawn body condition, since mule deer fawns employ a hiding strategy to escape predators during the first 2-4 weeks following birth (Wallmo 1981). Even fawns with higher birth weights discovered by predators while hiding would thus be unable to escape. Most mule deer populations also coexist with a larger suite of fawn predators (including mountain lions, bobcats, bears, and coyotes) than adult predators. However, the true effect of summer fawn predation on mule deer dynamics is currently hard to identify because few researchers have followed fawns for their entire first year of life (n=5 studies).

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

The importance of mortality from predation, nutrition, and weather depends on both mule deer age class and on the community of predator and prey species, but at this time there is not enough data to evaluate whether these interactions are driving dynamics, and further investigation is needed. Some modelling suggests that predation may exacerbate population declines caused by unfavourable weather (Laundre et al. 2006). In

this case nutrition and weather were the ultimate causes of mortality, and managers should be cautious when assessing populations, because finding additive mortality in a declining deer population is not proof that predation is driving the decline. Weather is likely to interact with predation through behavioural mechanisms. Ungulates in poor body condition take greater risks to forage (Sinclair & Arcese 1995) and prey selection of many predators can be influenced by prey body condition (e.g. Sinclair & Arcese 1995, Krumm et al. 2010) although results depend on predator species (Hornocker 1970, McLellan et al. 2012). Other mechanisms may also be operating, since nutritional supplementation lowered predation mortality even though predators were not selecting nutritionally stressed adults in control populations (Bishop et al. 2009).

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

varying deer population densities needs further investigation.

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

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

Feedback patterns driving mule deer population dynamics

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

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

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

survival that linger through cohort effects (Forchhammer et al. 2001, Coulson et al. 2006).

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

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

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

This pattern is likely to occur where human activities alter the landscape in a way that lowers nutritional carrying capacity (i.e. by development) or changes species interactions

within food webs (e.g. by expanding agriculture resulting in invasion by white-tailed deer). Mule deer are particularly susceptible to any alteration resulting in lower survival of adults (Robinson et al. 2002). Both food web and community composition and the spatial distribution of species are likely to be important in this scenario. In today's rapidly changing world, this pattern will become more important in future.

Recommendations for research

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

- 1) Interactions between predation, forage, and weather need to be studied, and it is highly unlikely that we will develop a predictive understanding of mule deer dynamics without understanding these interactions. The relationship between nutrition, fecundity, and predation risk is particularly interesting because of the high growth potential of mule deer populations.
- 2) Fecundity in free ranging populations is under-reported, and is needed to estimate population growth rates. In most studies we reviewed (20 out of 28), λ was not reported, lowering our ability to measure effects of environmental variables on vital rates and population growth quantitatively.
- 3) Much insight into general ungulate dynamics has come from long-term studies of marked individuals, and long-term mule deer research projects with marked individuals would probably yield substantial insights into population dynamics.

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

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

ACKNOWLEDGMENTS

We acknowledge support from the California Department of Fish and Game (Contract # P0880013), the Robert and Patricia Switzer Foundation Environmental Fellowship program and the UC Davis Graduate Group of Ecology. We thank J.-M. Gaillard, D. Kelt, A. Latimer, A. Sih and two anonymous reviewers for helpful comments on previous versions of this manuscript.

REFERENCES

Anderson AE (1981) Morphological and physiological characteristics. In: Wallmo OC (ed), *Mule and Black-tailed Deer of North America*, 27-97. University of Nebraska Press, Lincoln, Nebraska, USA.

- Atwood TC, Gese EM, Kunkel KE (2007) Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *Journal of Wildlife Management* 71: 1098-1106.
- Atwood TC, Gese EM, Kunkel KE (2009) Spatial partitioning of predation risk in a multiple predator–multiple prey system. *Journal of Wildlife Management* 73: 876-884.
- Ballard W, Lutz D, Keegan T, Carpenter L, Devos Jr J (2001) Deer predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29: 99-115.
- Bartmann RM, White GC, Carpenter LH (1992a) Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121: 3-39.
- Bartmann RM, White GC, Carpenter LH (1992b) Compensatory mortality in a Colorado mule deer population: Ridge area density reduction. *Wildlife Monographs* 121: 3-39.
- Bartmann RM, White GC, Carpenter LH (1992c) Compensatory mortality in a Colorado mule deer population: Shale oil tract cb predator removal. *Wildlife Monographs* 121: 3-39.
- Bender LC, Lomas LA, Browning J (2007) Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. *Journal of Wildlife Management* 71: 1118-1124.
- Bishop C J, Unsworth JW, Garton EO (2005) Mule deer survival among adjacent populations in southwestern Idaho. *Journal of Wildlife Management* 69: 311–21.
- Bishop CJ, White GC, Freddy DJ, Watkins BE, Stephenson TR (2009) Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172: 1-28.

- Bleich VC, Taylor T (1998) Survivorship and cause-specific mortality in five populations of mule deer. *Great Basin Naturalist* 58: 265-272.
- Bleich VC, Pierce BM, Jones, JL, Bowyer, RT (2006) Variance in survival of young mule deer in the Sierra Nevada, California. *California Fish and Game* 92: 24–38.
- Bowyer RT, Kie JG, Ballenberghe VV (1998) Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* 79: 415-425.
- Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* 85:1039-1052.
- Brown DE (2009) *Effects of Coyote Removal on Pronghorn and Mule Deer Populations in Wyoming*. MSc Thesis, Utah State University, Logan, Utah, USA.
- Connolly GE (1978) Predators and predator control. In: Schmidt JL, Gilbert DL (eds) *Big Game of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Connolly GE (1981) Limiting factors and population regulation. In: Wallmo OC (ed), *Mule and Black-tailed Deer of North America*, 245-285. University of Nebraska Press, Lincoln, Nebraska, USA.
- Cooley HS, Robinson HS, Wielgus RB, Lambert CS (2008) Cougar prey selection in a white-tailed deer and mule deer community. *Journal of Wildlife Management* 72: 99-106.
- Cooper H, Hedges LV, Valentine JC (eds; 2009) *The Handbook of Research Synthesis and Meta-analysis*, 2nd Ed. Russell Sage Foundation, New York, New York, USA.
- Coulson T, Benton TG, Lundberg P, Dall SRX, Kendall BE, Gaillard JM (2006) Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society B: Biological Sciences* 273: 547-555.

- Cox M, Lutz DW, Wasley T, Fleming M, Compton BB, Keegan T et al. (2009) *Habitat Guidelines for Mule Deer: Intermountain West Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.
- Darimont CT, Paquet PC, Reimchen TE (2007) Stable isotopic niche predicts fitness of prey in a wolf-deer system. *Biological Journal of the Linnean Society* 90: 125-137.
- Farmer CJ, Person DK, Bowyer RT (2006) Risk factors and mortality of black-tailed deer in a managed forest landscape . *Journal of Wildlife Management* 70: 1403-1415.
- Forchhammer MC, Clutton-Brock TH, Lindstrom J, Albon SD (2001) Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* 70: 721-729.
- Fox LB, Arsenault AA, Brewer CE, Carpenter LH, Jellison B, Jenks JA et al. (2009) *Habitat Guidelines for Mule Deer: Great Plains Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.
- Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13: 58-63.
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31: 367-393.
- Gaillard JM, Coulson T, Festa-Bianchet M (2010) Demographic processes: Lessons from long-term, individual-based studies. In: Owen-Smith N (ed), *Dynamics of Large Herbivore Populations in Changing Environments*, 201-245. Wiley-Blackwell, West Sussex, UK.

- Hamlin KL, Riley SJ, Pyrah D, Dood AR, Mackie RJ (1984) Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48: 489-499.
- Harrington JL, Conover MR (2007) Does removing coyotes for livestock protection benefit free-ranging ungulates? *Journal of Wildlife Management* 71: 1555-1560.
- Hatter IW (1988) *Effects of Wolf Predation on Recruitment of Black-tailed Deer on Northeastern Vancouver Island*. Wildlife Report no. R-23., British Columbia Ministry of Environment, Victoria, British Columbia, Canada.
- Hatter IW, Janz DW (1994) Apparent demographic changes in black-tailed deer associated with wolf control on northern vancouver island. *Canadian Journal of Zoology* 72: 878-884.
- Hayden JG, Ardt G, Fleming M, Keegan TW, Peek J, Smith TO, Wood A (2008) *Habitat Guidelines for Mule Deer: Northern Forest Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.
- Heffelfinger JR, Messmer TA (2003) Introduction. In: Devos Jr JC, Conover MR, Headrick NE (eds) *Mule Deer Conservation: Issues and Management Strategies*, 1-11. Jack Berryman Institute Press, Logan, Utah, USA.
- Heffelfinger JR, Brewer C, Alcalá-Galvan CH, Hale D, Weybright DL, Wakeling BF, Carpenter LH, Dodd NL (2006) *Habitat Guidelines for Mule Deer: Southwest Deserts Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.

- Hopcraft JGC, Olff H, Sinclair ARE (2010) Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25: 119-128.
- Hornocker MG (1970) An analysis of mountain lion predation upon mule deer and elk in the idaho primitive area. *Wildlife Monographs* 21:3-39.
- Hurley MA, Unsworth JW, Zager P, Hebblewhite M, Garton EO, Montgomery DM, Skalski JR, Maycock CL (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern idaho. *Wildlife Monographs* 178: 1-33.
- Johnson HE, Mills LS, Stephenson TR, Wehausen JD (2010) Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications* 20: 1753-1765.
- Johnstone-Yellin TL, Shipley LA, Myers WL, Robinson HS (2009) To twin or not to twin? Trade-offs in litter size and fawn survival in mule deer. *Journal of Mammalogy* 90: 453-460.
- Kie, JG, Bowyer RT, and Stewart KM (2003) Ungulates in western forests: habitat requirements, population dynamics, and ecosystem processes. In: Zabel CJ, Anthony RG (eds) *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*, 296-340. Cambridge University Press, New York, New York, USA.
- Krumm CE, Conner MM, Hobbs NT, Hunter DO, Miller MW (2010) Mountain lions prey selectively on prion-infected mule deer. *Biology Letters* 6: 209-211.

- Largo E, Gaillard JM, Festa-Bianchet M, Toigo C, Bassano B, Cortot H, et al. (2008) Can ground counts reliably monitor ibex *Capra ibex* populations? *Wildlife Biology* 14:489-499.
- Latch EK, Heffelfinger JR, Fike JA, Rhodes Jr OE (2009) Species-wide phylogeography of North American mule deer (*Odocoileus hemionus*): cryptic glacial refugia and postglacial recolonization. *Molecular Ecology* 18:1730-1745.
- Laundré JW, Hernández L, Clark SG (2006) Impact of puma predation on the decline and recovery of a mule deer population in southeastern Idaho. *Canadian Journal of Zoology* 84: 1555-1565.
- Lawrence RK, Demarais S, Relyea RA, Haskell SP, Ballard WB, Clark TL (2004) Desert mule deer survival in southwest Texas. *Journal of Wildlife Management* 68: 561-569.
- Lingle S (2000) Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer. *Canadian Journal of Zoology* 78: 85-99.
- Lingle S (2002) Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* 83: 2037-2048.
- Lingle S, Pellis SM, Wilson WF (2005) Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. *Journal of Animal Ecology* 74: 1140-1149.
- Lingle S, Feldman A, Boyce MS, Wilson WF (2008) Prey behavior, age-dependent vulnerability, and predation rates. *American Naturalist* 172: 712-725.
- Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M (1999) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80: 2539-2554.

- Lomas LA, Bender LC (2007) Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *Journal of Wildlife Management* 71: 884-894.
- Lukacs PM, White GC, Watkins BE, Kahn RH, Banulis BA, Finley DJ, Holland AA, Martens JA, Vayhinger J (2009) Separating components of variation in survival of mule deer in colorado. *Journal of Wildlife Management* 73: 817-826.
- Mackie RJ, Kie JG, Pac DF, Hamlin KL (2003) Mule deer (*Odocoileus hemionus*). In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild Mammals of North America: Biology, Management, and Conservation*, 889-905. Johns Hopkins University Press, Maryland, USA.
- Matthews PE, Coggins VL (1997) *Movements and Mortality of Mule Deer in the Wallowa Mountains*. Oregon Department of Fish and Game Enterprise, Oregon, USA.
- McConnell BR, Dalke PD (1960) The Cassia deer herd of southern idaho. *Journal of Wildlife Management* 24: 265-271.
- McCorquodale SM (1999) Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. *Journal of Wildlife Management* 63: 861-871.
- McCoy R, Murphie S (2011) Factors affecting the survival of black-tailed deer fawns on the Northwestern Olympic Peninsula, Washington. Makah Tribal Forestry, Neah Bay, Washington, USA.
- McLellan, BN, Serrouya, R, Wittmer, HU, Boutin, S (2010) Predator-mediated Allee effects in multi-prey systems. *Ecology* 91: 286-292.
- McLellan ML, Serrouya R, McLellan BN, Furk K, Heard DC, Wittmer HU (2012) Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia* 169: 853-860.

- McNay RS, Voller JM (1995) Mortality causes and survival estimates for adult female columbian black-tailed deer. *Journal of Wildlife Management* 59: 138-146.
- Messier F (1991) The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology* 60:377-393.
- Miller MW, Swanson HM, Wolfe LL, Quartarone FG, Huwer SL, Southwick CH, Lukacs PM (2008) Lions and prions and deer demise. *PLOS One* 3: e4019.
doi:10.1371/journal.pone.0004019
- Monteith KL, Bleich VC, Stephenson TR, Pierce BM (2010) *Population Dynamics of Mule Deer in the Eastern Sierra Nevada: Implications of Nutritional Condition*. California Department of Fish and Game, Bishop, California, USA.
- Nelson J, Cottam D, Holman EW, Lancaster DJ, McCorquodale S, Person DK (2008) *Habitat Guidelines for Mule Deer: Coastal Forest Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, town, state of publication, USA.
- Nicholson MC, Bowyer RT, Kie JG (1997) Habitat selection and survival of mule deer: Tradeoffs associated with migration. *Journal of Mammalogy* 78: 483-504.
- Nussey DH, Coulson T, Delorme D, Clutton-Brock TH, Pemberton JM, Festa-Bianchet M, Gaillard J-M (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* 92: 1936-1947.
- Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23: 57-69.
- Peek JM (1980) Natural regulation of ungulates (what constitutes a real wilderness?). *Wildlife Society Bulletin* 8: 217-227.

- Peek JM, Dennis B, Hershey T (2002) Predicting population trends of mule deer. *Journal of Wildlife Management* 66: 729-736.
- Pierce BM, Bleich VC, Terry Bowyer R (2000) Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* 81: 462-472.
- Pierce BM, Bowyer RT, Bleich VC (2004) Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management* 68: 533-541.
- Pojar TM, Bowden DC (2004) Neonatal mule deer fawn survival in west-central Colorado. *Journal of Wildlife Management* 68: 550-560.
- Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53: 7-15.
- Robinette WL, Baer CH, Pillmore RE, Knittle CE (1973) Effects of nutritional change on captive mule deer. *Journal of Wildlife Management* 37: 312-326.
- Robinson HS, Wielgus RB, Gwilliam JC (2002) Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Canadian Journal of Zoology* 80: 556-568.
- Sinclair ARE (1989) Population regulation in animals. In: Cherret JM (eds) *Ecological Concepts*, 197-241. Blackwell Publishers, Oxford, UK.
- Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: the serengeti wildebeest. *Ecology*. 76:882-891.
- Sinclair ARE, Krebs CJ (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357: 1221-1231.

- Sinclair ARE (2003) Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358: 1729-1740.
- Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator-prey system. *Nature* 425: 288-290.
- Smith RH, LeCount A (1979) Some factors affecting survival of desert mule deer fawns. *Journal of Wildlife Management* 43: 657-665.
- Sommer ML, Barboza RL, Botta RA, Kleinfelter EB, Schauss ME, Thompson JR (2007) *Habitat Guidelines for Mule Deer: California Woodland Chaparral Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.
- Statacorp 2011. *Stata Statistical Software: Release 12*. StataCorp LP, College Station, Texas, USA.
- Stenseth NC, Ottersen G, Hurrell JW, Mysterud A, Lima M, Chan K-S, Yoccoz NG, Adlandsvik J (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B* 270:2087–2096.
- Tollefson TN, Shipley LA, Myers WL, Keisler DH, Dasgupta N (2010) Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *Journal of Wildlife Management* 74: 974-986.
- Unsworth JW, Pac DF, White GC, Bartmann RM (1999) Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63: 315-326.
- Wallmo OC (1981) *Mule and Black-tailed Deer of North America*. University of Nebraska Press, Lincoln, Nebraska, USA.

Watkins BE, Bishop CJ, Bergman EJ, Bronson A, Hale B, Wakeling BF, Carpenter LH, Lutz DW (2007) *Habitat Guidelines for Mule Deer: Colorado Plateau Shrubland and Forest Ecoregion*. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Tuscon, AZ, USA.

White GC, Garrott RA, Bartmann RM, Carpenter LH, Alldredge AW (1987) Survival of mule deer in northwest Colorado. *Journal of Wildlife Management* 51: 852-859.

White GC, Bartmann RM (1998) Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62: 214-225.

Whittaker DG, Lindzey FG (1999) Effect of coyote predation on early fawn survival in sympatric deer species. *Wildlife Society Bulletin* 27: 256-262.

Wilson DE, Reeder DM (eds, 2005) *Mammal Species of the World: a Taxonomic and Geographic Reference*. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland, USA.

Woods LW, Swift PK, Barr BC, Horzinek MC, Nordhausen RW, Stillian MH, et al. (1996) Systemic adenovirus infection associated with high mortality in mule deer (*Odocoileus hemionus*) in California. *Veterinary Pathology Online* 33: 125-132.

Zager P, Pauley G, Hurley M, White C (2007) *Statewide Ungulate Ecology*. Idaho Dept.of Fish and Game, Boise, Idaho, USA.

Table 1.1 - The 48 studies of mule deer (*Odocoileus hemionus*) population dynamics reviewed, and the vital rates and causes of deer mortality presented in each.

Study	Vital rates reported				Cause of mortality	
	Adult survival	Fawn survival	Fecundity	λ (growth rate)	Cause of mortality	Other data on predation
Atwood et al. 2007						✓
Atwood et al. 2009						✓
Bartmann et al. 1992a+	✓	✓			✓	✓
Bender et al. 2007	✓				✓	
Bishop et al. 2005	✓	✓			✓	
Bishop et al. 2009	✓	✓	✓	✓	✓	✓
Bleich & Taylor 1998	✓				✓	✓
Bleich et al. 2006	✓	✓	✓		✓	
Bowyer et al. 1998						✓
Brown 2009						✓
Cooley et al. 2008						✓
Darimont et al. 2007						✓
Farmer et al. 2006	✓	✓			✓	✓
Hamlin et al. 1984		✓			✓	✓
Harrington & Conover 2007						✓
Hatter 1988		✓	✓		✓	
Hatter & Janz 1994	✓			✓		✓
Hornocker 1970						✓
Hurley et al. 2011	✓	✓	✓		✓	✓
Johnstone-Yellin et al. 2009		✓	✓	✓	✓	
Krumm et al. 2010						✓
Laundre et al. 2006						✓
Lawrence et al. 2004	✓	✓			✓	
Lingle 2000						✓
Lingle 2002						✓
Lingle et al. 2005						✓
Lingle et al. 2008						✓
Lomas & Bender 2007		✓			✓	
Lukacs et al. 2009	✓	✓				

Matthews & Coggins 1997	✓			✓	
McConnell & Dalke 1960					
McCorquodale 1999	✓		✓		
McCoy & Murphie 2011		✓			
McNay & Voller 1995	✓			✓	✓
Miller et al. 2008					✓
Monteith et al. 2010	✓	✓		✓	
Nicholson et al. 1997	✓				
Peek et al. 2002				✓	
Pierce et al. 2000					✓
Pierce et al. 2004					✓
Pojar & Bowden 2004		✓		✓	
Robinson et al. 2002	✓		✓	✓	✓
Smith & Lecount 1979					✓
Unsworth et al. 1999	✓	✓		✓	
White & Bartmann 1998	✓				
White et al. 1987	✓			✓	
Whittaker & Lindzey 1999		✓		✓	✓
Zager et al. 2007	✓				✓

Table 1.2 - Mule deer fawn survival rates (in three categories: summer, winter and first year) and causes of mortality. Weighted means and 95% confidence intervals are shown for each category.

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

* = survival was reported in multiple survival categories

† =not reported; calculated from general information in study

‡ =calculated from recruitment measures

R=calculated from recruitment measures such as composition counts

NR= not reported

Table 1.3 - Annual adult female mule deer survival rates and causes of mortality, with weighted means and 95% confidence intervals.

Study	Region	Survival	Cause of mortality as a percentage (%) of total mortality			
			Predation	Malnutrition /disease	Other	Unknown
Bartmann et al. 1992	CO Plateau	0.86	NR	NR	NR	NR
Bender et al. 2007	CO Plateau	0.81	13	61	9	17
Bishop et al. 2005	Intermountain West	0.81	23	7	36	34
Bishop et al. 2009	CO Plateau	0.91 (S)	35	16	35	16
Bleich & Taylor 1998	Intermountain West	0.75	63	9	4	24
Bleich et al. 2006	Intermountain West and Northern Forest	0.86	NR	NR	NR	NR
Farmer et al. 2006	Coastal Forest	0.80	45	25	30	0
Hatter & Janz 1994	Coastal Forest	0.84	NR	NR	NR	NR
Hurley et al. 2011	Intermountain West and Northern Forest	0.89 (S)	73	6	6	15
Lawrence et al. 2004	SW Desert	0.86 (S)	32	41	18	9
Lukacs et al. 2009	CO Plateau	0.84	38	13	25	25
Matthews & Coggins 1997	Northern Forest	0.85	12	28	48	12
McCorquodale 1999	Intermountain West	0.80	61	6	22	11
McNay & Voller 1995	Coastal Forest	0.74	73	6	6	15
Monteith et al. 2010	Intermountain West	0.89	NR	NR	NR	NR
Nicholson et al. 1997	SW Desert	0.81	NR	NR	NR	NR
Robinson et al. 2002	Northern Forest	0.72	62	10	10	19
Unsworth et al. 1999	CO Plateau, Intermountain West, Northern Forest	0.85	NR	NR	NR	NR
White & Bartmann 1998	CO Plateau	0.87	NR	NR	NR	NR
White et al. 1987	CO Plateau	0.83 (S)	11	37	17	34
Zager et al. 2007	Unknown	0.85	NR	NR	NR	NR
Weighted mean		0.84	44	17	21	18
95% confidence interval		0.75-0.94	22-66	11-23	14-28	12-24

S= senescence effects on survival are reported

NR=not reported.

Table 1.4 - Results from experimental studies of mule deer population dynamics, showing effects of changes in predators and nutrition.

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

Figure 1.1 - The geographical ranges of mule deer (*Odocoileus hemionus*) (light and dark grey areas) and black-tailed deer (*O. h. columbianus*) and (*O. h. sitkensis*) (dark grey area only) in western North America (Mackie et al. 2003). The 48 studies included in the review are shown as grey squares (mule deer) and black triangles (black-tailed deer).



Figure 1.2 - Mule deer habitat ecoregions: Southwest Deserts, California Woodland Chaparral, Colorado Plateau Shrublands and Forests (CO Plateau), Northern Forests, Coastal Forests, Intermountain West, and Great Plains. Locations of studies are shown, as in Figure 1.

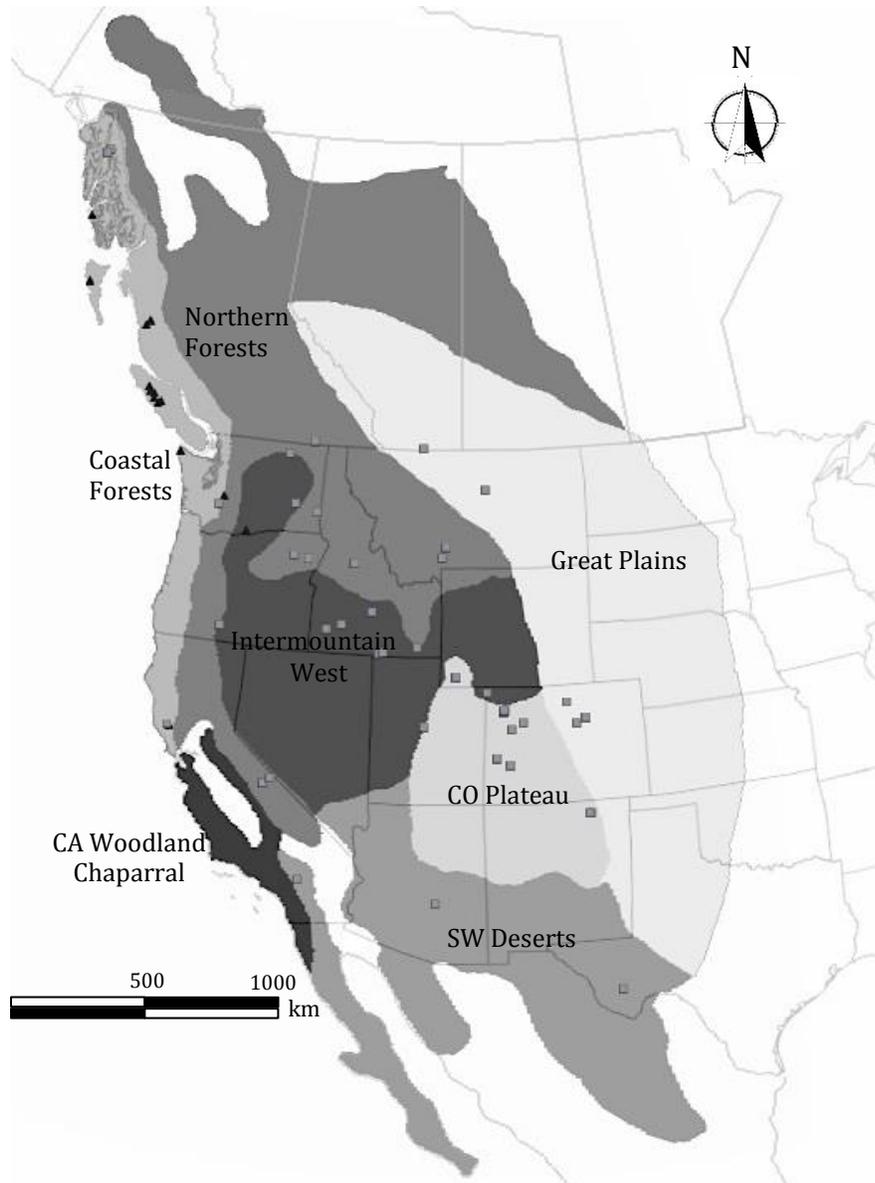


Figure 1.3 - Proximate causes of mule deer mortality (predation, malnutrition/disease, other and unknown) as percentages of reported total mortality for all age classes (error bars represent 95% confidence intervals; winter and summer mortality is calculated over 6 months, first year and annual rates are per year).

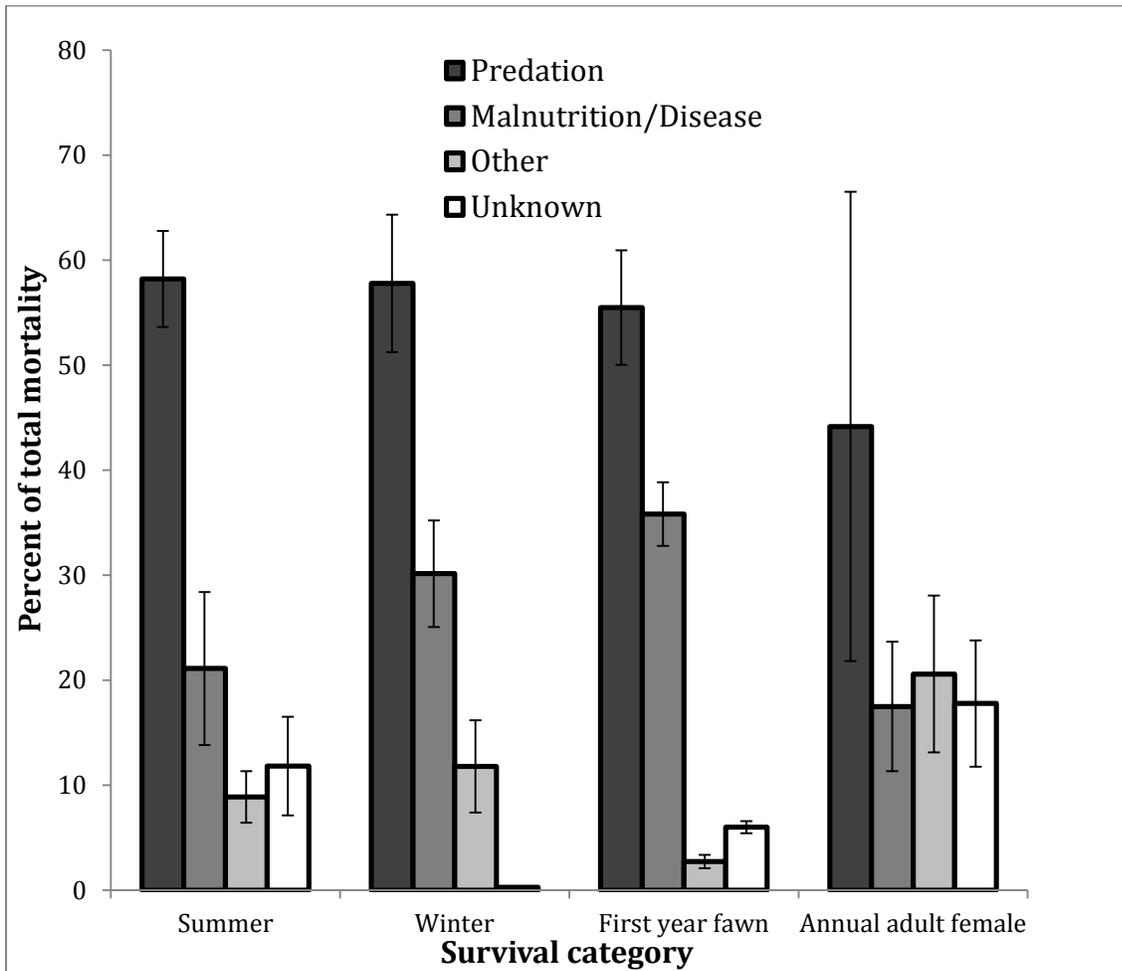
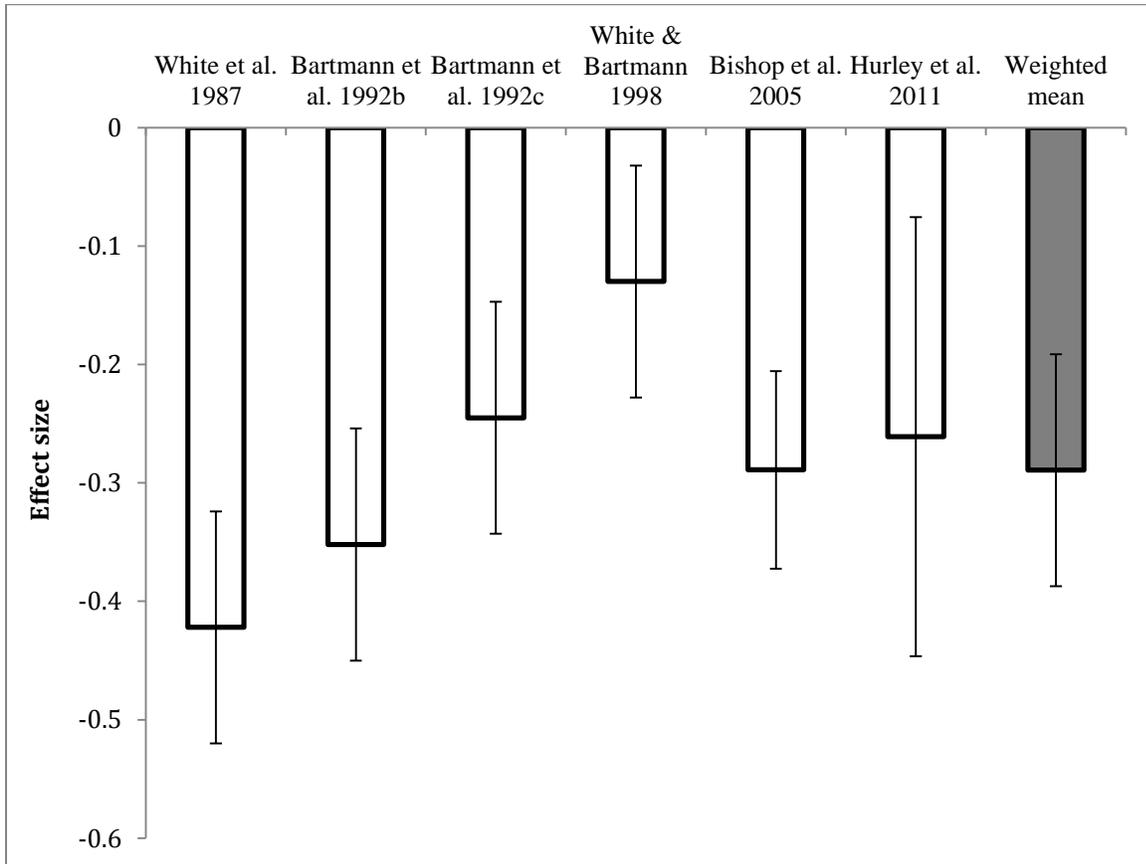


Figure 1.4 - Effect of high snowfall on winter fawn survival rates, as quantified in six studies, plus the weighted mean effect size (error bars represent 95% confidence intervals).



VI. Chapter 2: Forage availability modifies predation risk of black-tailed deer fawns

Tavis D. Forrester and Heiko U. Wittmer

Wildlife, Fish, and Conservation Biology, University of California, One Shields Ave., Davis, CA 95616, USA. (TDF, HUW)

Victoria University of Wellington, School of Biological Sciences, PO Box 600, Wellington 6140, New Zealand. (HUW)

Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA 22630, USA. (TDF)

Understanding how top-down and bottom-up effects influence population dynamics of ungulates is essential for effective management and conservation, and there is an emerging consensus that forage and environmental productivity interact with predation to influence survival. From 2009 to 2013, we captured and monitored 135 black-tailed deer (*Odocoileus hemionus columbianus*) fawns in coastal California to study possible interactions between forage and predation on survival. We estimated seasonal and annual survival rates, assessed the cause of all mortalities (n=93), measured available forage, estimated relative abundances of predators on summer range (i.e., fawning areas) each year, and used remote sensing to quantify habitat on winter range. We then used cumulative incidence and proportional hazards functions to evaluate how environmental covariates were related to fawn survival. Summer survival rates averaged 0.40 across all years ($SE=0.05$) and the mean annual survival rate was 0.26 ($SE=0.04$). We found that most fawn mortality resulted from predation during summer, mainly by black bears (*Ursus americanus*) and coyotes (*Canis latrans*), and spatial differences in summer survival persisted

until recruitment. Black bear predation, the single largest cause of mortality, appeared unrelated to forage availability. Observed spatial variation in mortality risk due to other causes was linked to the availability of oak forage but not predator abundance. Additionally, characteristics of deer including adult female condition and fawn birthweight, did not provide evidence for purely bottom-up limitation. Rather our results provided evidence that both bottom-up and top-down effects were influencing fawn survival in this declining population, and that predator identity and the timing of mortality affected these interactions.

Key words: age specific survival, black bear, coyote, fawn survival, predator hunting mode, seasonal survival, ungulate

A primary challenge in ecology is determining how top-down and bottom-up effects influence fitness and population dynamics in complex communities (Sinclair and Krebs 2002; Sinclair 2003; Owen-Smith and Mills 2008). Understanding the dynamical consequences of bottom-up and top-down effects is of particular interest in ungulates because they are dominant herbivores within ecological communities (Augustine and McNaughton 1998), help maintain predator diversity (Schmitz 2008), and are important components of trophic cascades (Ripple et al. 2014). Body size is one of the most important variables determining the relative contributions of predation and forage to survival in ungulates (Sinclair et al. 2003; Hopcraft et al. 2010). Smaller ungulates require higher quality forage because of their smaller digestive systems (Clauss and Hummel 2005) and are vulnerable to a larger number of predators than larger ungulates (Radloff and Du Toit 2004). Small ungulates (~3-25 kg) are thus thought to be primarily regulated by predation, large ungulates (>300 kg) by forage availability, and mid-sized (25-300 kg) ungulates by interactions between predation and forage quantity and quality (McNaughton et al. 1989; Hopcraft et al. 2010).

Juveniles of many ungulates are also vulnerable to a larger number of predators than adults (Linnell et al. 1995). In complex communities with multiple predators, juveniles may be preyed upon by up to 4 times as many predators as adults (Linnell et al. 1995), and even in simple communities there is often at least one predator killing juveniles (Moorter et al. 2009). Predation is thus the primary source of juvenile mortality in many ungulates, and predominantly occurs over the first summer when they are most vulnerable (Gaillard et al. 2000). The magnitude of the effect of predation on juvenile ungulates, however, also depends on prey selection and hunting mode of predators. For example, predation pressure on small bodied prey is higher in communities where large predators select all sizes of prey (size-nested predation)

versus where predators select only a certain size class (size-partitioned predation) (Radloff and Du Toit 2004). When size-nested predation occurs, seasonal and inter-annual shifts in prey selection by large predators can also change predation pressure on a given species (Owen-Smith and Mills 2008). The hunting mode of predators affects predation pressure through both species and individual differences. Different predator species may focus more or less on juvenile prey (Gervasi et al. 2012) or even target different ages of juveniles (e.g. neonates versus fawns following their mothers) (Griffin et al. 2011). Individual predators systematically searching for juveniles instead of opportunistically preying upon them will also have greater effects (Bastille-Rousseau et al. 2011).

Juvenile nutrition, in contrast to vulnerability to predators, is heavily affected by maternal condition (Parker et al. 2009). The highest nutritional demands of the year for female ungulates occur during late pregnancy and lactation (Clutton-Brock et al. 1989) and available nutrition during this time determines juvenile nutrition (White 1992). During lactation, females thus require forage that has high amounts of both energy and protein to support the rapid growth of fawns and to replenish body fat and mass (Parker et al. 2009).

Understanding contributions of predation and nutrition to juvenile survival is magnified by the importance of juveniles in determining future population growth of ungulates. Compared to adult survival, juvenile survival is lower and more variable in ungulates (Gaillard et al. 1998). Because of the observed higher variability among years in juvenile survival, it is typically survival of juveniles that determine the trajectory of population growth despite the generally higher elasticity of adult survival (Gaillard et al. 1998).

Unexpected population fluctuations of mule deer (*Odocoileus hemionus*), and black-tailed deer (*O. h. columbianus*), over the last several decades have highlighted the uncertainty

surrounding the role of predation and forage in juvenile survival and population dynamics (Ballard et al. 2001). The recovery of carnivores across the western USA, along with the current decline of mule and black-tailed deer in the same area, has brought increased attention to the importance of predation (Ballard et al. 2001; Forrester and Wittmer 2013). Forage availability is also important and has been linked to recruitment (Gilbert and Raedeke 2004) and fine-scale habitat selection of juveniles (Bowyer et al. 1998). Possible interactions between forage availability and predation risk of juveniles, however, have rarely been considered (Farmer et al. 2006). This is likely a consequence of predation and forage often being portrayed as a sharp dichotomy, where some populations are held far below a nutritional carrying capacity (K) by predation, some are regulated near K by forage availability, and others are in some short transition between the two states where both predation and forage impact populations (Ballard et al. 2001; Pierce et al. 2012). However, recent theoretical advances suggest that mid-sized ungulates, such as mule and black-tailed deer, should be experiencing interacting predation and forage effects (Hopcraft et al. 2010; Forrester and Wittmer 2013).

Although survival and cause-specific mortalities vary seasonally in both mule and black-tailed deer, only 5 studies have followed tagged juveniles (i.e. fawns) from birth to recruitment, and no year-round studies have directly linked available forage to survival (Forrester and Wittmer 2013). Here we investigated fawn survival from birth to recruitment in black-tailed deer in northern California and tested hypotheses about the relative importance and interactions of top-down and bottom-up effects. Specifically, we addressed the following competing hypotheses related to risk of death and bottom-up and top-down effects: 1) If top-down effects dominate fawn survival, most mortalities will be from predation, forage availability will have no influence on mortality risk, and characteristics of deer will show no signs of a nutritionally limited

population (i.e. good adult body condition, high fawn birth weights, high pregnancy and fecundity rates); 2) If bottom-up effects dominate survival, malnutrition will cause mortality, forage availability will explain mortality risk and risk of predation, and characteristics of deer will be consistent with nutritional limitation (i.e. poor adult body condition, low fawn birth weights, low pregnancy and fecundity rates); or 3) If top-down and bottom-up effects are both influencing survival, predation will be the dominant cause of mortality with some malnutrition, forage availability will modify the risk of mortality and possibly predation, and characteristics of deer will show a mix of top-down and bottom-up signs. We also investigated the more specific hypotheses that 4) Predation mortality risk will be linked to predator abundance; and 5) Forage availability will influence the risk of predation similarly regardless of predator species. We addressed the first 3 hypotheses for both the summer and winter periods, while the last 2 were only addressed during summer.

MATERIALS AND METHODS

Study Area.— Our study area covered ~1000 km² in the northwestern California Coast Range, and was composed of 2 major ridges that divided the area into 3 watersheds (named M1 and FH7 for the forest roads traversing them; Figure 1). The terrain was rugged with sharp gradients in elevation, ranging from 500 m in valley bottoms to >2000 m on ridgetops. The climate is considered Mediterranean and >85% of all precipitation occurred from October through April. Snow cover was generally limited to elevations >1000 meters and was irregular, particularly during mild winters.

Vegetation communities in the area were diverse due to elevational gradients, soil diversity, and land management practices. Plant communities at low elevations were a mix of oak woodlands (*Quercus* spp.), dense chaparral, and grasslands, while mid elevations were

mainly mixed-coniferous forests dominated by pine (*Pinus* spp.) and Douglas-fir (*Pseudotsuga menziesii*). High elevation areas supported a mix of true fir forests (*Abies* spp.), patches of shrub cover (mainly *Ceanothus* spp.) and included scattered dry and wet meadows. Past land management, including logging and grazing, left a mosaic dominated by even-aged conifers, with occasional mature timber stands, and grasslands dominated by exotic species. Important deer forage included *Ceanothus*, herbaceous vegetation, oak leaves, and oak mast in the fall.

Black-tailed deer wintered in valleys and moved to high quality habitats at high elevations during summer (hereafter termed fawning areas). Deer shared the study area with a diverse predator-prey community and common predators included American black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and pumas (*Puma concolor*). Black-tailed deer were the only resident ungulate and pumas were the principal predator of adult deer (Marescot et al., in press). Smaller prey species included lagomorphs (e.g., black-tailed jackrabbit *Lepus californicus*) and rodents (e.g., California ground squirrel *Otospermophilus beecheyi*).

Fawn Capture and Monitoring.— All handling procedures were approved by an Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886) and adhered to guidelines established by the American Society of Mammalogists (Sikes and Gannon 2011). We captured fawns from mid-June to mid-July of each year by driving along unpaved forest roads during daylight, by using spotlights to locate fawns at night, and by scanning meadows and forest habitat with binoculars for post-parturition does to find hidden fawns. We captured fawns by hand or with handheld nets wearing new latex gloves for each capture to avoid scent contamination. Upon capture, fawns were weighed, sexed, and then fitted with a small colored and numbered plastic ID tag in 1 ear and a very high frequency

(VHF) motion-sensitive transmitter (Sirtrack, Havelock North, New Zealand) in the other ear. Battery life of transmitters was 1 year. We estimated fawn age in the field using status of the umbilical cord, standing/walking coordination, and hoof growth line measurements (Sams et al. 1996). Fawn ages were estimated as a range of days and we used the median value as the age for analysis. Fawns were released near the capture site immediately after processing, which averaged approx. 10 minutes.

Fawn Monitoring and Mortality Investigation.— We monitored the status of fawns daily from June through mid-September and every 7-14 days from either the ground or air during the rest of the year. VHF transmitters switched to mortality signal after remaining stationary for 4 hours, facilitating assessment of mortality causes. Fawn mortalities during summer were investigated almost immediately following detection of a mortality signal ($AVG=1.1$ days, $SE=0.25$), while inclement weather and limited accessibility delayed investigations in winter ($AVG=24.2$ days, $SE=8.1$). Cause of mortality was determined during site investigations using systematic criteria including disposition of the carcass, predator sign, evidence of caching, bite marks, and blood (Atkinson and Janz 1994). If no obvious evidence of predation was found, a necropsy was performed. Deaths were considered capture related if they were a direct result of handling.

Life history characteristics.— As a part of a larger research project we also captured 60 adult female black-tailed deer and collected fetal and pregnancy rates as detailed in Marescot et al. (in press). During captures we also assessed body condition using a modified rump fat body condition scores (rBCS range from 1-5, Gerhart et al. 1996; Cook et al. 2010), which we analyzed using one-way analysis of variance (ANOVA). Helicopter based distance-sampling surveys (Buckland et al. 2001) provided approximate deer density estimates at the onset of our

study (D. Casady, unpublished data). We compared fawn weights at 2 days old, the youngest age group we captured in sufficient numbers (n=13), to fawn weights at 2 days old (n=17) born to captive does with *ad libitum* access to food (Cowan and Wood 1955; Parker and Wong 1987) using an unequal variance *t*-test. We delineated fawning areas and winter ranges using 95% minimum convex polygons from GPS locations of adults. We considered areas to be spatially separated if location data indicated gaps greater than twice the size of the average diameter of an adult home range and where geographic features created barriers to movement (Forrester 2014).

Vegetation Surveys.— We surveyed all fawning areas to quantify percent cover of deer forage types and to estimate biomass of shrubs, forbs, and grasses. Surveys were conducted along 100 m line transects with random starting points that we located on grids covering each fawning area with 1x1 km spacing. Shrub cover and species composition was estimated using line-intercept surveys on each transect (Bonham 1989) and shrub forage biomass was estimated using twig counts on three 1x3 m quadrats per transect (Shafer 1963). Herbaceous biomass was estimated using the comparative yield (CY) and dry weight ranking (DWR) methods using 10 0.25 m² quadrats per transect (Haydock and Shaw 1975; Jones and Hargreaves 1979). We identified shrubs to species, classified all small flowering plants as forbs, and categorized grasses as annual or perennial. We conducted 157 line transect surveys, conducted CY and DWR surveys on 1770 quadrats, and counted all twigs equal or smaller to typical deer browse diameter on 471 quadrats. We measured 100-200 browsed twigs to obtain the mean species-specific browse diameter for important deer browse, including *Ceanothus*, *Prunus*, *Arctostaphylos*, and *Quercus* species (see Appendix 1 for species list). We estimated habitat specific forage amounts for Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) cover types (Schwind and Gordon 2001); conifer, hardwood, mixed conifer and hardwood, shrub,

and herbaceous. Habitat weighted estimates of forage were created by estimating the amount of forage for each habitat type per fawning area (forage g/m² x habitat area), summing these values from all habitat types, and then dividing by the total area. Herbaceous biomass was variable among years so herbaceous forage values were calculated for each year, while shrub biomass was less variable and average shrub browse was calculated for all years combined.

We created a forage availability index for winter range by estimating the percent area of CALVEG vegetation types containing high-quality forage. High quality vegetation types were determined using past research (Dasmann and Taber 1956; Wallmo 1981; Livezey 1991) and included oak woodland, herbaceous meadows, and high quality shrub types (e.g., montane mixed chaparral). Winter ranges (n=4, Figure 1) were delineated as minimum convex polygons from GPS locations of adult deer (see above). Fawns spend their first winter exclusively with their mother (Wallmo 1981), and although we did not collar mother and offspring pairs we confirmed that winter fawn locations fell within wintering ranges.

Deer Diet Analysis.— We collected deer pellets in fawning areas on transects that followed deer trails with randomly located starting points distributed across available habitat types. Diet composition was analyzed using microhistological analysis (Holechek et al. 1982; Leslie et al. 1983) and diet quality was indexed using fecal nitrogen and diaminopimelic acid (DAPA) (Hodgman et al. 1996). We used previous work (Dasmann and Taber 1956; Wallmo 1981; Kie et al. 1984) and our dietary analysis to determine the most important shrubs for deer in our study area and estimated nutritional quality for these species, including crude protein, in vitro dry matter digestibility, and tannin analysis (Appendix 1). All diet analyses were performed by the Wildlife Habitat and Nutrition Laboratory at Washington State University. Differences in diet among fawning areas were assessed using one-way ANOVA.

Weather and Winter Range Elevation.— We acquired daily precipitation and temperature data from 4 United States Geological Survey (USGS) weather stations and winter and April snowpack depth from 2 California State monitoring areas located in the study area. We created a winter severity index for each deer that was the number of days on winter range below freezing ($0\text{ }^{\circ}\text{C}$) to a given week. We accounted for difference in elevation among winter ranges and weather stations by adjusting the temperature of the weather station nearest the winter range by the standard environmental lapse rate of $6.49\text{ }^{\circ}\text{C}$ per 1000 m. We measured total winter precipitation as precipitation from November-February and spring precipitation as all precipitation from March-June. We used the average monthly adult female elevation in each winter range as a proxy for the monthly average elevation of fawns. We assumed that this average value was biologically realistic because of the small individual variation in monthly elevation within each winter range (average SE=43 m).

Relative Abundance of Predators.— We estimated the occupancy and abundance of predators in summer fawning areas using heat and motion-triggered cameras (Bushnell Trophy Cam, Bushnell, Overland Park, KS and Cuddeback Capture IR, Cuddeback, Green Bay, WI). We randomly sampled fawning areas by placing a 12-14 km^2 grid with 1 km^2 cells over the 4 fawning areas and randomly selecting grid cell centers to place cameras. We placed cameras at areas of animal activity (trails, closed roads, springs, scrapes, etc.) within 100 m of randomly selected points (Rowcliffe et al. 2008). We used the average summer home range size (1 km^2) of adult female black-tailed deer (Bunnell and Harestad 1983; McCorquodale 1999) as a grid cell because this allowed us to estimate the probability of predator use of the average female deer home range per fawning area (MacKenzie et al. 2005). Cameras were deployed for 3 month periods beginning in mid-June of each year and ending in September. We deployed 8-10 cameras

in each of the 4 sampling grids for a total of 32-35 cameras per deployment, and a total of 275 camera deployments and 8,980 trap nights over 3 summers.

We used Program PRESENCE to model both probability of use of a deer home range and detection probability for each major fawn predator, but excluded pumas due to insufficient detections. Detection probabilities of fawn predators were not different among fawning areas, and probability of use often approached 1. Because detection probability was the same among fawning areas we used the monthly detection rate of predators (# predator detections/camera days * 30) to model the effect of predator relative abundance on variation in summer fawn mortality risk. We estimated predator relative abundance for 3 critical life history periods of black-tailed deer fawns; the neonate period (mid-June to mid-July), the hiding period (mid-July to mid-August), and following their mother (mid-August to mid-September) (Wallmo 1981).

Modeling Fawn Mortality Risk.— We defined summer separately for each fawn as the period from capture until their last location on summer range and winter as the time from the first relocation on winter range until recruitment as a yearling. The date of mortality signal was used as the date of death or the date between the last live location and the first mortality signal if there was a gap of >3 days. We tested for differences in survival among years and between fawning and winter ranges, the M1 and FH7 ridges, sex, twin status, and seasons using the log-rank test of Kaplan-Meier survival rates (Cleves et al. 2010). We tested for differences in age and weight at capture among years using one-way ANOVA or using Kruskal-Wallis rank tests for non-normal variables.

We used cumulative incidence functions (CIFs) to estimate cause-specific fawn mortality and survival rates by month throughout the first year of life (Heisey and Patterson 2006). Cumulative incidence functions model each mortality source while accounting for the probability

of dying from all other possible causes of mortality (Heisey and Patterson 2006). These functions are based on proportional hazards models (Cox 1972) and model the probability of a mortality from cause i occurring before time t .

(Equation 1)
$$\text{CIF}_i(t) = P(T \leq t \text{ and failure from cause } i).$$

We modeled fawn mortality risk with Cox proportional hazards because seasonal hazard functions could not be fit using parametric functions. We used the standard Cox proportional hazards formula

(Equation 2)
$$h(t|\mathbf{X}_j) = h_0(t)\exp(\mathbf{X}_j\beta_x),$$

where t is time as specified in the model (e.g., days since birth), $h(t|\mathbf{X}_j)$ is the hazard rate for the j th deer at time t , $h_0(t)$ is the baseline hazard, and the regression coefficients β_x are estimated from the risk covariates \mathbf{X}_j for the j th deer (Cox 1972; Therneau and Grambsch 2000). The β_x are used to estimate hazard ratios that are a measure of the risk of death similar to an odds ratio. The hazard ratios are the exponential functions of the β 's from equation 1 and a hazard ratio (HR) of less than or greater than 1 represents a smaller or greater risk of death respectively. We considered a HR significantly different than 1 if the 95% confidence interval did not overlap 1.

Because we captured fawns soon after birth we modeled survival as a function of age in days (Fieberg and DelGiudice 2009). We used a delayed entry design where we estimated risk beginning at birth but fawns entered the analysis at the day of capture for summer survival and the day of arrival on winter range for winter survival. We censored animals from analysis after death, after the last day on summer range (max value = 104 days of age), or after recruitment to a yearling (Hosmer et al. 2011).

We modeled the risk of summer and winter fawn mortality separately because seasonal ranges were spatially separated and fawns were at risk from a smaller number of predator species

during winter. Covariates of mortality risk during summer included biomass of oak and herbaceous forage, relative predator abundance, previous winter precipitation, spring precipitation, as well as sex, age and weight at capture, and twin status of fawns. Covariates of mortality risk during winter included amount of oak and shrub habitat types on winter range, cumulative winter precipitation, cumulative days below freezing, average weekly elevation, and a predation risk index that was the difference between average weekly elevation of deer and pumas (based on GPS locations of 7 collared pumas, data presented in Allen et al. 2014). We used pairwise correlation coefficients to assess if covariates were correlated (correlation >0.5). We evaluated all possible model subsets from remaining covariates (Whittingham et al. 2006; Arnold 2010) and used Akaike Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002). We considered a model to be strongly supported if the AIC_c score was <4 AIC_c from the next model (Burnham and Anderson 2002). We used Akaike weights (w_i) to calculate the relative importance of all covariates and model averaging methods to calculate average hazard ratios, standard errors, and confidence intervals from all models if no model was strongly supported (Burnham and Anderson 2002; Johnson and Omland 2004).

We tested possible linear and non-linear interactions using fractional polynomials (Royston and Sauerbrei 2004). We tested the assumption of proportional hazards for covariates in the model using graphical methods and Schoenfeld residual plots (Grambsch and Therneau 1994). If the proportional hazard assumption was violated, we assessed covariate fit and form using Martingale residuals and transformed variables or stratified the model by the appropriate variable (Hosmer et al. 2011). If variables that changed over time violated the proportional hazard assumption we split our dataset at the failure times and interacted the variables with a time

function (Hosmer et al. 2011). We chose the appropriate time function by fitting a locally weighted scatterplot smoothed (lowess) graph of the martingale residuals against the covariates interacted with various time functions, and used the function that created the most linear plot (Therneau and Grambsch 2000; Cleves et al. 2010). We assessed model fit by plotting the cumulative hazard function against the Cox-Snell residuals and testing for a 1:1 fit (Therneau and Grambsch 2000). We assessed if outliers unduly affected the model by graphing DFBETA residuals (Cleves et al. 2010) and likelihood displacement values (Collett 2003) against analysis time.

We modeled the cause specific risk of bear and coyote predation using cumulative incidence functions (CIFs) with the semi-parametric method formulated by Fine and Gray (1999). This method models the CIF for cause i as the cumulative sub-hazard function for that cause alone, and covariate effects for cause i can be interpreted similarly to a Cox proportional hazards model. We tested assumptions of the CIF models with the same methods as the Cox proportional hazards models, selected models using AIC_c , and used model averaging if we did not find one best model (Burnham and Anderson 2002). All statistical tests were performed in STATA ver. 12.1 (StataCorp, College Station, TX).

RESULTS

Fawn Capture and Monitoring.— We captured 137 fawns (72 females, 64 males, 1 unknown) during the summers of 2009-2012. Two fawns were censored due to tag failure ($n=1$) and capture related mortality ($n=1$). The mean capture date was June 27 ($SE_{\text{among years}}=6.40$ days, Range 6 June-19 July), the mean age at capture was 4.8 days ($SE=0.18$, Range of 0-10) and mean capture weight was 3.7 kg ($SE=0.08$, Range 2-7). Mean capture date differed significantly among years (ANOVA, $F_{3,134}=17.24$, $p<0.001$), but mean capture age (Kruskal-Wallis, $X^2_{df=3}=6.873$,

$p=0.076$) and capture weight (ANOVA, $F_{3,134}=0.80$, $p=0.493$) were not different. Mean capture age also did not differ between ridges (t -test, $t_{134}=0.13$, $p=0.89$). We categorized 42 fawns as twins and 93 as singles but did not capture both fawns of all sets of twins. Fawn weights at 2 days old were 14% lower than captive fawns, a significant difference ($t_{28}=1.989$, $p=0.021$).

Summer Diet and Fawning Area Vegetation.— Deer diet composition and forage quality results are reported in detail in Appendix 1. Diet was averaged between years and was mostly composed of shrubs (Cherry Hill=88%, Coyote Rock=83.1%, Cold Spring=85.8%, Plaskett Meadows=53.6%), while forbs contributed only a small proportion (Cherry Hill=2.1%, Coyote Rock=3.9%, Cold Spring=4.8%, Plaskett Meadows=11.5%). Oak leaves composed most of the diet in summer in all areas except for Plaskett Meadows (Cherry Hill=76.1%, Coyote Rock=65.4%, Cold Spring=73.6%, Plaskett Meadows=21.8%).

Population life history characteristics.— The average adult female rBCS score was 2.8 (SE=0.37), and there were no differences in body condition among fawning areas (one-way ANOVA, $F_{3,54}=0.91$, $p=0.44$). Pregnancy rates averaged 0.87 (SE=0.05) and average fecundity was 1.9 fawns per doe (Marescot et al., in press). Black-tailed deer density was approximately 20 deer/km² at the beginning of the study (D. Casady, unpublished data).

Temporal Patterns in Fawn Survival.— A total of 95 fawns died during our study, including 74 during summer. Summer survival rates for fawns averaged 0.42 across all years (SE_{among years}=0.05) and the mean annual survival rate was 0.26 (SE=0.04). Summer (Min=0.14; 2009, Max=0.51; 2011) and annual (Min=0.09; 2009, Max=0.37; 2011) fawn survival fluctuated greatly among years (Table 1), but the differences were not significant (*Log Rank (LR) test*, $X^2_{df=3}=5.24$, $p=0.15$). Winter survival of fawns averaged 0.62 across all years (SE_{among years}=0.06).

Predation was the primary source of fawn mortality (Figure 2), and black bear predation was the largest single source of mortality (Table 1). The majority (61%) of total mortality and of predation mortality (69%) occurred within 30 days of birth. During summer, there were low numbers of mortalities assessed as unknown predators (5.0% of summer mortality) or unknown cause (7.7% of summer mortality). Summer survival did not differ by sex (*LR test*, $X^2_{df=1}=0.17$, $p=0.68$), but trended lower for twins ($\phi=0.33$, $SE=0.08$) compared to single fawns ($\phi=0.46$, $SE=0.06$) (*LR test*, $X^2_{df=3}=1.93$, $p=0.16$). Only 22% of annual mortality occurred on winter range, and most known causes were attributed to predation. No winter mortalities were attributed to malnutrition but we could not assess the cause of mortality in most instances (unknown mortalities=16 of 21 total). Female fawns were more likely to die in the winter than males (*LR test*, $X^2_{df=1}=5.25$, $p=0.02$), but there was no difference in single or twin survival (*LR test*, $\chi^2=0.19$, $p=0.66$). Despite seasonal differences there were no annual differences in survival between sexes (*LR test*, $X^2_{df=1}=0.36$, $p=0.56$) or between single and twin fawns (*LR test*, $X^2_{df=1}=1.59$, $p=0.21$).

Spatial Patterns in Fawn Survival.— Summer survival trended lower in the 2 fawning areas on the FH7 ridge ($\phi=0.36$, $SE=0.06$) than the M1 ridge ($\phi=0.49$, $SE=0.07$) (*LR test*, $X^2_{df=1}=2.89$, $p=0.089$). Although winter survival did not differ for fawns from different fawning areas (*LR test*, $X^2_{df=1}=0.71$, $p=0.399$), differences in summer survival were large enough that there was some evidence for a difference in annual survival between ridges (Figure 3, *LR test*, $X^2_{df=1}=3.30$, $p=0.06$). There were no strong differences in survival among the 4 distinct wintering areas (*LR test*, $X^2_{df=3}=7.08$, $p=0.07$).

Summer Mortality Risk.— We limited the Cox proportional hazards analysis to the 3 cohorts captured from 2010-2012 ($n=121$, $mortality_{summer}=63$) since we did not collect covariate information for the 2009 cohort. We pooled data across years after confirming that summer

survival differences among years were not significant (*LR test*, $X^2_{df=2}=0.32$, $p=0.854$). Capture weight and age were correlated (>0.5 correlation coefficient) and capture weight was retained for the model because it was more accurately measured in the field. Correlation coefficients were < -0.5 between herbaceous forage and both overall shrub cover and *Ceanothus* species. We retained herbaceous forage for modeling because herbaceous forage is critical summer forage for mule deer (Wickstrom et al. 1984; White 1992), and dropped *Ceanothus* since these species did not contribute much to summer diets (see Appendix I). We also dropped percent cover because it was measured as vegetation composition and not specifically as deer cover. All remaining environmental covariates met proportional hazards assumptions, and capture weight was modeled as a linearly increasing and time varying covariate since it increased with age.

There was no clear best model for summer mortality risk so we summed Aikake weights (w_i) and estimated model averaged parameters to determine the importance of covariates. Capture weight and the amount of oak forage within fawning areas explained the most variation in mortality and were negatively related to mortality risk (Table 2). Herbaceous forage and twin status also explained variation in mortality; twins were 54% more likely to die than single fawns and increasing herbaceous forage showed a trend toward decreased mortality risk. Predator abundance, fawn sex, and spring and winter precipitation were not well supported in mortality risk models (Table 2).

Predation risk from bears during summer was not strongly explained by any covariates, but relative bear abundance had the strongest support ($w_i=0.64$). No predator abundance or forage covariates showed a significant effect on predation risk (Table 3). Predation risk from coyotes during summer was lower in areas with more oak forage (Table 3). No other covariate significantly affected coyote predation risk. The coyote predation risk CIF was higher on the

FH7 ridge compared to the M1 ridge ($LR\ test, X^2_{df=1}=7.50, p=0.006$) while the bear predation risk CIF was not different ($LR\ test, X^2_{df=1}=1.04, p=0.307$).

Winter Mortality Risk.— We pooled data since there was no significant difference in winter survival among years ($LR\ test, X^2_{df=2}=4.34, p=0.114$). All covariates in winter hazards models met proportional hazards assumptions. There was no single best model for winter mortality risk, so we report model averaged parameters and summed AIC_c weights for covariates from all subsets of models (Arnold 2010). Sex of fawns was the strongest predictor of mortality, and the amount of shrub habitat and predation risk index were also related to mortality risk, although not significantly (Table 4). Winter severity, precipitation, and the amount of oak habitat in winter home ranges were not related to mortality. We did not model predation-specific mortality risk in winter due to the high number of unknown mortalities.

DISCUSSION

Top-down effects dominated mortality of black-tailed deer fawns in our study area, particularly during the first 30 days of their life. Predation during that time was primarily driven by black bears, and there was no apparent sign that differences in forage or habitat moderated predation risk from bears. Forage and habitat availability became more important over subsequent months, and differences in forage and habitat availability during summer explained observed spatial variation in mortality and predation risk from coyotes among fawning areas. Overall, we thus found that an interaction of top-down and bottom-up forces affected annual survival probabilities of fawns in black-tailed deer, and that fawns of this mid-sized ungulate were subjected to intense top-down pressures because of their vulnerability to a large number of size-partitioned predators (Radloff and Du Toit 2004).

Almost all bear predation in our study was concentrated on fawns <30 days old, a pattern also found in other ungulates (Vreeland et al. 2004; Gustine et al. 2006; Griffin et al. 2011). The risk of being killed by a bear was unrelated to both the availability of forage and the relative abundance of bears in fawning areas, as well as individual differences among fawns in capture weight, sex, or twin status. Forage availability was likely of no importance because fawns at this young age have not yet accrued benefits of better forage (White 1992), are still relying on hiding from predators (Geist 1981), and are likely unable to evade predators once detected. Differences in hunting methods of individual bears may have contributed to the lack of correlation between bear abundance and fawn mortality. The hunting strategies of black bears in other areas have been found to vary significantly, with most individuals encountering fawns opportunistically and only a few actively searching for fawns (Zager and Beecham 2006; Bastille-Rousseau et al. 2011). This suggests that the number of bears actively searching for fawns in identified fawning areas may have influenced predation risk to a greater degree than overall bear abundance.

Mortality risks from other causes were modified by bottom-up effects, and the variation in the predation risk from coyotes and overall risk of mortality was lower in areas with more oak forage. Several mechanisms could be responsible for this observed pattern. Older fawns in better condition may have been able to escape coyotes more easily or mothers in better condition may have been able to defend against coyotes more effectively (Lingle et al. 2005, 2008). Oak forage was likely linked to better summer condition because it made up the majority of the summer diet and was used in much higher proportion than its availability. Furthermore, oak leaves had lower tannins and higher protein content than *Ceanothus* spp., the next most common shrub observed in the diets of deer in our study area. Protein is critical for early growth of fawns and is just as important for summer nutrition as digestible energy (Parker et al. 2009). There seemed to be no

carryover effects of nutrition from the preceding winter since there was no detectable difference in body condition of adult females across the study area at the beginning of the summer. Other mechanisms for the observed link between oak forage and lower coyote predation could be an increased escape ability in open habitats (Geist 1981), or coyotes switching to alternate prey in habitats dominated by oaks (Hamlin et al. 1984; Hurley et al. 2011).

The interaction between predation and forage was strongest in summer, but may have occurred during winter as well. During winter, fawns were vulnerable to fewer predator species and known predation was mainly due to pumas. The amount of dense brush in wintering areas and overlap with the average monthly elevation of pumas increased mortality risk, a result consistent with prey vulnerability to ambush predators in complex habitat (Miller et al. 2014). The amount of oak habitat had no effect despite the importance of oak in summer and the possible benefits of oak as thermal cover for black-tailed deer in winter (Bowyer and Kie 2009). However, we also observed sex-specific mortality risks of fawns during winter. Sex specific differences in fawn mortality have been previously observed in mule deer (Bartmann et al. 1992; Unsworth et al. 1999; but see Lomas and Bender 2007), but our ability to associate environmental variables with sex specific mortality was limited by our low precision in assessing the cause of death during winter. Winter precipitation and severity apparently held little explanatory power during this time of the year.

Determining the dynamical consequences of predation requires assessing the relationship of a population to its carrying capacity K and then estimating the proportion of the “doomed surplus” of fawns killed by predators (i.e., compensatory mortality) (Errington 1946; Bowyer et al. 2005). We used established indices of population level processes (Bowyer et al. 2005; Pierce et al. 2012) to determine the degree of resource limitation present in our strongly declining

black-tailed deer population ($\lambda=0.82\pm 0.13$; Marescot et al., in press). Evidence for the population being food limited included low fawn weights which at approx. 2 days old were significantly lower than those of captive fawns from does with *ad libitum* access to food (Bowyer et al. 2005; Pierce et al. 2012). Estimates of vital rates, however, did not match results typically observed in food-limited populations (Gaillard et al. 1998) including pregnancy and fetal rates which were higher (Marescot et al., in press) than averages reported for mule and black-tailed deer across their distribution (Forrester and Wittmer 2013). Since estimates for average fetal rates reported in Forrester and Wittmer (2013) were mostly from high-density populations with an average $\lambda=0.99$, they should provide a benchmark for equilibrium populations. Finally, body condition of adult females in the study area in early summer was approaching a level of “good” (mean rBCS=2.8 on a 1-5 scale). Fat reserves in early summer, however, should be near the low point for the year (White 1992; Parker et al. 2009), and a good body condition does not provide evidence for nutritional limitation (Pierce et al. 2012).

Our findings were consistent with the interplay of top-down and bottom-up effects expected in a mid-sized ungulate such as black-tailed deer (Hopcraft et al. 2010). Future work on fawn mortality in mule and black-tailed deer should focus on manipulative experiments to determine mechanisms in the relationships between the quantity and quality of forage and predation, particularly since better deer habitat may support alternate prey that sustain high predator populations (Monteith et al. 2014) but may also encourage prey switching (Hamlin et al. 1984). Meta-analysis similar to work in other ungulate communities (e.g., Hopcraft et al. 2010; Griffin et al. 2011) will also be vital to gaining deeper insight into the role of predation in fawn survival across a range of predator diversity and abundances.

ACKNOWLEDGMENTS

We acknowledge support from the California Department of Fish and Wildlife (Contract #P0880013), the California Deer Association and the Mendocino County Blacktail Association. TDF thanks the Robert and Patricia Switzer Foundation Environmental Fellowship Program, the UC Davis Graduate Group in Ecology, and the Stockton Sportsmen's Club. We thank D. Casady of CDFW and our field crew for their dedicated efforts. Finally, we thank D. Kelt, A. Latimer, and A. Sih as well as 3 anonymous reviewers for their comments that greatly improved this manuscript.

LITERATURE CITED

- Allen, M. L., L. M. Elbroch, D. S. Casady and H. U. Wittmer 2014. Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Canadian Journal of Zoology* 95:397-403.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175-1178.
- Atkinson, K. T. and D. W. Janz. 1994. Effects of wolf control on black-tailed deer on Vancouver Island. British Columbia Ministry of Environment, Lands, and Parks, Wildlife Bulletin No. B-73:1-43.
- Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-1183.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter and J. C. deVos. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99-115.

- Bartmann, R. M., G. C. White and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121:3–39.
- Bastille-Rousseau, G., D. Fortin, C. Dussault, R. Courtois and J.-P. Ouellet. 2011. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography* 34:588–596.
- Bonham, C. D. 1989. *Measurements for terrestrial vegetation*. John Wiley and Sons, New York, USA.
- Bowyer, R. T., J. G. Kie and V. van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: Climate, forage, or risk of predation? *Journal of Mammalogy* 79:415–425.
- Bowyer, R. T. and J. G. Kie. 2009. Thermal landscapes and resource selection by black-tailed deer: implications for large herbivores. *California Fish and Game* 95:128–139.
- Bowyer, R. T., D. K. Person and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pp. 342–361 in *Large carnivores and the conservation of biodiversity* (J. C. Ray, K. H. Redford, R. S. Steneck & J. Berger, eds.). Island Press, Washington, D.C.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press.
- Bunnell, F. L. and A. S. Harestad. 1983. Dispersal and dispersion of black-tailed deer: Models and observations. *Journal of Mammalogy* 64:201–209.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York, USA.

- Clauss, M. and J. Hummel. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. *Mammal Review* 35:174–187.
- Cleves, M. A., W. Gould, R. Gutierrez and Y. Marchenko. 2010. An introduction to survival analysis using Stata. Stata Press, College Station, Texas, USA.
- Clutton-Brock, T. H., S. D. Albon and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262.
- Collett, D. 2003. Modelling survival data in medical research. CRC Press, Boca Raton, USA.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. Mccorquodale, D. J. Vales, et al. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management* 74:880–896.
- Cowan, I. M. and A. J. Wood. 1955. The growth rate of the black-tailed deer (*Odocoileus hemionus columbianus*). *Journal of Wildlife Management* 19:331–336.
- Cox, D. 1972. Regression models and life tables. *Journal of the Royal Statistical Society* 34:187–220.
- Dasmann, R. F. and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *Journal of Mammalogy* 37:143–164.
- Errington, P. L. 1946. Predation and vertebrate populations. *The Quarterly Review of Biology* 21:144-177.
- Farmer, C. J., D. K. Person and R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management* 70:1403–1415.
- Fieberg, J. and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* 90:1687–1697.

- Fine, J. P. and R. J. Gray. 1999. A proportional hazards model for the subdistribution of a competing risk. *Journal of the American Statistical Association* 94:496–509.
- Forrester, T. D. and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Review* 43:292–308.
- Forrester, T. D. 2014. Fitness consequences of predation and forage for black-tailed deer in the California Coast Range. Ph.D. Dissertation. University of California, Davis.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58-63
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Geist, V. 1981. Behavior: adaptive strategies in mule deer. Pp. 157–223 in *Mule and black-tailed deer of North America* (O. C. Wallmo, ed.). University of Nebraska Press, Lincoln, NE.
- Gerhart, K. L., R. G. White, R. D. Cameron and D. E. Russell. 1996. Estimating fat content of caribou from body condition scores. *Journal of Wildlife Management* 60:713–718.
- Gervasi, V., E. B. Nilsen, H. Sand, M. Panzacchi, G. R. Rauset, H. C. Pedersen, et al. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. *Journal of Animal Ecology* 81:443–454.
- Gilbert, B. A. and K. J. Raedeke. 2004. Recruitment dynamics of black-tailed deer in the western cascades. *Journal of Wildlife Management* 68:120–128.

- Grambsch, P. M. and T. M. Therneau. 1994. Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–526.
- Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, et al. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology* 80:1246–1257.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165:1–32.
- Hamlin, K. L., S. J. Riley, D. Pyrah, A. R. Dood and R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48:489–499.
- Haydock, K. and N. Shaw. 1975. The comparative yield method for estimating dry matter yield of pasture. *Australian Journal of Experimental Agriculture* 15:663–670.
- Heisey, D. M. and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544–1555.
- Hodgman, T. P., B. B. Davitt and J. R. Nelson. 1996. Monitoring mule deer diet quality and intake with fecal indices. *Journal of Range Management* 49:215–222.
- Holechek, J. L., M. Vavra and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. *Journal of Range Management* 35:309–315.
- Hopcraft, J. G. C., H. Olf and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25:119–128.
- Hosmer, D. W., S. Lemeshow and S. May. 2011. *Applied survival analysis: regression modeling of time to event data*. John Wiley and Sons, Hoboken, New Jersey, USA.

- Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs* 178:1–33.
- Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.
- Jones, R. M. and J. N. G. Hargreaves. 1979. Improvements to the dry-weight-rank method for measuring botanical composition. *Grass and Forage Science* 34:181–189.
- Kie, J., T. Burton, J. Menke and W. Grenfell. 1984. Food habits of black-tailed deer, *Odocoileus hemionus columbianus*, in Trinity County, California. *California Fish and Game* 70:183–186.
- Leslie, D. M., Jr., M. Vavra, E. E. Starkey and R. C. Slater. 1983. Correcting for differential digestibility in microhistological analyses involving common coastal forages of the Pacific Northwest. *Journal of Range Management* 36:730–732.
- Livezey, K. 1991. Home range, habitat use, disturbance, and mortality of Columbian black-tailed deer in Mendocino National Forest. *California Fish and Game* 77:201–209.
- Lingle, S., A. Feldman, M. S. Boyce and W. F. Wilson. 2008. Prey behavior, age- dependent vulnerability, and predation rates. *The American Naturalist* 172:712–725.
- Lingle, S., S. M. Pellis and W. F. Wilson. 2005. Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. *Journal of Animal Ecology* 74:1140–1149.
- Linnell, J. D., R. Aanes and R. Anderson. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology*. 1:209–223.

- Lomas, L. A. and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *Journal of Wildlife Management* 71:884–894.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey and J. E. Hines. 2005. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, Elsevier, New York, USA.
- Marescot, L., T. D. Forrester, D. S. Casady and H. U. Wittmer. In Press. Using multistate capture-mark-recapture models to quantify effects of predation on age-specific survival and population growth in black-tailed deer. *Population Ecology*. DOI: 10.1007/s10144-014-0456-z
- McCorquodale, S. M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat basin of Washington. *Journal of Wildlife Management* 63:861–871.
- McNaughton, S. J., M. Oesterheld, D. A. Frank and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144.
- Miller, J. R. B., J. M. Ament and O. J. Schmitz. 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology* 83:214–222.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, et al. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Moorter, B. V., J.-M. Gaillard, P. D. McLoughlin, D. Delorme, F. Klein and M. S. Boyce. 2009. Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. *Oecologia* 159:669–678.

- Owen-Smith, N. and M. G. L. Mills. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator–prey web. *Ecology* 89:1120–1133.
- Parker, K. L., P. S. Barboza and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57–69.
- Parker, K. L. and B. Wong. 1987. Raising black-tailed deer fawns at natural growth rates. *Canadian Journal of Zoology* 65:20–23.
- Pierce, B. M., V. C. Bleich, K. L. Monteith and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *Journal of Mammalogy* 93:977–988.
- Radloff, F. G. T. and J. T. Du Toit. 2004. Large predators and their prey in a southern African savanna: a predator’s size determines its prey size range. *Journal of Animal Ecology* 73:410–423.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, et al. 2014. Status and ecological effects of the world’s largest carnivores. *Science* 343:1241484.
- Rowcliffe, J. M., J. Field, S. T. Turvey and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228–1236.
- Royston, P. and W. Sauerbrei. 2004. A new approach to modelling interactions between treatment and continuous covariates in clinical trials by using fractional polynomials. *Statistics in Medicine* 23:2509–2525.

- Sams, M. G., R. L. Lochmiller, E. C. Hellgren, W. D. Warde and L. W. Varner. 1996. Morphometric predictors of neonatal age for white-tailed deer. *Wildlife Society Bulletin* 24:53–57.
- Schmitz, O. J. 2008. Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 39:133–152.
- Schwind, B. and H. Gordon. 2001. CALVEG geobook: A comprehensive information package describing California's wildland vegetation, version 2. USDA Forest Service, Pacific Southwest Region, Sacramento, CA.
- Shafer, E. L. 1963. The twig-count method for measuring hardwood deer browse. *Journal of Wildlife Management* 27:428–437.
- Sikes, R. S. and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358:1729–1740.
- Sinclair, A. R. E. and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:1221–1231.
- Sinclair, A. R. E., S. Mduma and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425:288–290.
- Therneau, T. M. and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer, New York, USA.

- Unsworth, J. W., D. F. Pac, G. C. White and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315–326.
- Vreeland, J. K., D. R. Diefenbach and B. D. Wallingford. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. *Wildlife Society Bulletin* 32:542–553.
- Wallmo, O. C. (ed.). 1981. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln, USA.
- White, R. G. 1992. Nutrition in relation to season, lactation, and growth of north temperate deer. Pp. 407–417 in *The Biology of Deer* (R. D. Brown, ed.). Springer New York.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- Whittingham, M. J., P. A. Stephens, R. B. Bradbury and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75:1182–1189.
- Zager, P. and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17:95–108.

Table 2.1 – Cause specific mortality rates, total mortality, and survival rates calculate from cumulative incidence functions (CIF) for black-tailed deer fawns in Mendocino National Forest from 2009-2013.

Cause of Mortality	Month 1	Month 2	Summer Mortality	Month 6	Month 9	Annual Mortality
Bear	0.19	0.20	0.21	0.21	0.21	0.21
Coyote	0.09	0.13	0.14	0.14	0.14	0.14
All Feline Predation	0.02	0.04	0.05	0.06	0.06	0.06
Unknown Predation	0.02	0.03	0.03	0.03	0.04	0.05
Malnutrition	0.10	0.10	0.10	0.10	0.10	0.10
Unknown Cause	0.04	0.04	0.07	0.11	0.15	0.19
Total Mortality	0.46	0.54	0.60	0.65	0.70	0.75
Survival	0.54	0.46	0.40	0.35	0.30	0.25

Table 2.2 - Model averaged Cox proportional hazard ratios for summer hazards models including standard errors and confidence intervals with summed Akaike model weights (w_i) from all subsets of models. Hazard ratios >1 or <1 indicate an increase or decrease in mortality risk respectively, and covariates significantly explain mortality risk if the model averaged 95% confidence intervals do not overlap 1. The hazard ratio for the twin covariate is the risk of mortality of twins compared to single fawns and the sex hazard ratio is the risk of being a male fawn compared to female fawns.

Summer Mortality Risk Covariates	Summed Model Weights (w_i)	Model Avg. Hazard Ratios	Model Avg. SE	Model Avg. 95% CI
Capture Weight	0.98	0.98	0.01	0.97 – 0.99
Oak Forage Biomass	0.97	0.86	0.05	0.77 – 0.95
Twin Status	0.76	1.54	0.22	1.00 – 2.39
Herbaceous Forage Biomass	0.62	0.92	0.06	0.82 – 1.03
All Predators Relative Abundance	0.37	0.94	0.08	0.81 – 1.09
Sex	0.33	1.07	0.10	0.89 – 1.30
April Precipitation	0.29	0.96	0.08	0.81 – 1.13
Winter Precipitation	0.27	1.00	0.01	0.99 – 1.01

Table 2.3 - Summed Akaike model weights (w_i) from all subsets of models and model averaged sub-hazard ratios (SHR), covariate standard errors (SE), and confidence intervals (CI) calculated from cumulative incidence function (CIF) models for the summer predation risk of black-tailed deer fawns from black bear and coyote. Sub-hazard ratios indicate an increase or decrease in predation risk if they are >1 or <1 respectively, and covariates significantly affect predation risk if the model averaged 95% confidence interval do not overlap 1. The sub-hazard ratio for twin status is the risk of predation of twins compared to single fawns and the sex sub-hazard ratio is the risk of being a male fawn compared to female fawns.

Covariates	Black Bear Models				Coyote Models			
	w_i	SHR	SE	95% CI	w_i	SHR	SE	95% CI
Coyote Relative Abundance	0.54	0.86	0.25	0.53 – 1.41	0.29	0.96	0.23	0.63 – 1.47
Bear Relative Abundance	0.64	0.89	0.15	0.66 – 1.20	0.36	0.88	0.17	0.66 – 1.16
Herbaceous Forage Biomass	0.27	0.99	0.03	0.93 – 1.05	0.40	0.94	0.02	0.84 – 1.07
Oak Forage Biomass	0.32	0.98	0.03	0.93 – 1.03	0.89	0.77	0.13	0.60 – 0.98
Capture Weight	0.33	0.94	0.07	0.82 – 1.06	0.48	0.80	0.19	0.56 – 1.13
Twin Status	0.35	1.15	0.14	0.88 – 1.51	0.33	1.17	0.22	0.80 – 1.73
Sex	0.35	0.87	0.14	0.67 – 1.13	0.29	1.12	0.19	0.80 – 1.56

Table 2.4 – Winter mortality results from all possible subsets of Cox proportional hazards models, including the summed Akaike model weights (w_i) and model averaged hazard ratios, covariate standard errors (SE), and confidence intervals (CI). Hazard ratios values greater than one or less than one indicated an increase or decrease in mortality risk respectively, and covariates significantly explain mortality risk if the model averaged 95% confidence interval does not cross 1. Sex shows the risk of being male compare to being female, total browse shows the change in mortality risk for each hectare of shrub habitat in the winter range, puma risk is the change in risk for every 100 meter difference between puma and deer average winter elevation, winter severity is the number of days below freezing, precipitation is cumulative precipitation, total oak shows the change in mortality risk for each additional hectare of oak habitat on winter range, and twin status is the risk of being a twin compared to a single fawn.

Winter mortality risk covariate	w_i	Hazard Ratios	SE	95% CI
Sex	0.91	0.27	0.56	0.09 – 0.80
Total Browse	0.78	1.14	0.07	0.99 – 1.31
Puma Risk	0.66	1.44	0.24	0.90 – 2.30
Winter Severity	0.38	1.00	0.0001	1.00 – 1.01
Precipitation	0.35	0.98	0.02	0.94 – 1.02
Total Oak	0.29	1.01	0.01	0.98 – 1.03
Twin Status	0.28	0.90	0.18	0.63 – 1.29

Figure 2.1 - Study area in the context of the state of California, showing the 3 watersheds and 2 main ridges (M1 and FH7). White areas indicate higher elevation while darker areas are lower elevation. Deer fawning areas are named and shown in dark gray and winter ranges are shown in white.

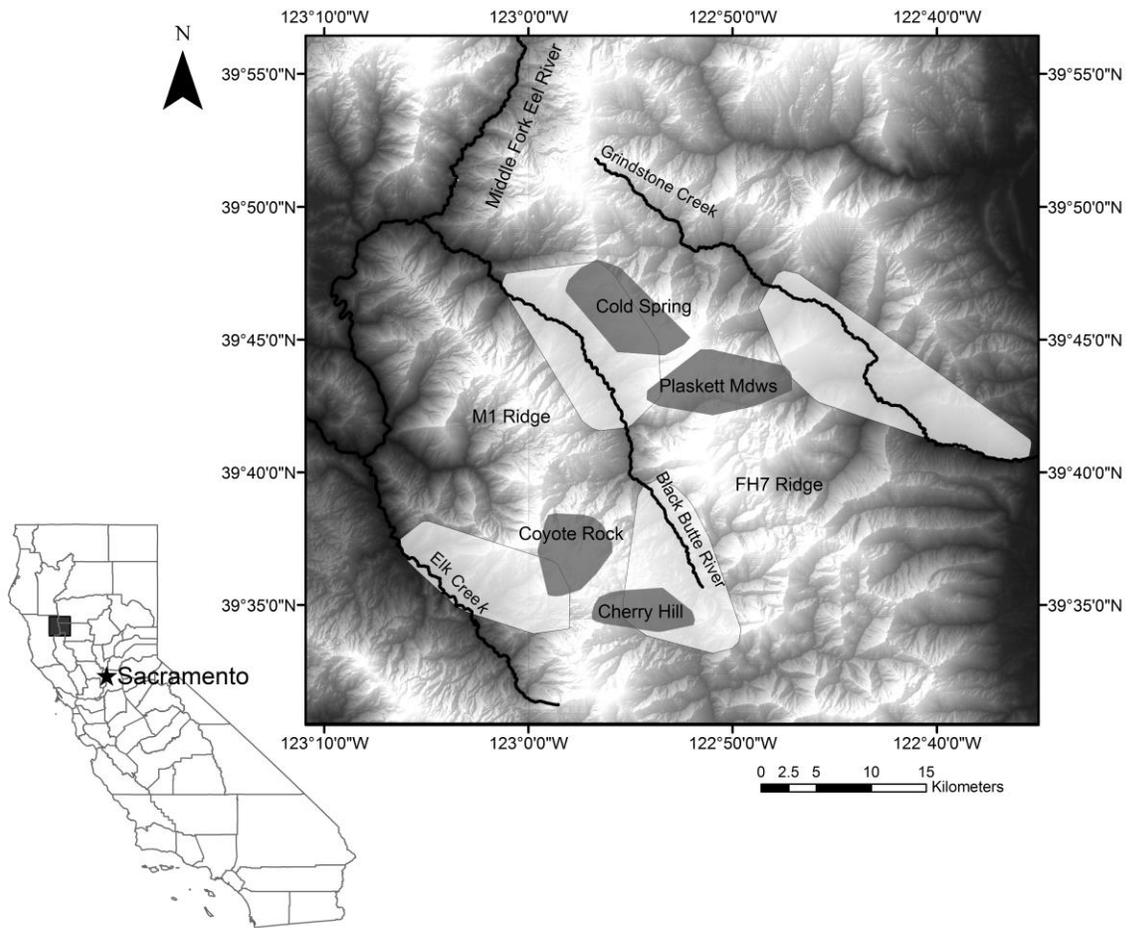


Figure 2.2 - Causes of mortality of black-tailed deer fawns in the Mendocino National Forest from 2009-2012 separately during the first 3 months of life and combined for the entire year.

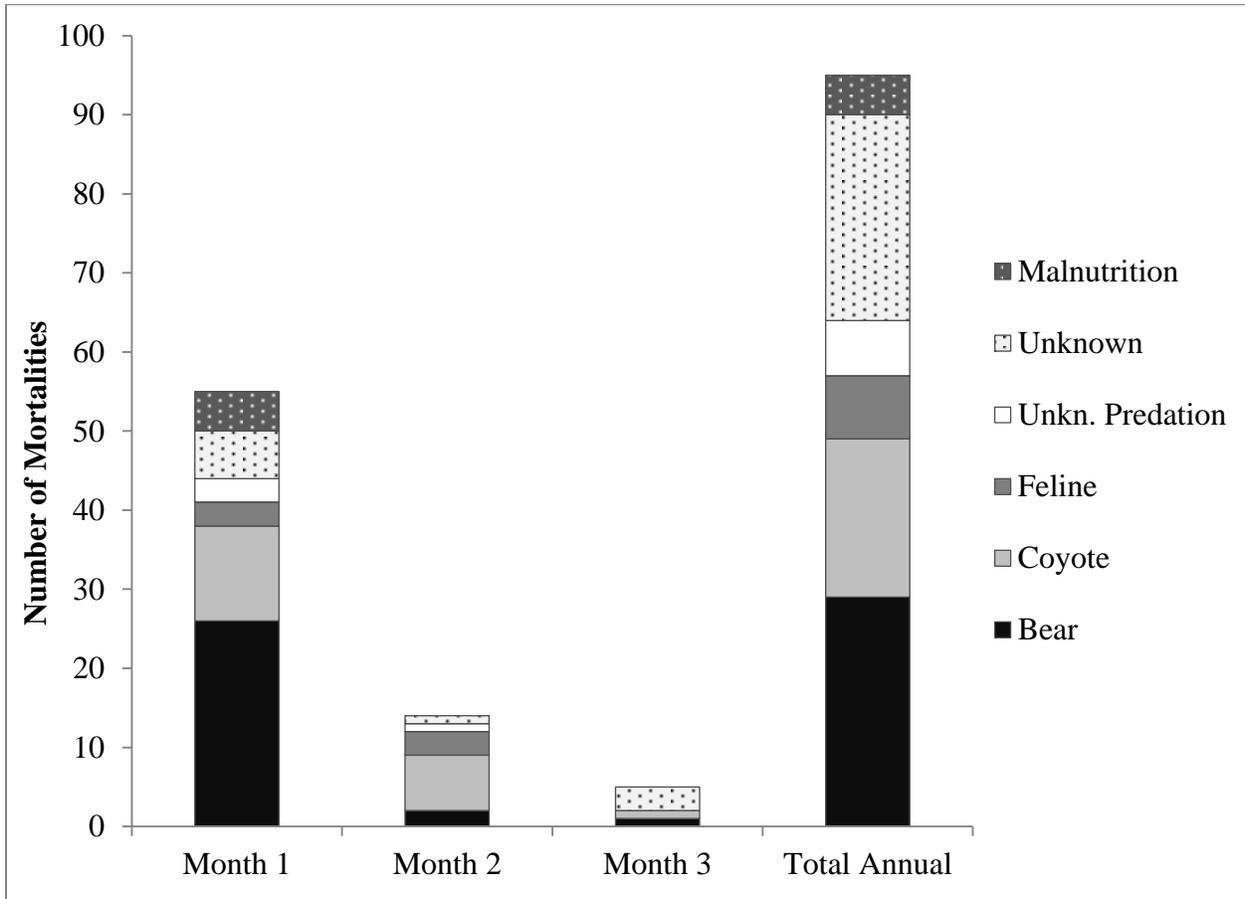
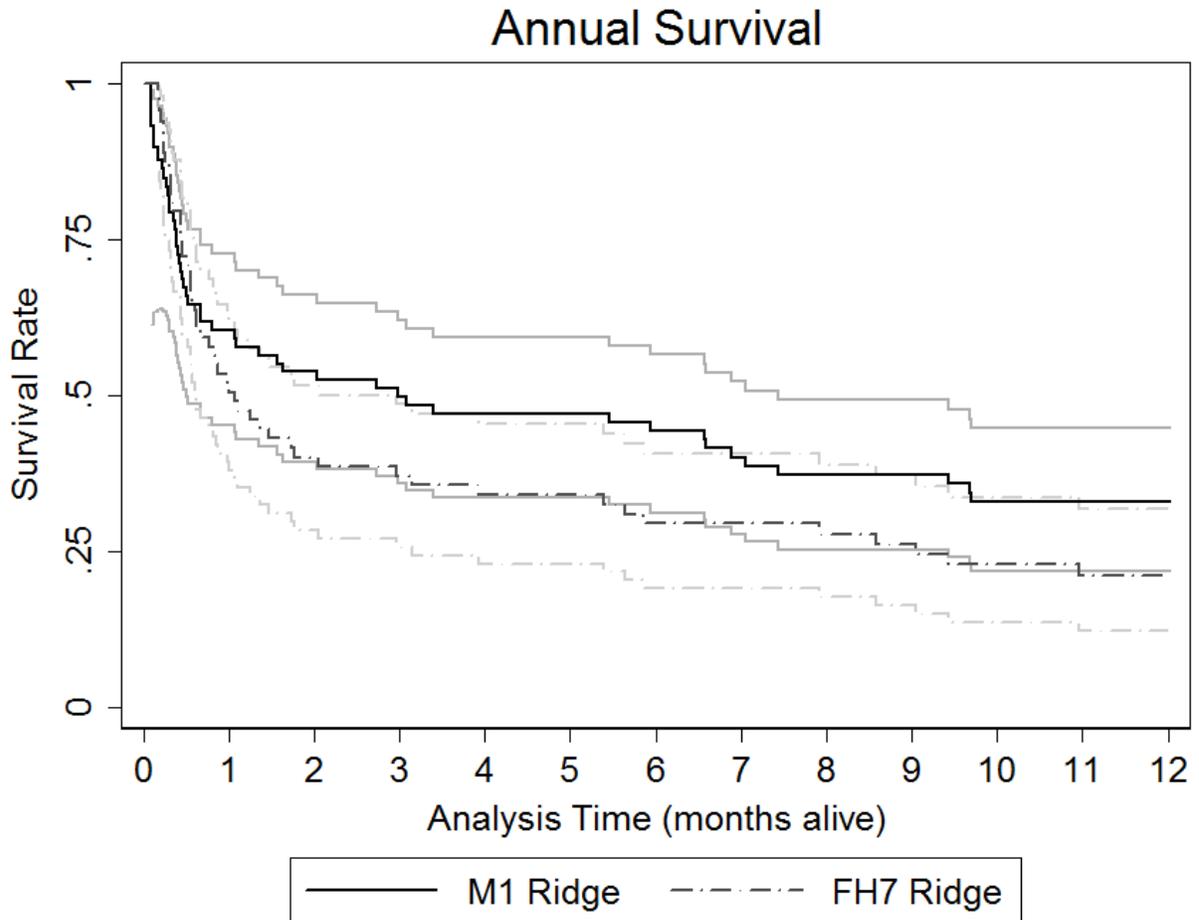


Figure 2.3 - Ridge specific Kaplan-Meier annual survival rates for black-tailed deer fawns in the Mendocino National Forest from 2009-2013. Confidence intervals (95%) are shown in gray.



Appendix 2.1 - Deer Diet, Forage Quality, and Common Shrub Species

1) We estimated deer diet based on microhistological analysis of deer pellets (Holechek and Gross 1982; Leslie et al. 1983) collected in the study area and as described in the Methods. A local plant list and samples of requested species were sent to the Wildlife Habitat and Nutrition Lab at Washington State University to aid with identification. The diet composition of black-tailed deer is presented in percent (\pm SE) for each of the 4 identified fawning areas in Table 1. Diet composition was similar across fawning areas with the exception of Plaskett Meadows which had a lower proportion of oak leaves (Kruskal-Wallis, $\chi^2 = 8.12, P = 0.043$) and a higher proportion of other shrub species (Kruskal-Wallis, $\chi^2 = 7.92, P = 0.047$) than other fawning areas.

2) Forage quality of Brewer's oak (*Quercus garryana breweri*) and mountain whitethorn ceanothus (*Ceanothus cordulatus*), the species most frequently eaten by deer in our study area, were estimated from plant samples collected from each fawning area. Samples of each species were collected at a minimum of 4 separate locations per fawning area (varied from 4-6), and from several different plants at each location. Multiple leaves were harvested from each plant from twigs smaller than the average deer browse diameter for the species (see Methods). The combined samples from each fawning area were analyzed for crude protein, gross energy (calories/gram), in-vitro dry matter digestibility (% IVDM), detergent fiber levels, and tannins (Martin and Martin 1982). Samples from distinct fawning areas were blended for analysis to obtain fawning area averages. Since averages did not vary among fawning areas, we calculated averages for each species across all fawning areas (Table 2). Whitethorn ceanothus had significantly higher gross energy than Brewer's oak ($t_{5,7} = 12.20, P < 0.001$), but lower IVDM

($t_{5,7} = -2.45, P = 0.028$), protein ($t_{5,7} = -2.06, P = 0.047$), and higher tannin concentrations ($t_{5,7} = 2.046, P = 0.048$).

3) We surveyed all fawning areas in 2010 and 2011 to quantify percent cover of deer forage types and to estimate biomass of shrubs, forbs, and grasses. Herbaceous vegetation was also surveyed in 2012. We calculated percent cover and forage biomass for each fawning area for use as covariates in survival models and report the percent coverage of all species in the entire study area in Table 3.

LITERATURE CITED

- Holechek, J. L. and B. D. Gross. 1982. Evaluation of different calculation procedures for microhistological analysis. *Journal of Range Management* 35:721–723.
- Leslie, D. M., Jr., M. Vavra, E. E. Starkey and R. C. Slater. 1983. Correcting for differential digestibility in microhistological analyses involving common coastal forages of the Pacific Northwest. *Journal of Range Management* 36:730–732.
- Martin, J. S. and M. M. Martin. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia* 54:205–211.

Table A2.1 – Diet composition (%) of black-tailed deer by fawning area in the Mendocino National Forest, California during the years of 2010-2013. Both the 3-year average and standard error (SE) are reported. Fawning area names are followed by the name of the ridge in parentheses.

Forage Type	Cherry Hill (M1)		Coyote Rock (M1)		Cold Spring (FH7)		Plaskett Meadows (FH7)	
	3-year average	SE	3-year average	SE	3-year average	SE	3-year average	SE
<i>Quercus</i> spp.	76.1	0.03	65.4	8.03	73.6	7.53	21.8	7.16
<i>Ceanothus</i> spp.	6.5	0.80	1.6	0.15	3.8	0.98	8.5	0.70
Other Shrubs	5.4	0.93	16.1	4.68	8.4	6.54	23.2	3.36
Conifers	1.0	0.67	2.9	0.78	1.4	0.52	5.0	1.80
Forbs	2.1	0.35	3.9	1.28	4.8	2.36	11.5	3.54
Grasses	0.9	0.38	1.0	0.67	2.7	1.19	4.4	1.44
Lichen	6.2	0.44	6.5	2.71	2.8	1.89	14.2	2.79
Other Forage	1.8	0.39	2.6	0.38	2.4	0.61	11.3	1.40

Table A2.2 – Forage quality of the two most common shrub species in the diet of black-tailed deer in the Mendocino National Forest, California during 2011-2013. IVDM stands for in-vitro digestible matter and tannins are reported as the milligrams precipitated with a standard assay divided by the amount of forage, and are a measure of the potential amount of tannin that can bind with protein and prevent digestion.

Shrub spp.	% Crude	Gross	% IVDM	% Neutral	% Acid	% Acid	Tannin
	Protein	Energy (cal/gm)		Detergent Fiber	Detergent Fiber	Detergent Lignin	
<i>Quercus</i>							
<i>garryana</i>	17.2	4746	68.4	36.6	21.8	7.5	0.11
<i>breweri</i>							
<i>Ceanothus</i>							
<i>cordulatus</i>	11.2	5062	56.9	26.3	18.3	7.0	0.16

Table A2.3 – Most common shrub species from line transect surveys on summer fawning areas in the Mendocino National Forest, 2010-2011. The barren cover type primarily encompasses the duff layer underneath dense forest canopy, as well as bare dirt and rock.

Cover Type or Species Name	Scientific Name	Overall Percent Cover
Barren	NA	47.1
Herbaceous	NA	13.1
Whitethorn Ceanothus	<i>Ceanothus cordulatus</i>	8.1
Brewer's Oak	<i>Quercus garryana breweri</i>	7.1
White Fir	<i>Abies concolor</i>	5.4
Snow Berry spp.	<i>Symphiocarpus</i> spp.	3.3
Red Fir	<i>Abies magnifica</i>	1.9
Live Oak spp.	<i>Quercus agrifolia</i> / <i>Q. wislizeni</i> / <i>Q. chrysolepis</i>	2.1
Gooseberry/Currant spp.	<i>Ribes</i> spp.	1.4
Whiteleaf Manzanita	<i>Arctostaphylos viscida</i>	1.4
Wild Rose	<i>Rosa</i> spp.	1.1
Fern spp.	<i>Polystichum</i> and <i>Pteridium</i> spp.	0.8
Bitter Cherry/Choke Cherry	<i>Prunus</i> spp.	0.8
Ponderosa Pine	<i>Pinus ponderosa</i>	0.8
Willow spp.	<i>Salix</i> spp.	0.7

VII. Chapter 3: Home sweet home: Fitness consequences of site familiarity in black-tailed deer

Tavis D. Forrester¹

Wildlife, Fish, and Conservation Biology, University of California, One Shields Ave., Davis, CA 95616, USA.

David S. Casady

California Department of Fish and Wildlife, Large Mammal Conservation Program, 1812 9th Street, Sacramento, CA 95811, USA.

Heiko U. Wittmer

Victoria University of Wellington, School of Biological Sciences, PO Box 600, Wellington 6140, New Zealand.

¹ *Current Address: Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Rd Front Royal, VA 22630, USA*

Abstract

Individual animals strive to maximize fitness by gaining access to food while minimizing predation risk, and spatial knowledge of both forage resources and predation risks has long been presumed to be advantageous. Actual fitness benefits of site familiarity, however, have rarely been demonstrated. We placed GPS collars on 57 female black-tailed deer (*Odocoileus hemionus columbianus*) in coastal California over 4 years to track seasonal movements, determine home ranges, and monitor survival and cause of mortality. We used the seasonal home range as a measure of site familiarity and modeled how mortality risk varied with use of familiar areas,

forage availability, age class, and elevational overlap with simultaneously collared pumas using Cox proportional hazards models. The use of familiar areas was the best predictor of mortality risk, and deer that had a 40% probability of leaving their home range in a given week were 4 times more likely to die than deer that never left their home range. Puma predation was the largest cause of mortality and deer whose average weekly elevation was above or below the average elevation of pumas were less likely to die. While forage availability was not related to mortality risk, deer with lower forage availability were more likely to leave their home range during both summer and winter. Our results provide a rare example of fitness benefits associated with site familiarity and the use of familiar areas as a refuge from predation. The benefits of site familiarity likely are widespread in ungulates, especially when there are stable home ranges, complex habitats, and few cues of predation risk.

Keywords forage availability, home range, *Odocoileus hemionus columbianus*, predation, private information, *Puma concolor*

Individuals maximize fitness by optimizing the trade-off between forage intake and the risk of predation (Sih 1980; Kie 1999). Both access to high quality forage and avoidance of predators are ultimately linked to the physical space or habitat individuals occupy. Individuals with better information should thus be expected to have greater fitness (Dall et al. 2005). This supposition has led to an enduring belief among behavioral ecologists that familiarity with a physical space, or site familiarity, improves individual fitness (Baker 1978; Greenwood and Harvey 1982; Stamps 1995; Harwood et al. 2003). Benefits associated with site familiarity have also been proposed as the mechanism underlying the widespread occurrence of site fidelity in multiple taxa (Switzer 1993; Wolf et al. 2009). Many species expend great effort to return to previously occupied seasonal ranges, often migrating over large distances, and such fidelity to a particular location has been shown to enhance survival and reproductive success (Switzer 1993). Although it is assumed that the mechanisms of these benefits are related to site familiarity, the actual fitness consequences of site familiarity have rarely been demonstrated (Piper 2011).

The main proximate mechanism underlying site familiarity is the spatial memory of resources and physical habitat features (Piper 2011; Spencer 2012), which can occur across different scales (van Beest et al. 2013). Home ranges (or territories in species defending exclusive access to an area) are the result of decisions made by individuals at multiple scales, ranging from the selection of habitats from those available over larger areas (Johnson 1980) to decisions made during daily movements and foraging bouts (Wolf et al. 2009; van Beest et al. 2013). The home range thus represents an animal's best solution to optimize energy intake while simultaneously minimizing the risk of predation. Within home ranges, familiarity has been linked to advantages such as increased use of high quality forage patches after an initial learning period (Wolf et al. 2009) and better ability to escape from simulated predators (Clarke et al.

1993). Fitness consequences associated with site familiarity should also occur at the home range scale.

Much of our understanding of the advantages associated with site familiarity comes from studies on birds (Piper 2011). Ungulates should also benefit from site familiarity because many species show high fidelity to seasonal home ranges (Edge et al. 1985; Purdue et al. 2000; Wittmer et al. 2006) and are long-lived, both important traits for spatial learning (Piper et al. 2008; Spencer 2012). Ungulates also utilize spatial knowledge at several scales, showing plasticity in home range size and seasonal movements (Fryxell and Sinclair 1988). Variation in these behaviors has already been linked to seasonal variation in forage quality (Garrott et al. 1987; Pettorelli et al. 2007) as well as predation risk (Fryxell et al. 1988; Wittmer et al. 2006), highlighting the potential benefits of site familiarity in ungulates (van Beest et al. 2013).

Black-tailed deer (*Odocoileus hemionus columbianus*), a subspecies of mule deer, occupy complex forested habitats in coastal areas of western North America. Both species are known to move between seasonal ranges, and their fidelity to these ranges is well documented (Geist 1981; Garrott et al. 1987; McCorquodale 1999). Seasonal home ranges are comparatively small for their body size, particularly in forested areas with high resource availability (Geist 1981). The small size of seasonal ranges combined with documented among-year fidelity suggests that site familiarity should be an important fitness determinant in these species.

Black-tailed deer, like other ungulates, also are well suited for studies of site familiarity since their body size allows researchers to fit them with GPS collars that provide data required to understand potential benefits of familiarity including habitat use and selection, movements, survival probabilities and cause of mortality. Here we report the fitness consequences of site familiarity determined from a study of black-tailed deer in northern California over 4 years. We

placed GPS collars on 57 female deer to a) track seasonal movements, b) determine seasonal home ranges, and c) monitor survival and cause of mortality. We used the seasonal home range as a measure of site familiarity to examine how predation risk varied in familiar and unfamiliar areas, while accounting for the effects of forage availability and age class on survival (Loison et al. 1999; Hopcraft et al. 2010). Specifically, we tested the following predictions of the effects of site familiarity on the use of space by black-tailed deer: H1) The risk of death will be lower inside compared to outside seasonal home ranges. H2) If H1 is true then deer with more forage availability within their home range will be less likely to leave identified home ranges. H3) Territory size should decrease with age as spatial learning occurs. H4) Older deer will be less likely to leave their home range due to improved familiarity with the distribution of forage and predation risk.

Materials and Methods

Study Area

Our ~1000 km² study area spanned three watersheds and two large ridges in the California coastal mountains and was located almost completely within the Mendocino National Forest (Figure 1). Terrain was rugged and steep except on ridge tops. Vegetation at low elevations included mixed oak woodlands (*Quercus* spp.), dense chaparral, and grasslands, while mid-elevations were comprised mainly of mixed coniferous forests dominated by pine (*Pinus* spp.) and Douglas-fir (*Pseudotsuga menziesii*). High elevation plant communities were a mix of true fir (*Abies* spp.), shrub species (e.g., *Ceanothus* spp., *Prunus* spp.), and scattered dry and wet

meadows. Important deer forage included herbaceous plants, *Ceanothus* shrubs, and oak leaves. Almost all precipitation (mean = 1320 mm) occurred from October through April. Snow was generally limited to elevations >950 meters and occurred irregularly during dry winters.

The study area supported a diverse predator community that included pumas (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Black-tailed deer were the only resident ungulate. Female black-tailed deer spent summer and winter clustered in habitats with high-quality forage (Figure 1). Summer ranges were located on ridge tops where females also gave birth, and winter ranges were in drainages at lower elevations. Deer usually traveled the short distance (typically 5-10 km) between their seasonal ranges in a single day (unpublished data). Pumas tracked elevational movements of deer, although GPS location data of simultaneously fitted individuals showed that the mean summer elevation used by collared deer was higher than that of pumas in our study area (Allen et al. 2014).

Adult deer capture, monitoring and mortality assessment

We captured 60 adult female deer on high-elevation summer ranges from 2009-2013 and fitted them with GPS collars (LotekTM or TelonicsTM) programmed to record locations every 1 to 5 hours. Capture methods were described in Casady and Allen (2013) and all procedures were approved by an Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886). Three individuals died from capture-related mortalities and were censored from all analyses. GPS collars of 7 individuals failed prior to retrieval of location data and were thus excluded from our mortality risk analysis (see below). Age of deer was

determined based on cementum annuli methods and based on observed differences in survival probabilities were grouped into the following 3 age categories: yearlings (1-2 years old), prime-aged adults (2-7 years old), and senescent individuals (>8 years) (Marescot et al. 2015).

We monitored deer status from the ground every 1-4 days from mid-June through mid-September, and every 7-14 days from the ground or the air during the rest of the year. Collars were programmed to switch to a mortality signal after 4 hours of inactivity to facilitate mortality recovery. Mortalities on summer range typically were recovered within 1 week of first detection (mean=8.2 days, SE=1.8), while investigation of mortalities during winter was often delayed due to inclement weather and difficulties accessing winter range (mean=147.5 days, SE=19.5). Cause of mortality was determined during site investigations using systematic criteria including disposition of the carcass, predator sign, evidence of caching, bite marks, and blood (Atkinson and Janz 1994).

Home range, vegetation, and weather

Home ranges were estimated at the 95% isopleth using the local convex hull (LoCoH) method with the “minimum spurious hole covering” rule (Getz and Wilmers 2004; Getz et al. 2007). We estimated individual home ranges for summer and winter separately based on observed patterns in space use and excluded locations during distinct elevational movements. We then calculated the weekly probability of deer leaving their home range by dividing the number of locations outside the home range by the total number of locations for each week. We chose a weekly interval because pumas in our study area killed an average of 1.07 deer per week (Allen et al. 2014). We assigned individuals to distinct summer and winter ranges using spatial gaps in the

GPS data greater than twice the size of the average diameter of an adult home range and geographic features that created barriers to movement. The extent of these distinct seasonal ranges was determined using 95% minimum convex polygons (MCPs) from GPS locations of all collared deer within each seasonal range.

Detailed vegetation data were collected on summer and winter ranges using a combination of remote sensing and vegetation surveys. All vegetation types were classified according to the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG), a vegetation classification system developed by the United States Forest Service that uses infrared satellite imagery and field verification to classify multiple vegetation types in terms of overall cover type (e.g., conifers, shrubs) and detailed vegetation classes (e.g., ponderosa pine *Pinus ponderosa*) (Brohman et al. 2005). In addition, we quantified the biomass of important deer forage (including forbs, grasses, shrubs and trees) on summer range using plant surveys (Forrester 2014). We focused on summer vegetation because of the critical need for quality nutrition during late pregnancy and lactation (Parker et al. 2009).

We estimated the amount of summer forage available to each deer by calculating the amount of forage for each CALVEG habitat type within individual home ranges (forage $\text{g/m}^2 \times$ habitat area), summing these values for all habitat types and then dividing by the total area. Herbaceous biomass varied among years and therefore was calculated separately for each year. Shrub biomass varied little among years and its availability was calculated for all years combined. We also created a forage availability index for summer and winter home ranges by calculating the area of high-quality forage CALVEG vegetation types in individual home ranges using ArcGIS. High-quality CALVEG vegetation types included oak woodland, herbaceous, and shrub species preferred by black-tailed deer (Dasmann and Taber 1956; Wallmo 1981).

We acquired daily precipitation and temperature data from 4 United States Geological Survey (USGS) weather stations and snowpack depth from 2 California state snow monitoring areas located in the study area. We defined a winter severity index as the number of days below freezing (0°C) from arrival on winter range to each week during the year. We accounted for difference in elevation between deer home ranges and weather stations by adjusting the temperature of the weather station nearest the winter range by the standard environmental lapse rate of 6.49°C per 1000 meters elevation. Our weather variables included winter severity index, total precipitation to date, previous total winter precipitation, and total April snowpack.

Statistical analysis

We used Kaplan-Meier procedures (Pollock et al. 1989) based on weekly encounter histories to determine survival rates. We tested for differences in survival among years, age classes, and seasons, and between individual summer and winter ranges using log-rank tests (Cleves et al. 2010).

We used cumulative incidence functions (CIFs) to calculate the summer, winter, and annual cause-specific mortality rates of deer, and used the delta method to calculate associated standard errors (Coviello and Boggess 2004). Cumulative incidence functions model the risk of death occurring from one of several causes as the probability of the time of death (T) from cause i occurring before time t :

(Equation 1)
$$\text{CIF}_i(t) = P(T \leq t \text{ and death from cause } i).$$

We examined how forage availability, proximity to predators, weather, and individual deer characteristics affected the risk of mortality and the probability of a deer spending time

outside its home range using an *a priori* set of models (Appendix 1). We used the amount of summer herbaceous and oak forage and the area of herbaceous and oak CALVEG cover types within a seasonal home range in the “forage” model. We used the distance between the mean monthly elevation of pumas and deer (Allen et al. 2014) in the “proximity to predators” model. We created a “weather” model with precipitation and the number of freezing days as time varying covariates for each weekly encounter date. The “individual deer” model consisted of age class and the probability a deer was inside or outside the 95% isopleth of its seasonal LoCoH home range. We also tested for combinations of each of the variables (e.g., forage + proximity to predators + weather). Prior to our analysis, we ensured covariates were not highly correlated (i.e., correlation coefficients $<|0.7|$).

We modeled the risk of mortality using Cox proportional hazards (Cox 1972; Therneau and Grambsch 2000), following the standard form:

$$\text{(Equation 2)} \quad h(t|\mathbf{X}_j) = h_0(t)\exp(\mathbf{X}_j\beta_x),$$

where $h(t|\mathbf{X}_j)$ is the hazard rate for the j th deer at time t , $h_0(t)$ is the baseline hazard function, and the regression coefficients β_x are estimated from the risk covariates \mathbf{X}_j for the j th deer. The β_x are used to estimate hazard ratios that are a measure of the risk of death, where the hazard ratios are the exponential functions of the β 's from equation 1 and a hazard ratio (HR) of less than or greater than 1 represents a smaller or greater chance of death respectively. We considered a hazard ratio significantly different than 1 if the 95% confidence interval did not overlap 1. We used a delayed entry design with left and right censored data with survival time based on biological years (Fieberg and DelGiudice 2009) beginning on June 1st where deer entered the analysis at capture and exited upon death or dropping their GPS collar (Hosmer et al. 2011).

We modeled the probability a deer stepping outside the 95% isopleth of its seasonal home range with a multiple failure Cox proportional hazards model (Therneau and Grambsch 2000). Deer were counted as outside of their range if any locations fell outside the home range on the day selected for the encounter history. In this application of the model the hazard ratio was an odds ratio that measured the probability of leaving the home range, and the β_x were used to estimate the odds ratios for each covariate. We used the same model set described in the survival analysis above.

We tested the assumption of proportional hazards for covariates in Cox hazards and CIF models using graphical methods and Schoenfeld residual plots (Grambsch and Therneau 1994). If time varying variables violated the proportional hazard assumption we interacted the variables with an appropriate time function (Therneau and Grambsch 2000; Cleves et al. 2010; Hosmer et al. 2011). We assessed model fit by plotting the cumulative hazard function against the Cox-Snell residuals and testing for a 1:1 fit (Therneau and Grambsch 2000).

We selected models using Akaike Information Criterion adjusted for small sample sizes (AIC_c) and present models within 4 AIC_c units of the best model (Burnham and Anderson 2002). We considered nested models as competitors for best model only if parameters in the model were significant at the 0.1 level or if parameters were not merely a subset of the competing model (Burnham and Anderson 2002; Arnold 2010). If multiple non-nested models were within 4 ΔAIC_c of the best model we report model-averaged parameters (Burnham and Anderson 2002).

We conducted post-hoc analyses to test if lower survival probabilities of senescent deer could be attributed to differences in home range composition and habitat selection between age classes. We tested for differences in the amount of forage inside home ranges of prime-aged and senescent individuals using repeated measures analysis of variance (rANOVA), or Friedman's

test for repeated measures if variables could not be transformed to meet normality assumptions, with age class as the independent variable and amount of specific habitats as dependent variables. We tested if the amount of forage within a home range was normally distributed with the Shapiro-Wilk test and used Bartlett's test to determine if variance was homoscedastic.

Results

Survival rates

A total of 21 deer died during the study. There were no differences in survival between winter and summer ranges (LR test, $\chi^2_{df=1}=0.15$, $p=0.70$) or among the 9 identified seasonal ranges (LR test, $\chi^2_{df=8}=9.28$, $p=0.319$). There also was no significant difference in annual survival among years (LR test, $\chi^2_{df=3}=4.81$, $p=0.308$). Annual survival differed among age classes (LR test, $\chi^2_{df=2}=6.15$, $p=0.046$), with prime-aged females experiencing higher survival (0.78, SE=0.06, CV=0.10) than both yearlings (0.64, SE=0.16, CV=0.39) and senescent individuals (0.60, SE=0.15, CV=0.69).

Predation was the primary cause of mortality in all seasons, although delays retrieving winter mortalities resulted in a high number of unknown mortalities on winter range (Table 1). All predation mortalities but one were due to pumas. A 2-year-old nutritionally stressed deer was killed by a black bear.

Mortality risk analysis and mortality location

We pooled data across years since there were no significant differences in survival. All environmental covariates met proportional hazard assumptions. Three competing models were within 4 ΔAIC_c of the top model so we averaged model parameters. The best predictor of mortality risk was the probability of leaving an individual home range. Individuals with a 40% probability of stepping outside their respective home ranges within a given week were 4 times more likely to die than deer that never left their home range (Table 2). Of the 21 observed mortalities, 13 occurred outside respective 95% home range isopleths. Distances of mortalities to nearest home range boundaries averaged 1171 m (SE = 325 m), with 8 mortalities >700 m outside identified home ranges. Mortality risk was reduced by 3% for each additional hectare of herbaceous habitat within a home range and by 10% for every 100 m difference in mean monthly elevations of simultaneously collared pumas. Senescent individuals were 2 times more likely to die than prime aged deer, although the 95% confidence interval for the hazard ratio slightly overlapped 1. Mortality risk for deer remained constant for most of the year but declined in spring (Figure 2). Weather, biomass of summer forage, and amount of oak habitat within individual home ranges did not predict variation in mortality risk.

Factors influencing leaving individual home ranges

A single model explaining the probability of an individual leaving its home range was strongly supported ($w_i=0.93$). After controlling for the amount of precipitation and freezing days, both of which reduced the probability that deer would leave their home ranges, the amount of

herbaceous forage habitat within home ranges and the biomass of herbaceous and oak forage on summer range reduced the probability of stepping outside identified ranges (Table 3). Deer were also 65% more likely to leave their home range during winter despite the significantly larger range size (ANOVA, $F_{1,143}=11.95$, $p<0.001$). Age class had no impact on the likelihood of leaving home ranges in either summer or winter (Table 3).

Effects of senescence

There was no difference in home range sizes of prime-aged and senescent individuals during summer (0.62 vs. 0.60 km², rANOVA, $F_{2,46}=0.02$, $p=0.98$) or winter (0.89 vs. 0.72 km², rANOVA, $F_{2,43}=0.13$, $p=0.88$). The mean seasonal range size for all deer >2 years of age was 0.71 km² (SE=0.04), with summer home ranges averaging 0.61 km² (SE=0.05 km²) and winter home ranges averaging 0.86 km² (SE=0.07 km²). Yearlings utilized slightly larger summer (0.82 ± 0.37 km²) and winter ranges (1.17 ± 0.27 km²) than other age classes. There was no difference in the amount of forage habitat within home ranges of prime-age and senescent individuals in either summer (rANOVA, $F_{2,46}=0.01$, $p=0.99$) or winter (rANOVA, $F_{2,43}=0.24$, $p=0.78$).

Senescent deer (n = 12, 50 ± 1.85 kg) weighed more than prime-aged deer (n = 44, 45 ± 1.04 kg) in our study area (unequal variance *t*-test, $t_{54}=-2.383$, $p=0.02$).

Discussion

The fitness effects of site familiarity have rarely been demonstrated despite the expected widespread relevance of the concept (Piper 2011). We found strong fitness benefits of using

familiar areas in a medium-sized ungulate, the black-tailed deer, that is negatively affected by predation across much of its distribution (Forrester and Wittmer 2013). The observed fitness benefits linked to familiarity were lower risks of mortality and predation inside identified seasonal home ranges. Furthermore, we found a link between bottom-up effects and the probability of use of familiar spaces. Specifically, deer with access to greater amounts of forage within seasonal home ranges and access to higher quality summer range were less likely to leave their home range during weekly monitoring intervals and thus venture into risky areas. Given that the home range is one of the most widely used metrics to describe the spatial ecology and habitat requirements of vertebrates (Burt 1943; Kie et al. 2010), these findings have significance for our understanding of the role of site familiarity and private information on space use and survival.

One of the presumed benefits of site familiarity is an improved knowledge of the spatial distribution of both forage quantity and quality. In mid-sized ungulates such as black-tailed deer, a high concentration of digestible energy (or forage quality) is more important than the amount of forage (Kie 1999; Parker et al. 2009; Hopcraft et al. 2010). Selecting and ingesting high quality forage takes more time than searching for forage patches (Kie 1999), and familiarity with high quality forage patches minimizes the time an individual spends foraging in potentially risky habitats. The very small size of seasonal home ranges we observed in our study (mean = 0.74 km²) make it highly likely that deer were familiar with the seasonal distribution of forage and also had sufficient access to high quality forage to operate at such small scales.

Familiarity with very small home ranges also resulted in lower predation risk for deer within their seasonal home range, and this relationship was consistent among seasons and various habitat types. The consistency of the effect shows the direct link between familiarity and

lower risk of predation, but it is unlikely that deer actively avoided predators. Actively avoiding predation depends on the ability of prey to interpret predator and habitat specific cues of risk (Lima 2002; Creel and Winnie Jr. 2005; Laundré 2010) as well as the characteristics of predators and the space in which they interact with prey (Lima 2002). Pumas are the primary predators of adult deer in our study area and are ambush predators that prefer to hunt in structured habitat (Holmes and Laundré 2006). Pumas also operate at much larger spatial scales than their ungulate prey (Logan and Sweanor 2010), and the home ranges of female and male pumas were 375 and 490 times larger (Allen et al. 2014), respectively, than the mean annual range of black-tailed deer in our study area. Due to this mismatch in spatial scale puma activity would be sporadic within a deer home range, providing few active cues (e.g., scent markings, regular travel paths, etc.) that deer could detect and use to avoid them. Thus it is unlikely deer actively avoided predation based on private information they gathered about pumas inside their home ranges.

It is more likely that the higher survival rates we observed for deer remaining within their home ranges were simply a consequence of reduced encounter probabilities with pumas. Minimizing the time spent foraging reduces predation risk as it allows individuals to minimize movement and return to bedding areas to ruminate and digest their food (Kie 1999). Such an interpretation would be consistent with predictions from the theory of predator-prey “shell games” (Mitchell and Lima 2002). Predator-prey shell game theory predicts that the risk of attack from a predator is determined by the predictability of prey occurrence in a given area, prey vigilance, and the killing efficiency of the predator (Mitchell and Lima 2002). The optimal strategy of prey facing predators with a high killing efficiency is to avoid all predator encounters by remaining stationary (Mitchell and Lima 2002), while the prey response to a low killing efficiency predator should be large-scale random movements (Lima 2002). Deer are unlikely to survive an attack by

pumas (Hornocker 1970), and if deer perceive the known area of their home range as safer than unknown territory (a de facto refuge), the response of staying within a small home range is adaptive against a predator with high killing efficiency whose location is uncertain (Sih 1992; Mitchell and Lima 2002).

The concept of a home range as a refuge is also consistent with our results regarding forage availability and the probability of a deer leaving a home range. If some areas are safe and some areas are risky, deer should only forage in risky areas when forced there by hunger (Sinclair and Arcese 1995). Our results agree with this prediction, as lower forage availability increased the chance of a deer leaving their home range and abandoning the advantages of site familiarity for a higher risk area. The role of forage limitation varied seasonally given that deer were more likely to step outside their home ranges in winter. Our results suggest that access to summer forage may have carried into winter, given that deer with more forage biomass on the summer range were less likely to leave their home range in both summer and winter.

There were physiological constraints to the benefits of site familiarity. Senescent individuals were twice as likely to die as prime age adults, even though senescent individuals did not present lower weight, as reported elsewhere (Nussey et al. 2011). Additionally, the increased probability of older deer dying was not linked to differences in forage availability or to the likelihood of leaving the home range. Senescence may have affected the ability of older deer to detect and avoid pumas in ways not measured by weight or body condition (Boyd et al. 1994; Réale and Festa-Bianchet 2003). These changes, combined with the fact that the cumulative probability of encountering a puma during a deer's lifetime likely increases towards 1, may explain higher observed mortalities of older deer.

Given the wide occurrence of site fidelity in ungulates (Switzer 1993; Wolf et al. 2009), the fitness benefits of site familiarity are likely to be widespread. We predict that site familiarity will be important for ungulates with high site fidelity under 3 conditions: 1) when there are enough forage resources for stable home ranges, 2) when habitat has structure and biotic complexity, and 3) when the direct cues of predation risk are unclear and do not allow ungulates to determine well-defined spatial refuges. Habitat structure is important because ungulates in complex habitats are more likely to be solitary and rely on individual predator evasion rather than group defense strategies (Jarman 1974). The value of private information gained by an ungulate familiar with a site will also increase in areas with more habitat complexity (Piper 2011). The importance of site familiarity in the fitness of ungulates that fit these criteria remains to be investigated, as well as the role of spatial knowledge in balancing predation risk from multiple predators with different hunting strategies (e.g., social and cursorial carnivores such as wolves (*Canis lupus*) versus solitary and ambush predators such as pumas in the same community). The importance of site familiarity to reproductive success also remains unknown yet likely is important. We suggest that benefits of site familiarity within home ranges will be widespread, and inclusion of this concept will improve our understanding of both ungulate behavior and predator-prey interactions (Piper 2011) and help predict how ungulates may react to large-scale habitat changes (Faille et al. 2010).

Acknowledgments

This study was funded by the California Department of Fish and Wildlife (Contract #P0880013 to HUW) and the California Deer Association. TDF thanks the Robert and Patricia Switzer

Foundation Environmental Fellowship Program, the UC Davis Graduate Group in Ecology, and the Stockton Sportsmen's Club. We thank our dedicated field crew for their efforts during 4 years of fieldwork. Finally, we thank D. A. Kelt, A. Latimer, and A. Sih for their comments that greatly improved this manuscript.

Literature Cited

- Allen ML, Elbroch LM, Casady DS, Wittmer HU (2014) Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Can J Zool* 92:397–403. doi: 10.1139/cjz-2013-0284
- Arnold TW (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J Wildl Manag* 74:1175–1178.
- Atkinson KT, Janz DW (1994) Effects of wolf control on black-tailed deer on Vancouver Island. British Columbia Ministry of Environment, Lands, and Parks, Wildlife Bulletin No. B-73:1-43.
- Baker RR (1978) The evolutionary ecology of animal migration. Holmes & Meier Pub, New York
- Boyd DK, Ream RR, Pletscher DH, Fairchild MW (1994) Prey taken by colonizing wolves and hunters in the Glacier National Park area. *J Wildl Manag* 58:289–295. doi: 10.2307/3809393
- Brohman RJ, Bryant LD, Tart D, et al. (2005) Existing vegetation classification and mapping technical guide: Version 1.0. US Department of Agriculture, Forest Service, Ecosystem Management Coordination Staff

- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: A practical information-theoretic approach. Springer, New York, USA
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352. doi: 10.2307/1374834
- Casady DS, Allen ML (2013) Handling adjustments to reduce chemical capture related mortality in black tailed deer. *Calif Fish Game* 99:104–109.
- Clarke MF, Silva KB da, Lair H, Pocklington R, Kramer DL, McLaughlin RL (1993) Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. *Oikos* 66:533–537. doi: 10.2307/3544949
- Cleves MA, Gould W, Gutierrez R, Marchenko Y (2010) An introduction to survival analysis using Stata. Stata Press, College Station, Texas, USA
- Coviello V, Boggess M (2004) Cumulative incidence estimation in the presence of competing risks. *Stata J* 4:103–112.
- Cox D (1972) Regression models and life tables. *J R Stat Soc* 34:187–220.
- Creel S, Winnie Jr. JA (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim Behav* 69:1181–1189. doi: 10.1016/j.anbehav.2004.07.022
- Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193. doi: 10.1016/j.tree.2005.01.010
- Dasmann RF, Taber RD (1956) Behavior of Columbian black-tailed deer with reference to population ecology. *J Mammal* 37:143–164.

- Edge WD, Marcum CL, Olson SL (1985) Effects of logging activities on home-range fidelity of elk. *J Wildl Manag* 49:741–744. doi: 10.2307/3801704
- Faille G, Dussault C, Ouellet J-P, et al. (2010) Range fidelity: The missing link between caribou decline and habitat alteration? *Biol Conserv* 143:2840–2850. doi: 10.1016/j.biocon.2010.08.001
- Fieberg J, DelGiudice GD (2009) What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* 90:1687–1697. doi: 10.1890/08-0724.1
- Forrester TD (2014) Effects of predation and forage availability on the survival of black-tailed deer (*Odocoileus hemionus columbianus*) in the Mendocino National Forest, California. Ph.D. Dissertation. University of California, Davis.
- Forrester TD, Wittmer HU (2013) A review of the population dynamics of mule and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Rev* 43:292–308. doi: 10.1111/mam.12002
- Fryxell JM, Greever J, Sinclair ARE (1988) Why are migratory ungulates so abundant? *Am Nat* 131:781–798.
- Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. *Trends Ecol Evol* 3:237–241. doi: 10.1016/0169-5347(88)90166-8
- Garrott RA, White GC, Bartmann RM, Carpenter LH, Alldredge AW (1987) Movements of female mule deer in northwest Colorado. *J Wildl Manag* 51:634–643. doi: 10.2307/3801282
- Geist V (1981) Behavior: Adaptive strategies in mule deer. In: Wallmo OC (ed) *Mule Black-Tailed Deer N. Am.* University of Nebraska Press, Lincoln, NE, pp 157–223

- Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC (2007) Locoh: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* 2:e207. doi: 10.1371/journal.pone.0000207
- Getz WM, Wilmers CC (2004) A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27:489–505. doi: 10.1111/j.0906-7590.2004.03835.x
- Grambsch PM, Therneau TM (1994) Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–526. doi: 10.1093/biomet/81.3.515
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annu Rev Ecol Syst* 13:1–21.
- Harwood AJ, Griffiths SW, Metcalfe NB, Armstrong JD (2003) The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon. *Anim Behav* 65:1141–1149. doi: 10.1006/anbe.2003.2125
- Holmes BR, Laundré JW (2006) Use of open, edge and forest areas by pumas *Puma concolor* in winter: are pumas foraging optimally? *Wildl Biol* 12:201–209. doi: 10.2981/0909-6396(2006)12[201:UOOEAF]2.0.CO;2
- Hopcraft JGC, Olf H, Sinclair ARE (2010) Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol Evol* 25:119–128. doi: 10.1016/j.tree.2009.08.001
- Hornocker MG (1970) An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. *Wildl Monogr* 21:3–39.
- Hosmer DW, Lemeshow S, May S (2011) Applied survival analysis: Regression modeling of time to event data. John Wiley & Sons, Hoboken, New Jersey, USA

- Jarman PJ (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–267. doi: 10.1163/156853974X00345
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71. doi: 10.2307/1937156
- Kie JG (1999) Optimal foraging and risk of predation: Effects on behavior and social structure in ungulates. *J Mammal* 80:1114–1129. doi: 10.2307/1383163
- Kie JG, Matthiopoulos J, Fieberg J, et al. (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philos Trans R Soc B Biol Sci* 365:2221–2231. doi: 10.1098/rstb.2010.0093
- Laundre J (2010) Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology* 91:2995–3007.
- Lima SL (2002) Putting predators back into behavioral predator-prey interactions. *Trends Ecol Evol* 17:70–75. doi: 10.1016/S0169-5347(01)02393-X
- Logan KA, Sweanor LL (2010) Behavior and social organization of a solitary carnivore. In: Hornocker M, Negri S (eds) *Cougar Ecol. Conserv.* University of Chicago Press, Chicago, IL, pp 105–117
- Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M (1999) Age-specific survival in five populations of ungulates: Evidence of senescence. *Ecology* 80:2539–2554. doi: 10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2
- Marescot L, TD Forrester, DS Casady, HU Wittmer (2015) Using multistate capture-mark-recapture models to quantify effects of predation on age-specific survival and population growth in black-tailed deer. *Pop Ecol.* doi: 10.1007/s10144-014-0456-z

- McCorquodale SM (1999) Movements, survival, and mortality of black-tailed deer in the Klickitat basin of Washington. *J Wildl Manag* 63:861–871. doi: 10.2307/3802799
- Mitchell WA, Lima SL (2002) Predator-prey shell games: Large-scale movement and its implications for decision-making by prey. *Oikos* 99:249–259. doi: 10.1034/j.1600-0706.2002.990205.x
- Nussey DH, Coulson T, Delorme D, et al. (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* 92:1936–1947. doi: 10.1890/11-0308.1
- Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. *Funct Ecol* 23:57–69.
- Pettorelli N, Pelletier F, Hardenberg A von, Festa-Bianchet M, Côté SD (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88:381–390. doi: 10.1890/06-0875
- Piper WH (2011) Making habitat selection more “familiar”: a review. *Behav Ecol Sociobiol* 65:1329–1351. doi: 10.1007/s00265-011-1195-1
- Piper WH, Walcott C, Mager JN, Spilker FJ (2008) Nestsite selection by male loons leads to sex-biased site familiarity. *J Anim Ecol* 77:205–210. doi: 10.1111/j.1365-2656.2007.01334.x
- Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival Analysis in Telemetry Studies: The Staggered Entry Design. *J Wildl Manag* 53:7–15. doi: 10.2307/3801296
- Purdue JR, Smith MH, Patton JC (2000) Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. *J Mammal* 81:179–185.
- Réale D, Festa-Bianchet M (2003) Predator-induced natural selection on temperament in bighorn ewes. *Anim Behav* 65:463–470. doi: 10.1006/anbe.2003.2100

- Sih A (1980) Optimal behavior: Can foragers balance two conflicting demands? *Science* 210:1041–1043. doi: 10.1126/science.210.4473.1041
- Sih A (1992) Prey uncertainty and the balancing of antipredator and feeding needs. *Am Nat* 139:1052–1069.
- Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76:882–891. doi: 10.2307/1939353
- Spencer WD (2012) Home ranges and the value of spatial information. *J Mammal* 93:929–947. doi: 10.1644/12-MAMM-S-061.1
- Stamps J (1995) Motor learning and the value of familiar space. *Am Nat* 146:41–58.
- Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. *Evol Ecol* 7:533–555. doi: 10.1007/BF01237820
- Therneau TM, Grambsch PM (2000) Modeling survival data: extending the Cox model. Springer, New York, USA
- Van Beest FM, Wal EV, Stronen AV, Paquet PC, Brook RK (2013) Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. *Oecologia* 173:409–420. doi: 10.1007/s00442-013-2647-2
- Wallmo OC (ed) (1981) Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA
- Wittmer HU, McLellan BN, Hovey FW (2006) Factors influencing variation in site fidelity of woodland caribou (*Rangifer tarandus caribou*) in southeastern British Columbia. *Can J Zool* 84:537–545. doi: 10.1139/z06-026

Wolf M, Frair J, Merrill E, Turchin P (2009) The attraction of the known: The importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32:401–410.
doi: 10.1111/j.1600-0587.2008.05626.x

Table 3.1 – Cause specific mortality rates shown as cumulative incidence functions by season and annually for adult female black-tailed deer in Mendocino National Forest from 2009-2013.

Cause of Mortality	Summer	<i>SE</i>	Winter	<i>SE</i>	Annual	<i>SE</i>
Predation	0.12	0.04	0.06	0.02	0.18	0.05
Unknown Cause	0.01	0.01	0.08	0.03	0.09	0.03
Poaching	0.01	0.01	0.02	0.01	0.03	0.02

Table 3.2 – Model averaged results for Cox proportional hazards models within $\Delta 4$ AIC_c of the top model. Hazard ratios greater or less than 1 indicate an increase or decrease in mortality risk respectively, and 95% confidence intervals indicate if the hazard ratio is significantly different than 1. Hazard ratios for the probability of leaving the range and herbaceous area indicate the change in mortality risk for a 10% increase in probability of leaving the range and a 1 ha increase in herbaceous habitat in the home range respectively. Hazard ratios of the Young and Senescent age classes are in comparison to Prime Age adults. Results for the Young age class should be interpreted cautiously since the sample size is small (n=4). Puma overlap is an index of predation risk that indicates the change of risk for every 100-meter increase in the difference between the average elevation of deer and pumas in the study area.

Covariate	Hazard Ratio	Standard Error	95% Confidence Interval
Probability of leaving home range	1.42	0.09	1.19 – 1.69
Herbaceous area in home range (ha)	0.97	0.02	0.94 – 1.00
Young Age Class	3.22	0.63	0.94 – 11.06
Senescent Age Class	2.38	0.48	0.93 – 6.10
Puma Overlap	0.90	0.04	0.82 – 0.98

Table 3.3 – Cox proportional hazards model results for the top model of the probability of leaving the home range for adult female deer in Mendocino National Forest from 2009-2013. Odds ratios greater or less than 1 indicate an increase or decrease in probability of leaving the home range, respectively, and *p* values indicate if the hazard ratio is significantly different than 1.

Covariate	Odds Ratio	<i>p</i> value	95% Confidence Interval
Seasonal Range	1.65	0.005	1.162 – 2.349
Herbaceous area in home range	0.99	0.019	0.987 – 0.998
Summer home range herbaceous biomass	0.95	0.049	0.906 – 0.999
Summer home range oak browse biomass	0.97	0.024	0.948 – 0.996
Cumulative Precipitation	0.98	0.049	0.957 – 0.999
Cumulative days below freezing	0.99	<0.001	0.996 – 0.998

Figure 3.1 – The study area in the context of the state of California showing the three watersheds and two main ridges (M1 and FH7). The relief in the map shows elevation with darker areas indicating lower elevation. Summer seasonal areas are shown in dark gray and winter seasonal areas are in white.

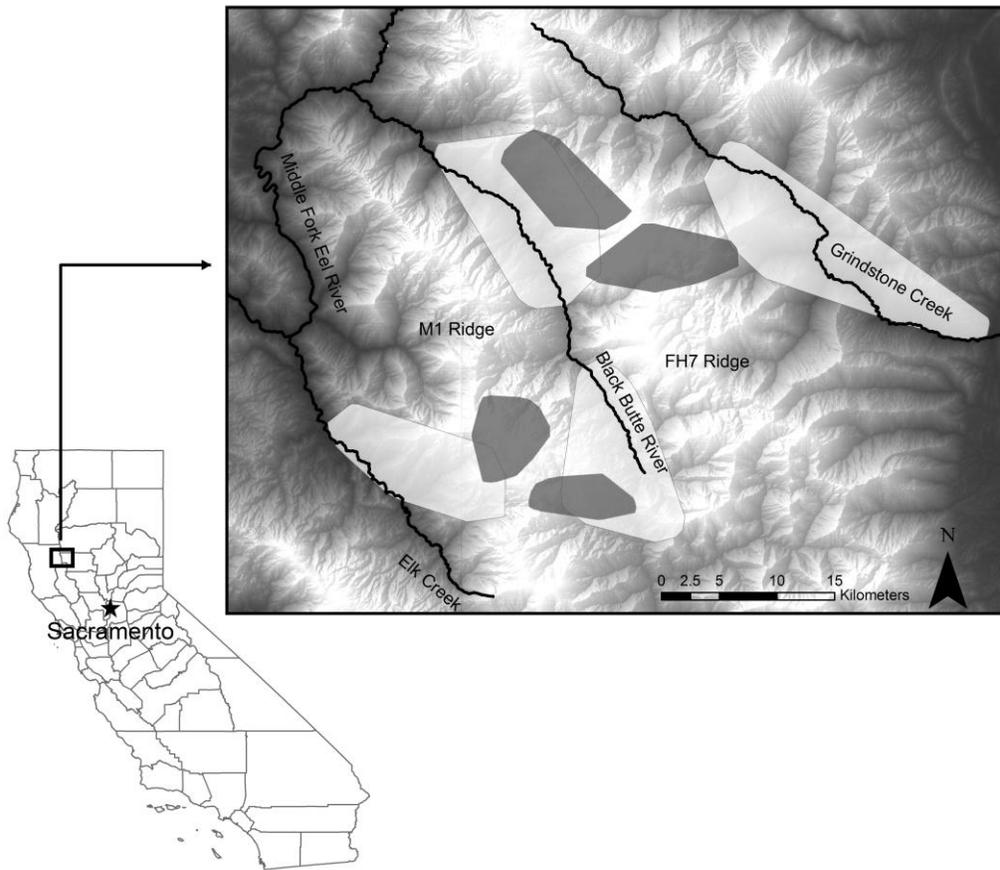
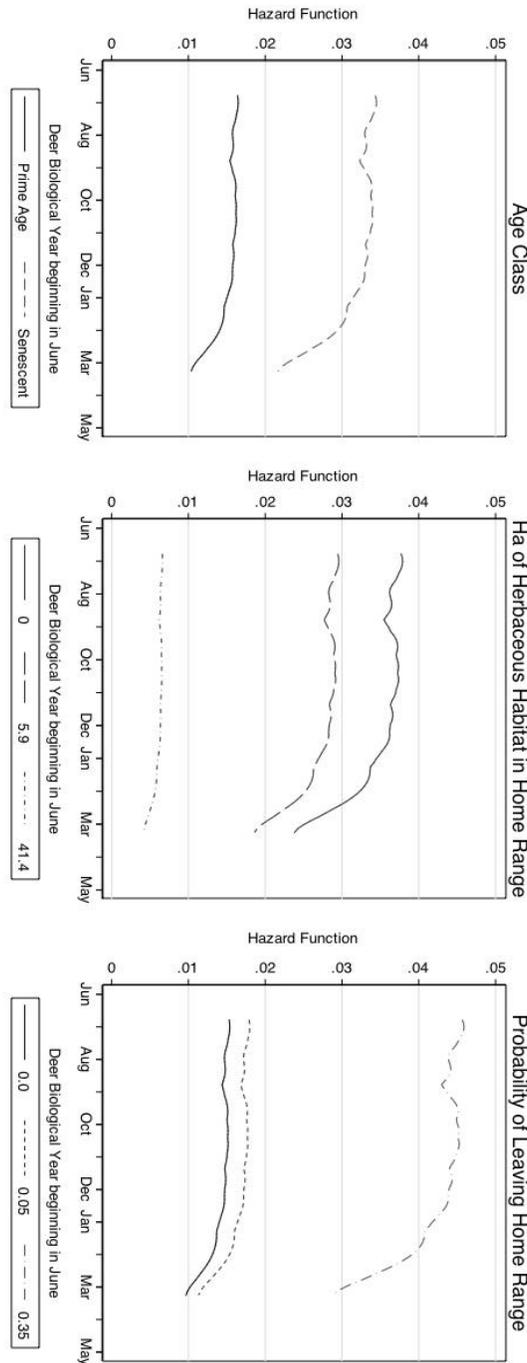


Figure 3.2 – Hazard rates for age class, forage area within home range, and the probability of leaving the home range for adult female black-tailed deer in the Mendocino National Forest from 2009-2013. Values for hectares of herbaceous habitat and probability of leaving the home range are the 10%, 50%, and 90% quantiles of covariate values.



Appendix 3.1 - *a priori* survival models

We examined how forage availability, proximity to predators, weather, and individual deer characteristics affected the risk of mortality and the probability of a deer spending time outside its home range using the following *a priori* set of models (Table 1). We used the amount of summer herbaceous and oak forage and the area of herbaceous and oak CALVEG cover types within a seasonal home range in the “forage” model. We used the distance between the mean monthly elevation of pumas and deer (Allen et al. 2014) in the “proximity to predators” model. We created a “weather” model with precipitation and the number of freezing days as time varying covariates for each weekly encounter date. The “individual deer” model consisted of age class and the probability a deer was inside or outside the 95% isopleth of its LoCoH seasonal home range (Getz et al. 2007). We also tested for combinations of each of the variables (e.g., individual deer + proximity to predators + forage).

We selected models using Akaike Information Criterion adjusted for small sample sizes (AIC_c) and present models within $\Delta 4 AIC_c$ of the best model (Burnham and Anderson 2002). We considered nested models as competitors for best model only if parameters in the model were significant at the 0.1 level or if parameters were not merely a subset of the competing model (Arnold 2010; Burnham and Anderson 2002). Weather variables were never significant and did not reduce the AIC_c of combination models (e.g. forage + weather) by $>\Delta 2 AIC_c$ (the penalty for adding an additional parameter), showing that they did not explain enough variation to justify inclusion in the model (Burnham and Anderson 2002; Arnold 2010).

Literature Cited

- Allen ML, Elbroch LM, Casady DS, Wittmer HU (2014) Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Can J Zool* 92:397–403. doi: 10.1139/cjz-2013-0284
- Arnold TW (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J Wildl Manage* 74:1175–1178
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: A practical information-theoretic approach. Springer, New York, USA
- Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmsers CC (2007) Locoh: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* 2:e207. doi: 10.1371/journal.pone.0000207

Table A3.1 – All *a priori* Cox proportional hazards survival models with informative parameters for female black-tailed deer 1 year old and older in the Mendocino National Forest 2009-2013. Model types names indicate the main factors considered in the model. Covariates include the probability of leaving the home range in a given week (Outside Range), the young, prime, or senescent age class of deer (Age Class), the difference between the average elevation for an individual deer and the mean elevation of simultaneously collared pumas (Puma), and the amount of precipitation or days with temperatures below freezing to date in the analysis (Precipitation; Freezing). The biomass of herbaceous and oak forage on summer range was also included (Summer Herb; Summer Oak).

Model Type	Model Covariates	ΔAIC_c	$AIC_c w_i$
Individual Deer + Predator Proximity + Forage	Outside Range + Age Class + Puma + Herb Area	0.00	0.53
Individual Deer + Predator Proximity	Outside Range + Age Class + Puma	1.65	0.23
Individual Deer + Forage	Outside Range + Age Class + Herb Area	2.20	0.18
Individual Deer	Outside Range + Age Class	5.67	0.03
Individual Deer	Outside Range	5.75	0.03
Forage	Herb Area	12.19	0.00
Individual Deer	Age Class	13.33	0.00
Weather	Freeze	13.89	0.00
Weather	Precipitation + Freeze	14.03	0.00
Predator Proximity	Puma	14.20	0.00
Forage	Summer Herb + Summer Oak	14.98	0.00
Weather	Precipitation	14.99	0.00
Forage	Summer Oak	15.33	0.00
Forage	Summer Herb	15.55	0.00

VIII. Summary

There are few places where the debate over the role of predation in population dynamics has been enjoined as vigorously as the management of deer in North America (Leopold 1943; Ballard et al. 2001; Ripple and Beschta 2004; Kauffman et al. 2010). This argument was formalized in the infancy of wildlife management by Aldo Leopold's direct, but simplistic, story about the ecological destruction of the Kaibab Plateau by an overabundant deer herd (Leopold 1943; Binkley et al. 2006). After decades of research, the same debate erupted again as federal predator control was curtailed across the western USA (Connolly 1978) and gray wolves (*Canis lupus*) were reintroduced to the Greater Yellowstone Ecosystem (Smith et al. 2003). This question about the impact of predators on deer formed the central theme of my research, and I worked to determine how both predation and forage resources affected the survival of black-tailed deer.

Top-down and Bottom-up Effects on Black-tailed Deer Survival

The unanticipated fluctuations in the populations of mule and black-tailed deer in the last century have highlighted the uncertainty surrounding the role of predation and forage in deer dynamics (Ballard et al. 2001). The role of predation in particular remains controversial (Connolly 1978; Ripple and Beschta 2005). I reviewed all available literature to compare mule and black-tailed deer vital rates with general patterns observed for all ungulates (Gaillard et al. 1998, 2000) and to assess the role of predation in population dynamics. I found that mule and black-tailed deer had lower (mule deer=0.44 vs. other ungulates=0.64) and more variable fawn survival rates than other ungulate species (mule deer CV=0.42 vs. other ungulates CV=0.27) (Gaillard et al. 2000). Adult survival, however, was high and stable and similar to other ungulates. Mule deer fecundity was over twice as high as the average for other ungulates (1.70 in

mule deer vs. 0.82 for all ungulates), and my results indicate that mule deer may depend heavily on high fecundity and high and stable adult survival to prevent long-term population declines.

Predation was the largest proximate cause of mortality for both adults and fawns in all studies. However, there was little evidence that predation mortality was additive, or that predation drove mule deer declines. Most predator removal studies showed that predation was compensatory, including an example of compensatory predation on adult mule deer by pumas (Hurley et al. 2011). Nutritional supplementation increased survival in both fawns and adult females (Bishop et al. 2009), and nutrition seemed to have a stronger influence on the equilibrium density of deer than predation. Nutrition is likely to be more important for mule deer than other ungulates because mule deer seem to depend on higher fecundity to stabilize populations, and fecundity (up to triplets in mule deer) and fawn birth weight are driven by nutritional status (Anderson 1981; Parker et al. 2009). Forage quality is also important since mule deer are mid-sized ungulates that depend on forage quality more than quantity (Wallmo 1981; Hopcraft et al. 2010). These results highlight the important distinction between the proximate and ultimate causes of mule deer mortality, and that assessing proximate causes of mortality alone may result in poor predictors of mule deer dynamics.

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

to escape. Most mule deer populations also coexist with a larger suite of fawn predators than adult predators.

Fawn mortality in my study area fit this general pattern of summer fawn mortality that was dominated by the effects of predation. There were more 4 main fawn predators (black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and pumas (*Puma concolor*)) and only a single predator of adult deer (pumas) in my study area. The majority of annual mortality occurred during the summer (80% of all mortality). Predation was the largest source of mortality (62% of all mortality), and black bears were the greatest single cause of death (28% of all mortality). Black bear predation was focused on fawns <30 days of age and was not related to forage availability, while the risk of coyote predation and overall mortality in the summer were lower in areas with more oak forage. Spatial differences in summer mortality persisted until recruitment (*LR test*, $X^2_{df=1}=3.69$, $p=0.05$), showing the importance of the summer period for fawn survival and for deer dynamics.

The interaction between predation and forage was weaker during winter. The amount of dense brush in wintering areas and overlap with the average monthly elevation of pumas did show a trend of increased mortality risk, a result consistent with prey vulnerability to ambush predators in complex habitat (Miller et al. 2014). The amount of oak habitat had no effect despite the importance of oak in summer and the possible benefits of oak as thermal cover for black-tailed deer in winter (Bowyer and Kie 2009). Winter precipitation and severity were unrelated to mortality.

The importance of both predation and forage influences on fawn survival were shown by population level indices that are measures of the relation of a deer population to the nutritional carrying capacity (K), and include female body condition, fawn birthweight, and fetal rates

(Pierce et al. 2012). Low fawn birthweights showed some effects of nutritional limitation, while high fecundity rates (1.9 vs. 1.70 mule deer average) and an average body condition of “good” with detectable fat reserves in early spring were consistent with populations that were top-down limited.

The survival of adult females was also influenced by an interaction of top-down and bottom-up influences. Adult survival was lower than expected in our study area (0.70 vs. 0.84 range-wide average) and the primary cause of death was predation by pumas. The risk of mortality was most strongly affected by individual behavior, and deer that had a 40% chance of leaving their home range during a given week were 4x more likely to die. Of the 21 observed mortalities, 13 occurred outside respective 95% home range isopleths. Distances of mortalities to nearest home range boundaries averaged 1171 m (SE = 325 m), with 8 mortalities >700 m outside home ranges. Forage availability did not directly affect the risk of mortality, but deer with less forage in their home range were more likely to leave and venture into risky territory (10 ha of herbaceous habitat reduced the chance of leaving by 5%).

Higher survival in familiar areas likely occurred because of spatial knowledge of forage resources (Wolf et al. 2009; Piper 2011) and a lower probability of encountering pumas, a highly efficient deer predator (Mitchell and Lima 2002). Deer behaved as if their home range was a predation refuge, only venturing into riskier territory outside when they had less available forage (Sinclair and Arcese 1995). The advantages of site familiarity had limits, and senescent individuals (0.60, SE=0.15, CV=0.69) experienced lower survival than prime-aged females (0.78, SE=0.06, CV=0.10) that was unrelated to home range size (summer: 0.60 vs. 0.62 km², rANOVA, $F_{2,46}=0.02$, $p=0.98$; winter: 0.72 vs. 0.89 km², rANOVA, $F_{2,43}=0.13$, $p=0.88$) or forage availability (summer: rANOVA, $F_{2,46}=0.01$, $p=0.99$; winter: rANOVA, $F_{2,43}=0.24$,

$p=0.78$). Finally the strong effects of site familiarity on the survival of adult female deer were evidence how individual behavior can scale up to affect population level processes.

My results provide evidence that both bottom-up and top-down effects were influencing deer survival in this declining population ($\lambda=0.82\pm 0.13$; Marescot et al. 2015), and that predator identity, the seasonal timing of mortality, and individual behavior of adult deer affected these interactions.

Implications for Management of Black-tailed Deer

The black-tailed deer population in the Mendocino National Forest is declining, confirming the fears of managers and hunters. The question of concern for stakeholders and managers is whether predation or forage limitation is causing this decline. I found evidence that both factors were contributing, but little evidence that predators were the sole reason for decline or that predators were holding deer populations in a “predator pit” (a stable population level lower than could be supported by available forage) (Sinclair 2003). Heavy predation on young fawns by black bears may have caused additive summer mortality. Black bear predation was unrelated to available forage, and fecundity rates and deer body condition were inconsistent with strong forage limitation. The survival rate of adult females was also low compared to the range wide average (study=0.70 vs. spp. avg=0.84), and predation was the largest cause of mortality. However, all other mortality sources for fawns were lower in areas with more forage, and fawn birth weights showed some evidence of food limitation. I also found evidence for predation-sensitive foraging in adult females (Sinclair and Arcese 1995), which is indicative of a population where predation is acting as a regulating force even though it may be holding the population a small distance below forage carrying capacity (Sinclair and Arcese 1995; Sinclair and Krebs 2002).

These findings show that management of deer in the Mendocino National Forest should focus on habitat and not predators. The population is likely below the forage carrying capacity but not far below, and predation rates are not the sole reason for the population decline. This pattern has been found in other mule deer populations that have undergone cyclical fluctuations in population size (Laundré et al. 2006; Pierce et al. 2012). Predation in these populations exacerbated declines but a combination of weather and nutrition were the ultimate cause behind the population fluctuations, and the deer herds went through periods of both decline and growth despite large predator populations (Laundré et al. 2006; Pierce et al. 2012). Large-scale predator reductions in other areas have also been shown to be ineffective in increasing mule deer density (see Forrester and Wittmer 2013). However, habitat management should account for the fact that female black-tailed deer show high site fidelity in the study area (unpublished data), and any habitat changes will have localized effects.

Leveraging this information for effective management will require educating stakeholders in a way that acknowledges the history of deer in the Mendocino National Forest. The deer population in this area has been high for decades. Aldo Leopold identified it as one of many overpopulated deer ranges in the United States in the 1940's (Leopold et al. 1947). Deer populations peaked again in the 1960's and 1970's and record deer harvests were taken by hunters in the counties that comprise our study area (Booth et al. 1982). Research has consistently shown that people form their view of what is ecologically normal in the early part of their lives (Pauly 1995), and most of the current stakeholders in deer management were young adults or children during the time of peak deer abundance in the area (Booth et al. 1982). What people here view as "normal" is in fact a population that was likely outstripping its own food supply (Leopold et al. 1947; Longhurst et al. 1952, 1976). Convincing stakeholders that

predation and increased puma populations are not destroying the deer herd will require educating them about this history as well.

I hope that my research will encourage future deer research in California to move away from the false dichotomy of predators vs. forage and investigate the dynamical relationship between the two. Like it or not, the relationship between people and deer guarantees that money and time will be focused on the deer herds of California, and it is my hope that the insight gained from studying deer can be used in management focused on the ecosystem, not just one species. Predators play an important ecological role, and we continue to discover the large impacts they have (Ripple et al. 2014). It is my hope that just as the first population surveys of deer led to the creation of wildlife management in America, the study of deer today can be part of the transition of wildlife management to an ecosystem approach that has room for both predators and prey.

Thank you for reading.

Literature Cited

- Anderson, A. E. 1981. Morphological and physiological characteristics. Pp. 27–97 in Mule and black-tailed deer of North America (O. C. Wallmo, ed.). University of Nebraska Press, Lincoln, NE.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter and J. C. deVos. 2001. Deer-predator relationships: A review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99–115.
- Binkley, D., M. M. Moore, W. H. Romme and P. M. Brown. 2006. Was Aldo Leopold Right about the Kaibab Deer Herd? *Ecosystems* 9:227–241.

- Bishop, C., G. White, D. Freddy, B. Watkins and T. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172:1–28.
- Booth, J., P. Yull and L. Murray. 1982. Mendocino Deer Herd Management Plan. California Department of Fish and Game.
- Bowyer, R. T. and J. G. Kie. 2009. Thermal Landscapes and Resource Selection by Black-Tailed Deer: Implications for Large Herbivores. *California Fish and Game* 95:128–139.
- Connolly, G. 1978. Predators and predator control. Pp. 369–394 in *Big Game of North America* (J. Schmidt & D. Gilbert, eds.). Stackpole Books, Harrisburg, USA.
- Forrester, T. D. and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Review* 43:292–308.
- Gaillard, J.-M., M. Festa-Bianchet and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison and C. Toigo. 2000. Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Hopcraft, J. G. C., H. Olf and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25:119–128.
- Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs* 178:1–33.

- Kauffman, M. J., J. F. Brodie and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Laundré, J. W., L. Hernández and S. G. Clark. 2006. Impact of puma predation on the decline and recovery of a mule deer population in southeastern Idaho. *Canadian Journal of Zoology* 84:1555–1565.
- Leopold, A. 1943. Deer Irruptions. *Publ. Wis. Conserv. Dep.*:351–366.
- Leopold, A., L. K. Sowls and D. L. Spencer. 1947. A Survey of Over-Populated Deer Ranges in the United States. *The Journal of Wildlife Management* 11:162–177.
- Longhurst, W. M., E. O. Garton, H. F. Heady and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. *Transactions of the Western Section of the Wildlife Society* 12:1–41.
- Longhurst, W. M., A. S. Leopold and R. F. Dasmann. 1952. A survey of California Deer Herds : their ranges and management problems. State of California, Dept. of Fish and Game, [Sacramento].
- Marescot, L., T. D. Forrester, D. S. Casady and H. U. Wittmer. 2015. Using multistate capture-mark-recapture models to quantify effects of predation on age-specific survival and population growth in black-tailed deer. *Population Ecology*.
- Miller, J. R. B., J. M. Ament and O. J. Schmitz. 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology* 83:214–222.
- Mitchell, W. A. and S. L. Lima. 2002. Predator-prey shell games: Large-scale movement and its implications for decision-making by prey. *Oikos* 99:249–259.

- Parker, K. L., P. S. Barboza and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57–69.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution* 10:430.
- Pierce, B. M., V. C. Bleich, K. L. Monteith and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *Journal of Mammalogy* 93:977–988.
- Piper, W. H. 2011. Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology* 65:1329–1351.
- Ripple, W. J. and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience* 54:755–766.
- Ripple, W. J. and R. L. Beschta. 2005. Linking Wolves and Plants: Aldo Leopold on Trophic Cascades. *BioScience* 55:613.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, et al. 2014. Status and ecological effects of the world’s largest carnivores. *Science* 343:1241484.
- Sinclair, A. R. E. 2003. Mammal Population Regulation, Keystone Processes and Ecosystem Dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 358:1729–1740.
- Sinclair, A. R. E. and P. Arcese. 1995. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76:882–891.

- Sinclair, A. R. E. and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:1221–1231.
- Smith, D. W., R. O. Peterson and D. B. Houston. 2003. Yellowstone after Wolves. *BioScience* 53:330.
- Wallmo, O. C. (ed.). 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.
- Wolf, M., J. Frair, E. Merrill and P. Turchin. 2009. The attraction of the known: The importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32:401–410.