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Pronghorn (Antilocapra americana) Offspring Recruitment on the Carrizo Plain National Monument: Evaluating the Effects of Low Population Density and Marginal Habitat Quality.

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PRONGHORN (*ANTILOCAPRA AMERICANA*) OFFSPRING RECRUITMENT ON THE CARRIZO PLAIN NATIONAL MONUMENT: EVALUATING THE EFFECTS OF LOW POPULATION DENSITY AND MARGINAL HABITAT QUALITY.

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ABSTRACT

Pronghorn (*Antilocapra americana*) Offspring Recruitment on the Carrizo Plain National Monument: Evaluating the Effects of Low Population Density and Marginal Habitat Quality.

By

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Demographic fluctuation among ungulate populations is strongly linked to variability in recruitment. Rates of recruitment are subject to various forms of density-dependent and density-independent regulation. For species which benefit from the presence of conspecifics, reduced population density can decrease rates of recruitment and trigger a decline in per capita growth. Termed the Allee effect, this scenario can cause demographic collapse and population extinction. For many ungulate species, predation on juveniles is reduced when the timing and distribution of births is synchronized within a local population. Because birth synchrony is density-dependent, it may act as a mechanism for the Allee effect if offspring production in small populations is not sufficient to limit predation. In addition to risks associated with the Allee effect, marginal quality habitat and stochastic environmental fluctuation can limit recruitment and contribute to declines in reduced populations. An understanding of how small populations are affected by density-dependence and habitat quality is critical for the ecology and conservation of ungulates. This study examines recruitment in a highly reduced population of pronghorn occupying sub-marginal habitat on the Carrizo Plain National Monument (CPNM) in California.

In Chapter 2, I address the potential for birth synchrony to act as a mechanism for a component Allee effect by comparing survival of individuals born during “peak” and “non-peak” periods within annual birth distributions. Twenty of forty-five pronghorn fawns born on the CPNM from 2009-2011 were equipped with lightweight, detachable GPS/VHF collars. The status of uncollared fawns was monitored via the VHF tracking of a collared sibling, general location of fawning site and/or the pelage of individual does. All 12 surviving fawns in the study (26.7%) were born during peak periods of productivity. I then tested for the presence of a demographic Allee effect by investigating the density dependent feedback of population size on logarithmic per capita population growth rate using ten years of regional flight count information from 2000-2011. Using multi-model inference and Akaike’s information criterion (AIC) I developed and selected a set of candidate models to best describe the pattern in the dataset. Results indicated that, at small population size, per capita growth rate tended to decline providing evidence for the presence of an Allee effect.

In Chapter 3, I evaluate the effect of macro- and micro-environmental conditions on recruitment. I modeled fawn habitat selection and survival, as well as examined diet composition and forage quality/availability for adults. Fawn locations, in comparison to random locations, were closer to drinking water and large shrub communities and contained lower percent slope of terrain. Survival of fawns appeared to increase with closer proximity to water sources, greater distance from main roads, and with increased slope of terrain. Low seasonal precipitation and high summer temperatures appeared to negatively affect survival. Forage abundance and quality were adequate during spring, but low during summer and fall. Low overall shrub cover appeared to provide inadequate concealment opportunities for fawns and likely limited nutrient availability during summer and fall for adults. Collectively, this study demonstrates that low density pronghorn populations are likely at risk for Allee effects and that Allee effects may be manifested through mechanisms associated with birth synchrony. Additionally, this study provides information on specific environmental conditions which affect survival of pronghorn fawns associated with micro- and macro-habitat availability and selection by does and fawns.

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CHAPTER 1

INTRODUCTION

Introduction

Understanding how populations are regulated is a central theme in ungulate ecology and conservation (Caughley 1977, Tulijapurkar 1997). For temperate herbivores, offspring recruitment has been demonstrated to play a fundamental role in population dynamics (Coulson et al. 1997, Pettorelli et al. 2005). Iteroparous reproduction among large, long-lived herbivores contributes to strongly age-structured populations and survival rates among particular age classes respond differently to various limiting factors (Gaillard 1998). For instance, juvenile survival is typically lower and more variable than survival of prime-aged adults (Gaillard et al. 2000, Eberhardt 2002). The importance of recruitment in influencing long-term demographic variation is particularly apparent for polytocous species (Gaillard et al. 2000), such as pronghorn (*Antilocapra americana*). Pronghorn consistently produce relatively large numbers of young annually (i.e., one set of twins per adult female per year) and exhibit the highest reproductive investment of any North American ungulate (Byers and Moodie 1990). However, mortality of neonatal fawns can be highly variable (40-80%) causing considerable fluctuations in annual recruitment rates (O'Gara and Shaw 2004). Causes of mortality for pronghorn fawns commonly include predation, disease, starvation, and exposure to inclement weather (O'Gara and Shaw 2004). Although predation is often the primary cause of mortality, the importance of predation as a limiting factor for pronghorn populations covaries with habitat quality. Alone, predation on fawns is not generally considered to drive population dynamics of pronghorn and many populations remain stable despite enduring considerable neonatal losses (Byers 1997). Nonetheless, the effect of predation on pronghorn recruitment appears to increase for low density populations (Gasaway et al. 1983, Cantrell 2001) and populations occupying habitats of marginal quality (Kohlmann 2004, Vriend and Barrett 1978).

Recruitment in low density populations

Recruitment, and ultimately population size, of pronghorn and other North American ungulates is regulated by both density-dependent and density-independent factors. Density-dependence in ungulate populations commonly involves forage limitation, predation, and disease. Density-independence is typically characterized by the effects of climatic variables. In populations where density-dependence is the primary form of regulation, there commonly exists a negative or “classical” relationship between density and per capita growth. However, when populations are low in density this relationship can become positive or “inverse” such that smaller populations have lower per capita growth. Termed the Allee effect, positive density-dependence at small population size can produce catastrophic demographic collapse and ultimately increases the risk of localized extinction (Courchamp et al. 1999).

Allee effects are generally classified as being either a component or demographic Allee effect (Courchamp et al. 1999). Component Allee effects refer to a positive relationship between population size or density and any measurable component of individual fitness (e.g., rates of births, deaths, or overall recruitment). When component Allee effects are strong they can result in a demographic Allee effect, a population level interaction where per capita growth rate is positively rated to population size or density.

The occurrence of Allee effects has been documented among a broad range of wildlife species, including pronghorn. Allee effects arise via such mechanisms as predator dilution, anti-predator vigilance, social thermoregulation, and decreased genetic diversity (Dennis 1989, Fowler and Baker 1991, Courchamp et al. 1999). For pronghorn, however, mechanisms for the Allee effect are poorly understood. Allee effects are typically manifested through behavioral or physiological characteristics that are intrinsic to the species' life history (Courchamp et al. 1999). For instance, pronghorn exhibit birth synchrony which is thought to saturate predators (e.g., time spent hunting or prey item consumption) and increase overall offspring survival rates (Rutberg 1987, Gregg et al. 2001, Kohlmann 2004). However, the benefits of birth synchrony are density-dependent, and small populations may not exhibit sufficient offspring production to reduce predation (i.e., component Allee effect). Small pronghorn populations, with reduced offspring production and increased predation rates may experience zero or negative per capita growth (i.e., demographic Allee effect).

Recruitment in marginal quality habitat

Beyond the constraints of population density on offspring recruitment are the effects of habitat quality. Pronghorn are endemic to North America and range from southern Canada to northern Mexico. Pronghorn abundance and dispersal vary among habitat types. Roughly two-thirds of all individuals inhabit grasslands, one-third live in shrub-steppe habitats, and less than one percent occupy deserts (Yoakum 1972, Sundstrom et al. 1973, Wildlife Management Institute 2001). Within each biome type, specific biotic and abiotic environmental attributes influence various aspects of fitness for both fawns and adults. For example, fawns require adequate vegetative and/or topographic concealment from predators during the early hiding phase of development (first two weeks of age) (Byers 1997b). However, adult does require open, high visibility terrain with relatively shorter vegetation height to maintain vigilance against approaching ground predators.

Pronghorn population density is strongly linked to forage quality, diversity, and availability (Yoakum 2004a). Populations regulated by forage conditions tend towards dynamic equilibria when food resources are constant (Caughley 1976). However, if interannual forage conditions are variable, considerable fluctuations in population size may occur (DeAngelis and Waterhouse 1987, Ellis and Swift 1988). Forage conditions not only affect adult survival but also impact recruitment by influencing reproductive success, birth site-selection, and nutritional quality during lactation (Canon and Bryant 1997, Yoakum 2001, 2003, Johnson et al. 2007). Pronghorn are highly selective, opportunistic foragers that consume the most palatable and succulent plant items available (Salwasser 1980). Pronghorn diets are generally divided into three main plant types: Grasses, shrubs and forbs (i.e., forbaceous plant). Although the availability of plant types may vary among different biomes, pronghorn preference for certain forage classes is remarkably consistent (Yoakum 2004c). Forbs comprise the majority of pronghorn diet and shrub composition is generally equal to, or far greater than, grass composition (Yoakum 2004a). Forbs tend to provide the best nutritional value and high forb abundance during winter and spring has been shown to contribute to increased fawn productivity and survival (Yoakum 2004c). Shrubs, however, become an important food source for both adults and fawns during late summer and fall, especially if annual forbs and grasses become desiccated and are no longer available (O’Gara and Yoakum 1992).

Objectives and justification

In this thesis, I evaluate how fawn recruitment is affected by low population density and habitat quality for a translocated population of pronghorn on the Carrizo Plain National Monument (CPNM) in California. Over two decades, the number of pronghorn at this site has decreased from 135 animals to approximately 30 individuals (Sommer 2012) and habitat quality has previously been ranked as moderate to poor for pronghorn (Longshore and Lowrey 2008). Prior research on pronghorn has been limited and information on recruitment has not been previously available. At such low population density, pronghorn on the CPNM may be affected by an Allee effect and, if so, may be at risk of local extinction due to demographic fluctuation. Testing for the presence of an Allee effect and evaluating the potential for birth synchrony to act as a mechanism for the Allee effect is the focus of Chapter Two. Recruitment on the CPNM may also be affected by the apparent low quality of habitat, which may also influence and impede population recovery. Evaluating how environmental conditions on the CPNM affect fawn habitat selection and survival is the aim of Chapter Three.

Understanding how recruitment is affected by population density and habitat conditions is not only critical for immediate management of pronghorn on CPNM, but also holds large scale implications for population ecology and conservation of pronghorn across the species' range. Over the past several decades, many pronghorn populations have become critically small, particularly those located within isolated and/or arid habitats. Examples include the federally endangered Sonoran subspecies in Arizona (*A. americana sonoriensis*) and the threatened Peninsular subspecies in Mexico's Baja California (*A. americana peninsularis*) (IUCN 2014, U.S. Fish and Wildlife Service

1997, respectively). Many declining populations are derived from translocated groups of individuals. Although the translocation of animals to reestablish extirpated populations or augment critically small populations is a common conservation practice (Griffith et al. 1989, Fischer and Lindenmayer 2000, World Conservation Union 1993), the success of such efforts depends on two important factors: the number of animals released and the quality of habitat available (Wolf et al. 1996, Griffith et al. 1998, O'Gara et al. 2004). Results described within this research thesis can be used by population ecologists and conservation managers to better understand the factors affecting recruitment and ultimately population dynamics of pronghorn and other ungulates.

Background

The remarkable, and perhaps unparalleled, population recovery of Pronghorn (*Antilocapra americana*) represents a success story for the conservation and management of North American megafauna (O'Gara and Yoakum 2004, Sparrowe 2004). Prior to European settlement, between 30 and 40 million pronghorn are estimated to have inhabited the expansive, open plains of western North America (Nelson 1925). However, numbers were reduced by more than 99% due to anthropogenic impacts associated with rapid agricultural development, unregulated year-round hunting, competition with domestic livestock, disease, construction of fencing, and the overall alteration and transformation of native rangelands (Yoakum 2004a). By 1915 a historic low of 13,000 individuals remained (Yoakum 2004b). Wildlife conservation practices became increasingly popular during the 20th century and pronghorn populations began to recover from near extinction through improved hunting policies and rangeland management (Yoakum 2004b). By 1924 the estimated population size increased to 30,500 and by 1983 that number had climbed to over one million (Yoakum 2004b).

Although pronghorn experienced more than half a century of significant population recovery, numbers plateaued between 1984 and 1995, and have since decreased by approximately one-third (Yoakum 2004b). This population decline is particularly apparent for pronghorn occupying arid habitats of the southwestern U.S. and Mexico (i.e., *A.americana sonoriensis* and *A. americana peninsularis* subspecies). California, which is composed of large areas of semi-arid habitat, once contained one of the highest pronghorn densities west of the Continental Divide (Yoakum 2004b). The species was widely distributed throughout the state, occupying ranges from the Modoc Plateau in the northeast, throughout the Sacramento and San Joaquin valleys, and along both sides of the coastal range in southwest California (Yoakum and Koch 2009). However, as California's human population expanded during the early 1900's, pronghorn populations exhibited similar trends as elsewhere in North America (Yoakum 2004b). The species became regionally extinct in all areas except the northeast (McLean 1944) and presently are absent from an estimated 70% of their historic range (Yoakum and Koch, 2009).

From 1987 to 1990, the California Department of Fish and Game (CDFG) conducted a series of reintroductions, during which 340 pronghorn were translocated from the Modoc Plateau region to several sites in Kern and San Luis Obispo counties (Maher 1994). Approximately 135 of these animals were released onto the Carrizo Plain National Monument (CPNM). Information from aerial surveys, conducted by the CDFG in 1995 and biannually from 2000-2011, indicate that this translocated pronghorn population has declined significantly. Today, pronghorn on the CPNM exist at low density as fewer than 30 individuals consistently utilize habitat within the monument boundary (Sommer 2012).

Study area

The Carrizo Plain National Monument (CPNM) is located within the coast range in southeastern San Luis Obispo County, California (Goodwin Education Center: N 35° 11' 23.51", W 119° 51' 47.87"; UTM 35.189864, -119.863298) (Fig 1.1). The monument encompasses 102,639 hectares (253,628 acres) co-managed by the CDFG, Bureau of Land Management (BLM) and The Nature Conservancy (TNC) (BLM 2011, Sisk et al. 2008). Topography within the monument is primarily composed of an expansive plain bordered by two mountain ranges: the Temblor Range along the northeast boarder and the Caliente Range along the southwest boarder. Elevation along the valley floor averages 615 meters (2,018 ft). The highest elevation is Caliente Peak at 1,556 meters (5,105 ft). Annual rainfall occurs primarily between December and April and can be highly variable among years (mean = 24.56 cm, SE = 2.31 cm). Runoff from rainfall drains collects in Soda Lake, a shallow, alkali terminal lake in the center of the valley floor (Penrod et al. 2010). The semi-arid nature of the Carrizo Plain results in the lake being ephemeral in nature. Average minimum daily temperature during the past two decades since 1992 was 5°C (41°F, SE = 8.72) and average maximum daily temperature was 24°C (75°F, SE = 13.04). Historically, the area was used for dry land wheat farming and is now inundated with non-native annual plant species. Annual grasses, notably brome (*Bromus* spp.) and wild oats (*Avena* spp.) are dominant on the plain. Alkali sink vegetation including spiny saltbush (*Atriplex spinifera*) and iodine bush (*Allenrolfea* *occidentalis)* are found at the lowest elevations. Juniper-oak cismontane woodland and cismontane juniper woodland and scrub are found in the higher elevations. Although anthropogenic disturbances within the monument are minimal, portions of the valley floor have been converted to agricultural fields and some livestock grazing does occur. The CPNM is generally considered to be at the far southwest portion of the Central Valley ecoregion (Hickman 1993). It provides habitat for a number species which are either federally listed as endangered or considered species of management concern: San Joaquin kit fox (*Vulpes macroitis mutica*), blunt-nosed leopard lizard (*Gambelia sila*), giant kangaroo rat (*Dipodomys ingens*), longhorn fairy shrimp (*Branchinecta longiantenna*), Nelson's antelope squirrel (*Ammospermophilus nelson*), and burrowing owl (*Athene cunicularia*) (Sommer 2012).

Literature Cited

Bureau of Land Management (BLM). 2011. BLM Fact Sheet, Mission Statement. Carrizo Plain National Monument page. http://www.blm.gov. Accessed 11 Nov. 2011.

Byers, J. A. and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn and the question of a limit on differential provisioning in ungulates. Behavioral Ecology and Sociobiology. 26:157-164.

Byers, J.A. 1997a. Methods and Materials. Pages 15-22. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Byers, J.A. 1997b. Birth and the hiding Strategy. Pages 52-78. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Canon, S. K. and F. Bryant. 1997. Bed site characteristics of pronghorn fawns. Journal of Wildlife Management. 61(4):1134-1141.

Cantrell, R., C. Cosner, W. F. Fagan. 2001. How predator incursions affect critical patch size: the role of functional response. The American Naturalist 158: 368-375.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Applied Biology 1:183-246.

Caughley, G. 1977. Analysis of Vertebrate Populations, John Wiley & Sons.

Coulson, T., S. Albon. F. Guinness, et al. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology 78:852-863.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the allee effect. Trends in Ecology and Evolution 14:405-410.

DeAngelis, D. W., and J. C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. Ecological Monographs 57:1-21.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling. 3, 481-538.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Ellis, J. E., and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. Journal of Range Management 41:450-459.

Fisher J. and D.B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation. 96: 1-11.

Fowler, C.W. and J.D. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. Report to the International Whaling Commission 41: 545-554.

Gaillard, J.M., M. Festa-Bianchet, N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution. 13 (2): 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 Ecological Systematics 31:367-393.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey and man in interior Alaska. Wildlife Monographs. Number 84.

Gregg, M. A., Bray, M., Kilbride, K. M., and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management. 65(1):19-24.

Griffith, B., J. M. Scott, J. W. Carpenter and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477-480.

Hickman, J. C. (Editor). 1993. Jepson Manual. Higher Plants of California. University of California Press.

IUCN 2013. The IUCN Red List of Threatened Species. Version 2013.2. http://www.iucnredlist.org. Downloaded on 11 February 2014.

Johnson, H. E. V. C. Bleich, P. R. Krausman. 2007. Mineral deficiencies in Tule elk, Owens Valley, California. Journal of Wildlife Diseases. 43(1): 61-74.

Kohlmann, S. G. 2004. Population dynamics and modeling. Pages 645-674. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Longshore, K. and C. Lowrey. 2008. Habitat analysis and food habits of pronghorn antelope in the Carrizo Plain National Monument, California. Final Report prepared for the Bureau of Land Management, Bakersfield, California. 43 pp. U.S. Geological Survey, Western Ecological Research Center, Henderson, Nevada, USA.

Maher, C. R. 1994. Pronghorn male spatial organization: population differences in degree of non-territoriality. Canadian Journal of zoology. 72:455.

Nelson, E. W. 1925. Status of the pronghorned antelope, 1922-1924. Bull. 1,346. U.S. Department of Agriculture. Washington, D.C. 64 pp.

O'Gara, B. W. 2004. Mortality Factors. Pages 379-408. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. and J. D. Yoakum.1992. Pronghorn management guides. Proceedings of the 15th biennial pronghorn antelope workshop. 101 pp.

O'Gara, B. W. and J. D. Yoakum. 2004. Forward. Page xxv. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. and H.G. Shaw. 2004. Predation. Pages 337-377. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

Penrod, K., W. Spencer, E. Rubin, and C. Paulman. April 2010. Habitat Connectivity Planning for Selected Focal Species in the Carrizo Plain. Prepared for County of San Luis Obsipo by SC Wildlands, http://www.scwildlands.org.

Pettorelli, N., J.M. Gaillard, N. G. Yoccoz, P. Duncan, D. Maillard, D. Delorme, G. V. Laere, C. Toigo. 2005. Journal of Animal Ecology. 74:972-981.

Rutberg, A. T. 1987. Adaptive hypothesis of birth synchrony in ruminants. The American Naturalist 130: 692-710.

Salwasser, H. 1980. Pronghorn antelope population and habitat management in the northwestern Great Basin environments. USDA, Forest Service, Pacific Southwest Region.

Sommer, M. L. 2012. California pronghorn antelope status report and management update. State of California Natural Resources Agency. California Department of Fish and Game.

Sisk, R. L., J. Tysdal-Sisk, and J. A. Sisk. 2008. Carrizo Plain National Monument, a natural history guide. Fenske Media Corporation, Rapid City, South Dakota, USA.

Sundstrom, C., W. G. Hepworth and K. L. Diem. 1973. Abundance, distribution and food habits of the pronghorn. Bull. 12. Wyoming Game and Fish Commission, Cheyenne. 62 pp.

Tuljapurkar, S. and Caswell, H. 1997. Structured-Population Models in Marine, Terrestrial, and Freshwater System, Chapman & Hall.

U.S. Fish and Wildlife Service. 1997. Appendices 1, 2 and 3 to Convention on international trade in endangered species of wild fauna and flora. U.S. Government Print. 1999:454-786/94969, Washington, D. C. 24 pp.

Vriend, H. G. and M. W. Barrett. 1978. Low pronghorn recruitment-is it an issue? Pronghorn Antelope Workshop Proceedings. 8:360-379.

Wildlife Management Institute. 2001. Unpublished survey of pronghorn populations in North America. Wildlife Management Institute, Washington, D. C.

Wolf, C. M., b. Griffith, and C. Reed. 1996. Avian and mammalian tranlocations: update and reanalysis of 1987 survey data. Conservation Biology 10(4):1142-1154.

World Conservation Union. 1993. Draft guidelines for re-introductions. Gland. Switzerland.

Yoakum, J. D. 1972. Antelope-vegetative relationships. Antelope States Workshop Proceedings. 5:171-177.

Yoakum, J. D. 2004a. Habitat characteristics and requirements. Pages 409-446. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. 2004c. Foraging Ecology, diet Studies and Nutrient Values. Pages 447-502. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D., A. J. Koch. 2009. A review of literature pertaining to pronghorn in California from 1769 to 2009. Trans. West. Sect. Wildl. Soc. 45:2009.

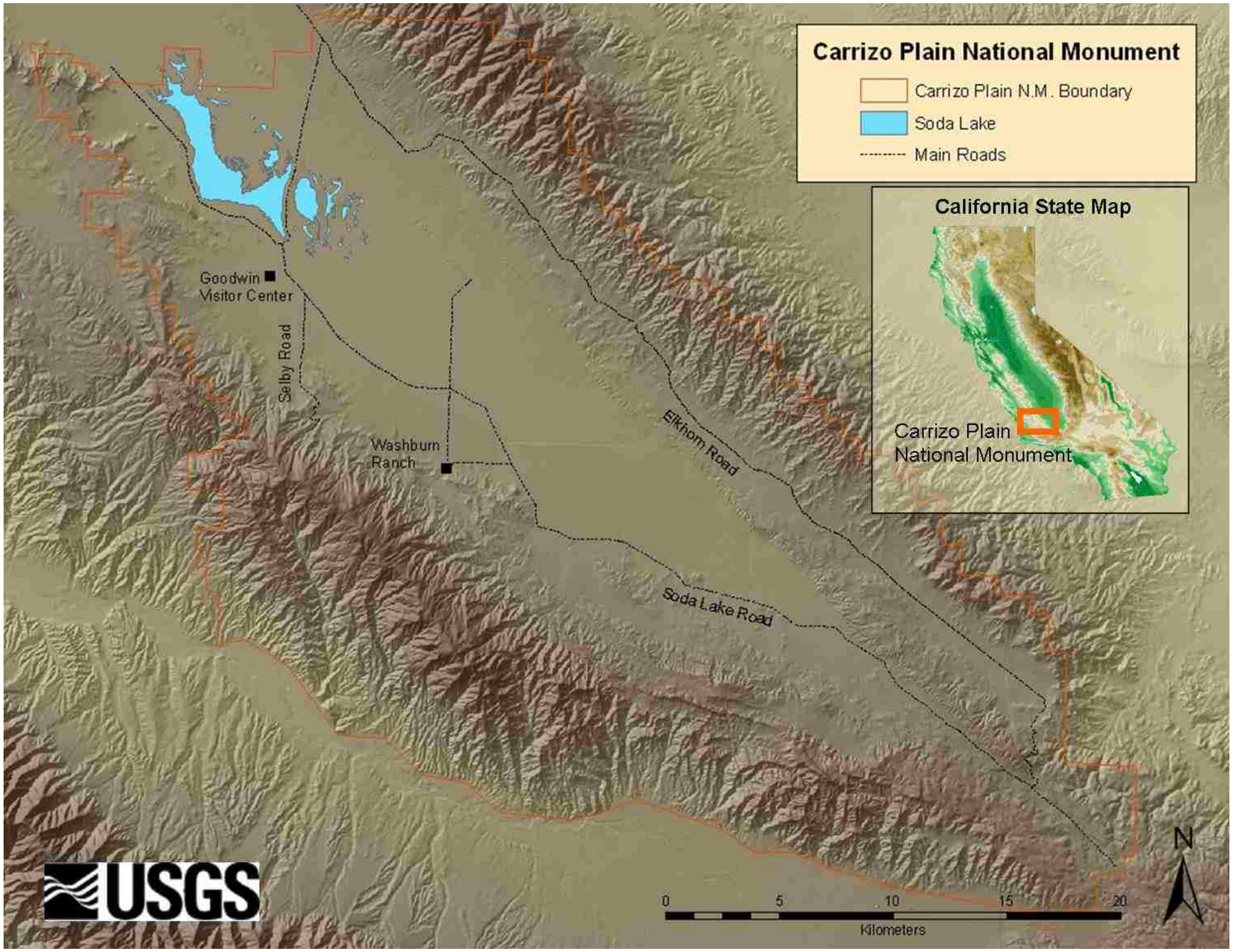


Figure 1.1. Carrizo Plain National Monument, CA. Goodwin Visitor Center is located at N 35° 11' 23.51", W 119° 51' 47.87"; UTM 35.189864, -119.863298.

CHAPTER 2

ALLEE EFFECTS, BIRTH SYNCHRONY, AND NEGATIVE DENSITY DEPENDENCE IN A TRANSLOCATED POPULATION OF PRONGHORN (ANTILOCAPRA AMERICANA)

Introduction

Understanding how wildlife populations are regulated is a principal concern in ecology and conservation (Caughley 1977, Tuljapurkar and Caswell 1997). For most temperate ungulates density-dependent and density-independent factors, in concert, directly affect individual fitness and ultimately regulate population size (Saether 1997, Clutton-Brock 1985, 1991). Density-independent regulation commonly involves the effects of climatic variables (Post and Stenseth 1998) whereas density-dependent regulation is often associated with forage availability (Kie et al. 1980; Skogland 1986), predation, (Wittmer et al. 2005), and disease (Shrauder 1984). Studies on density-dependence have largely focused on the effects of overcrowding, where a negative or "classical" relationship between population size and per capita growth (Fig 2.1) is formed as populations approach carrying capacity (the maximum number of animals supported within a particular habitat in relation to available resources) (Fowler 1981, Kohlmann 1998, Hess 1986, Hess 1999, Pojar 1997). Less studied, however, are the contrasting effects of positive or "inverse" density-dependence. Termed the Allee effect, positive density-dependence at low population size causes per capita growth rates to decline (Fig 2.1; Allee 1931). When Allee effects are strong, per capita growth rates can reach zero or negative values and cause catastrophic population collapse (Dennis 1989, McCarthy 1997, Poggiale 1998, Stephens et al. 1999, Courchamp et al. 1999).

Allee effects have profound implications for threatened wildlife populations (Stephens and Sutherland 1999, Courchamp et al. 2008). Thus, understanding how Allee effects arise is important for population ecology and conservation. Allee effects are generally classified as being either a component or demographic Allee effect (Courchamp et al. 1999). Component Allee effects refer to a positive relationship between population size or density and any measurable component of individual fitness (e.g., rates of births or deaths). When component Allee effects are strong enough, they may then result in a demographic Allee effect, where population size or density is positively related to per capita growth rate. Mechanisms for both component and demographic Allee effects have been documented for a large variety of taxa and can include cooperative breeding, predator dilution, foraging efficiency, mate finding and reduced genetic diversity (Dennis 1989, Fowler and Baker 1991, Stephens and Sutherland 2000, Berec et al. 2007). For ungulates, however, it is not well understood how Allee effects are produced (Hoffman 2010). Allee effects generally arise via mechanisms that are intrinsic to the species' life history (Courchamp et al. 2008). For social ungulate species, in which selection has favored large group sizes, fitness benefits are associated with the presence of conspecifics (Stephens and Sutherland 1999). Many ungulate species produce large numbers of young during tightly synchronized birth periods (Estes 1976, Rutberg 1987). Birth synchrony is an important adaptation which acts to saturate predation thresholds (e.g., energy and time foraging required) and ultimately decrease per capita predation rates (Rutberg 1987, Gregg et al. 2001, Kohlmann 2004). However, the benefits of birth synchrony are density-dependent and, in small populations, predation rates may increase if offspring production is low (i.e., component Allee effect). Thus, demographic Allee effects may arise in low density populations if a collapse of birth synchrony produces low or negative per capita growth rates.

In this study, I investigate potential Allee effects and evaluate birth synchrony as a possible mechanism for the Allee effect within a highly reduced population of pronghorn (Antilocapra americana) on the Carrizo Plain National Monument (CPNM) in California. The CPNM is located along the southwest edge of California's Central Valley, a region which once contained one of the highest pronghorn densities in North America (Pyshora 1977, Yoakum 2004b). However anthropogenic effects associated with agricultural development and overhunting resulted in regional elimination of the species by the 1930's (Yoakum 2004a). During a series of reintroduction efforts conducted in 1987, 1988 and 1990, 240 pronghorn were translocated to various locations surrounding the CPNM.

Information from aerial surveys indicates that descendants of the originally released individuals presently exist in two distinct groups (i.e., herds) (Sommer 2012). Although these groups occupy sites adjacent to one another, geographic and anthropogenic barriers (e.g., mountain ranges, salt flats, roads, fences, and residential development) restrict movement and minimize immigration and/or emigration (Sommer 2012). For purposes of clarity, these two groups will hereby be referred to as the CPNM and California Valley (CV) populations. Although the CPNM population utilizes expansive, undeveloped and federally protected habitat on the southern end of the Carrizo Plain, pronghorn abundance and fawn:doe ratios have consistently been higher for the

CV population occupying the mostly private agricultural areas on the northern end of the Carrizo Plain (Sommer 2012). The demographic contrast between the two populations provides an opportunity to compare relative strengths of potential Allee effects.

To assess ecological processes related to density-dependence in small populations, I first determine how fawn survival is affected by the timing and distribution of birth dates and evaluate the potential for birth synchrony to act as a mechanism for a component Allee effect. I then test for a demographic Allee effect by measuring the density-dependent feedback of population size on logarithmic per-capita growth for the CPNM and CV populations.

Methods

Birth synchrony and fawn survival

To examine the degree of synchronicity for annual birth distributions I divided the range of days in which births occurred for each year into four equal periods using the first, second and third quartiles (Gregg et al. 2001). I then totaled the number of births which occurred during each of the four periods. The two periods with the most number of births were considered peak periods and the two periods with the least number of births were considered non-peak periods. I defined birth synchrony as a distribution with two adjacent peak periods (e.g., the first and second periods are peak). Distributions in which the two peak periods were separated by one or more non-peak periods were considered to be asynchronous. The survival rates for fawns born during peak and non-peak periods were then compared to determine the effect that timing of birth had on recruitment (Gregg et al. 2001).

Fawn survival and causes of mortality

Neonatal pronghorn fawns were equipped with GPS/VHF expandable, breakaway collars during April and May, 2009-2011. Total weight of each collar was ≤ 120 grams. Fawn captures were conducted using methods described in O'Gara et al. (2004) and Gregg et al. (2001). Heidi Zurawka D.V.M., California Dept. Fish & Game, assisted with captures and trained the field crew in fawn processing techniques in 2009. Pronghorn fawns were captured at < 5 days of age. Bedded fawns were approached on foot and a large net (approx. 1 m dia.) was placed gently over the fawn to assure capture and prevent bolting. If a birth was witnessed, capture was conducted at least 4-6 hours afterwards to allow for fawn-doe imprinting. Once captured, every effort was used to minimize stress to the animals. Fawns were blindfolded and kept still to reduce the chance of injury. Surgical gloves, capture net, and collars were all previously stored in local vegetation to minimize human scent. I recorded sex, weight, body measurements, condition of fawns, and estimated the date of birth. For fawns whose birth was not observed, birth date was estimated by behavioral criteria, condition of pelage, hoof and dental development, and desiccation of umbilical cord (see O'Gara et al. 2004). Blood samples (18-20 ml) were collected from individuals that did not appear stressed (e.g. fawns that struggled more than normal). Blood samples were sent to the California Department of Fish and Game Wildlife Investigations Laboratory. All pronghorn fawns observed on the CPNM were monitored daily. Collared fawns were located using VHF telemetry receivers. Positive identification of uncollared fawns was possible through the collaring of a sibling, location, or identifiable pelage of the mother (Byers 1997a). Fawns which lived > 90 days were considered to have been recruited based on abundant evidence from similar studies which have documented that 95% of fawn mortality takes place ≤ 18 days of age (Gregg et al. 2001). Both collared and uncollared fawns which were not again observed after the regrouping of individuals during late summer, were considered to have died based on results from numerous studies (reviewed in Gaillard et al. 2000) indicating that young ungulates die either within their first weeks or during their first winter (Pettorelli et al. 2005). Results for survival rates were compared to eighteen other similar studies conducted within 10 different states as reported by O'Gara and Shaw (2004).

In addition to collaring fawns, I conducted standardized road surveys from 2008-2011. The purpose of these surveys was to: 1) monitor the distribution and condition of uncollared fawns and adults; 2) verify count information from flights conducted by the CDFG during that same period; and 3) locate and recorded potential predators of fawns (i.e., coyotes and golden eagles) (predators were recorded for 2010 and 2011 only). The CPNM contains an extensive network of paved and unpaved roads (>150 km in total), so that any one point within suitable pronghorn habitat is no more than 4.2 km from a drivable location. I was able to use binoculars and spotting scopes to effectively survey all pronghorn habitat from vehicles and by accessing areas of elevated topography on foot. Animal locations were calculated using the observer location (Garmin map76 handheld GPS unit) and the estimated distance and bearing to the animal. Female pronghorn detected during ground surveys were monitored for the presence of fawns using methods described by Byers (1997a).

I calculated seasonal fawn survival rates using the Kaplan–Meier (K-M) procedure (Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989). Due to the small sample size of collared individuals and the large quantity of censored data (i.e., telemetry failure) interpretation of K-M results was limited. However, when I compared K-M survival curves between collared fawns and fawns which were uncollared, but monitored regularly for survival, I found that results did not differ. I therefore grouped all fawns born during individual seasons and then compared seasons using a log rank procedure.

Fawns which did not survive were recovered as quickly as possible to determine whether death was due to predation and if so, to identify the predator species using criteria described in O’Gara and Shaw (2004). When possible, carcasses of deceased fawns were taken to the California Department of Fish and Game’s Wildlife Investigations Laboratory for necropsy results.

Density-dependence and the Allee effect

To test for Allee effects, and overall density-dependence, I used a multi-model inference approach (Burnham and Anderson 2002). First, I measured the density-dependent feedback of population size on logarithmic per-capita growth for both the CPNM and CV populations (Hoffman et al. 2010). Annual population sizes were estimated using winter count totals from aerial surveys conducted by the CDFG from 2000 to 2011. Population size was used instead of population density because the two areas occupied by each herd are similar in size (Courchamp et al. 2008). To evaluate the potential for immigration and emigration to have occurred between the CPNM and CV, and to justify analyzing the two populations as separate and demographically distinct, I compared the linear relationships of annual population change between the two groups. For all years, excluding 2008, there existed a positive relationship of annual population change between the two groups, indicating the population growth and/or decline occurred similarly, and that interchange between each group was likely limited and insignificant. Information from aerial counts was compared to information from ground surveys (from 2009-2011) to assess the accuracy of the data set. Logarithmic per capita population growth rate (log(g(N)) was calculated using log transformed data from the discrete-time model of population dynamics ($g(N) = \log(N_{t+1}/N_t)$; where N_t represents the population size at time t (Courchamp et al. 2008). I then developed a suite of models to test possible linear and non-linear (i.e., exponential) relationships between population size and per-capita growth (Burnham and Anderson 2002). Akaike's Information Criterion adjusted for small sample size (AIC_c) was used for model selection (Burnham and Anderson 2002). Residual sum of squares values from each of the alternative models were used to determine AIC_c and ΔAIC_c values. I used the AIC_c differences to rank the set of candidate models. I considered approximating models with ΔAIC_c of ≤ 3 as a conservative approach to determine the fit of possible competing models. I used Akaike weights (w_i) and evidence ratios to assess the relative strength of evidence for each model.

Results

Birth synchrony and fawn survival

Births for all three seasons (from 2009-2011) occurred within a one month period, between April 25 and May 25 (Fig. 2.2). The date range and synchronicity of fawn birth distributions varied between years (Fig. 2.2). The mean range in which births took place was 22.7 days (SE = 6.4). Birth synchrony was detected for the first two years, during 2009 and 2010, where peak offspring productivity occurred during the first two quarters of each year's respective birth distribution (before quartile 1 and between quartile 1 and 2). Birth synchrony was not detected for 2011, where peak periods of offspring productivity occurred at the beginning (before quartile 1) and at the end (after quartile 3) of the birth distribution. Survival was higher during peak periods than non-peak periods (Table). All 12 surviving fawns in the study were born during peak periods and none of the fawns born during non-peak periods survived in any year of the study. Survival was not related to overall offspring production across the three years ($\chi^2 = 6.00$, df = 4, p = 0.20).

Fawn survival and causes of mortality

Forty-five pronghorn fawns were born on the CPNM during three seasons from 2009 to 2011. Of these individuals, 20 (7 males and 13 females) were equipped with GPS/VHF collars and released. Mean age at capture was 2.07 days (SE = 0.33). Body measurements and processing data for each fawn can be found within Appendix A. Survival between male and female collared fawns did not differ (z = -0.32, p = 0.75). The remaining 11 uncollared fawns were monitored through field observation. Percent survival of collared fawns (20.0%) and uncollared fawns (32%) did not differ (z = -0.25, p = 0.81). Percent survival of all fawns (both collared and uncollared; 26.7%) did not differ from that found for other populations (29.4%, n = 995) as reported by O'Gara and Shaw (2004) (z = 0.22, p = 0.82). Annual fawn productivity and survival was variable across years (mean productivity = 15.0 fawns, SE = 3.5 and mean survival = 30.7%, SE = 8.5) (Table 2.2). Of 13 recovered collars, 10 functioned properly while deployed (i.e., consistently recorded locations); and of these 10 functioning collars, 9 were from deceased fawns. The mean number of days lived for the 9 deceased collared fawns was

14.4 days (SE = 2.9) and all but one of these fawns died at ≤ 18 days of age. Results for the Kaplan-Meier survival curve (Fig. 2.3) indicated that 50% of fawn mortality occurred prior to 20 days of age and that the greatest rate of mortality took place between 16 and 18 days. Kaplan-Meier survival curves did not differ between years (Log-Rank Statistic = 3.34, DF = 2, P = 0.19).

Causes of mortality for the 20 collared fawns and 1 uncollared fawn included predation (28.6%; n = 6), health-related issues (0.1%; n = 2) and undetermined causes (61.9%; n = 13). For the 6 predator related mortalities, predation by coyote (n = 6) and golden eagle (n = 1) were detected. Results from laboratory necropsies performed for the two health-related mortalities indicate that death was caused by an infected umbilical cord for one individual and a lacerated liver (possibly from being stepped on by its mother) for the other (Appendix B).

To evaluate the potential for additional predator related mortalities to have occurred, I analyzed age-specific mortality and movement patterns of fawns that did not survive. Byers (1997b) reported that fawn mortality was highest for individuals between 11 and 20 days; and suggested that, as fawns develop, increases in movement make individuals more visible to predators. On the CPNM, fawns made significant increases in movement between 16 to 18 days of age (Fig. 2.4). During that same period, the mortality rate was higher than for any other ages (Fig. 2.3). Eight of the 10 mortalities occurred between 16 and 18 days of age, indicating that mortality risk may have been associated with increased movement.

Density-dependence and the Allee effect

Pronghorn abundance and distribution on the CPNM were consistent between ground and aerial surveys conducted during the fawning seasons from 2009 to 2011 (Fig. 2.5). The pattern in the relationship between population size and logarithmic per-capita growth for the CPNM and CV populations are shown in Fig. 2.6. Analysis of variance and regression analyses of the data produced a set of possible models with varying fit to the data (Table 2.1). Parameters in the global model included population type (i.e., CPNM and CV), population size, population size squared, interaction between population type and population size, and interaction between population type and population size squared (Table 2.1). AIC model selection results indicated that four candidate models, Model 1 ($w_i = 0.40$), Model 2 ($w_i = 0.27$), Model 3 ($w_i = 0.14$) and Model 4 ($w_i = 0.12$), showed support as the best approximating models ($\Delta AIC_c < 3.0$) (Table 2.1). Important parameters indicated by the four top candidate models were population type (i.e., CPNM and CV), population size, and population size squared (Table 2.1).

Discussion

Birth synchrony and fawn survival

Synchronous birth distributions were detected for the two years of highest offspring productivity and largest population size, suggesting that birth synchrony is density dependent and may degrade in reduced populations. Birth peaks, however, contained only limited numbers of individuals due to low population size and did not reflect a strong pattern of synchronicity. All recruited individuals were born during the highest periods of offspring productivity (i.e., *peak periods*) within their respective annual birth distributions. In contrast, the total number of offspring produced each year was not related to the probability of survival. Therefore, it appears that the timing and clustering of birth dates (i.e., birth synchrony) was more important than the raw number of fawns produced. Though it is likely that birth synchrony and total offspring production are working together to influence fawn survival. Decreased recruitment rates due to a loss of birth synchrony in reduced populations would produce a component Allee effect, and possibly a demographic Allee effect. However, directly testing for birth synchrony as a mechanism for a component or demographic Allee effect would require more than three years of fawn survival information. Increased population size is likely to create a more synchronous birth distribution and therefore increase offspring survival. Additionally, variables which influence timing and breeding are likely to be important for maintaining synchronous birth distributions. Gregg et al. (2001) suggested that excessive disturbance of adults during breeding season may disrupt social breeding structure (Copeland 1980), which could reduce birth synchrony by lengthening the breeding period. Gregg et al. (2001) also suggested that female nutrition and body condition during breeding and pregnancy are important for maintaining normal estrous cycles and gestation periods; and that birth synchrony may be promoted through management practices which enhance summer and fall forage quality and abundance, or include supplemental feeding during breeding season (Lee et al. 1998).

Fawn survival and causes of mortality

Mean percent survival of pronghorn fawns on the CPNM did not differ from mean percent survival reported for other populations across the species' range (O'Gara and Shaw 2004). It is important to consider, however, that for small populations, having the same mean percent survival as larger populations may not be adequate for population growth and stability because the raw numbers of recruited individuals are very limited. During this study, the total number of fawns that survived during any one year was only between 3 and 5 fawns. In addition, offspring productivity and percent survival varied substantially between years. Although pronghorn commonly exhibit high variability in annual recruitment (Vriend and Barrett 1978, Kohlmann 2004), small or sparse populations are likely to become vulnerable to environmental and demographic stochasticity (e.g., drought and chance variation of births/deaths, respectively) (Courchamp et al. 2008). Increased rates of fawn survival are likely required to sustain a viable pronghorn population on the CPNM and management actions which increase recruitment will reduce the risk of localized extinction.

The primary causes of mortality typically attributed to deceased pronghorn fawns include predation, starvation, exposure and disease (O’Gara and Shaw 2004). Of these mortality factors specifically, I found evidence for predation only. Mortalities related to health appeared to be separate and unrelated events. Predation on the CPNM (29%) was substantially lower than for other populations (53%; O’Gara and Shaw 2004). Although predation is not generally considered to drive pronghorn population dynamics, the importance of predation increases for static or declining populations; as well as for populations occupying marginal habitats or areas where the number of predators is high in relation to the number of pronghorn (Lee et al. 1998, O’Gara and Shaw 2004). In addition, the abundance of alternate prey species (e.g., lagomorphs, rodents, etc.) can alleviate pronghorn fawn predation (Beale 1986). For the CPNM, population density estimates of predators and alternative prey species would be useful to provide an indication of how predator-prey relationships function at this site; and how interspecific interactions may affect fawn survival and predation.

Information for the direct causes of individual mortalities was absent for the majority of deceased individuals. Weak or non-existent VHF signals on collars delayed and/or impeded the ability to recover carcasses and conduct effective necropsies. Often, fawns were consumed entirely before arrival and/or only small tooth or bone fragments remained. Scavengers (e.g., vultures, corvids, coyotes, etc.) are common on the CPNM, and differentiating between scavenging and predation events becomes increasingly difficult with delayed recovery times (e.g., > 48 hours). To investigate the potential for additional predator related deaths to have occurred, I examined patterns in movement in relation to age-specific mortality. Byers (1997b) found that predation is highest for fawns between 11 and 20 days of age, suggesting that the transition from hiding to cursorial (i.e., running) behavior causes fawns to become increasingly visible to predators while still vulnerable to attack. These results support Byers (1997b) and provide evidence that mortality is associated with increased movement patterns during development. Of the 10 mortalities which occurred during ages of increased fawn movement, the cause of death was reported as unknown for 8 individuals. I consider it likely that predation was involved for a portion of these undetermined cases. Long-term information on fawn survival and causes of mortality is likely required to accurately assess the importance of predation in driving recruitment and ultimately population size on the CPNM.

Density-dependence and the Allee effect

Three broad conclusions can be interpreted through evaluation of the candidate models for density-dependence. First, Model 2 and Model 4 indicate that, independent of population size, growth rates differ between the two populations. That is, the CPNM population has lower rates of growth at any given population size than does the CV population. This may indicate that a habitat effect is involved in which environmental variables (e.g., forage conditions or predator densities) influence population growth. Second, Model 3 indicates that both populations exhibit an Allee effect but do not differ in the magnitude or position of shift from an Allee effect to negative density dependence. Third, Model 1 indicates that both populations exhibit negative density-dependence but do not differ in the amount of reduction in population growth caused by increased population size. The apparent contradiction between Model 1 and Model 3 is best understood by noting that the average size of each population differs within the data set; average population size on the CPNM (53 adults) is lower than in CV (67 adults). Accordingly, it is unknown how growth rates respond to large population sizes on the CPNM or how growth rates respond to small population sizes in CV. Examination of the dataset indicates that at low population size, growth rates respond differently between the two populations, suggesting the presence of an Allee effect for pronghorn on the CPNM and the presence of negative density-dependence for pronghorn in CV.

Summary

In summary, two lines of evidence from this study support the hypothesis that birth synchrony in small populations can act as a mechanism for component Allee effects, and possibly for demographic Allee effects. First, survival was higher for fawns born during peak birth synchrony and lower for those born during outlier dates (component Allee effect). Second, results from multi-model inference and the fact that population growth rates between CPNM and CV appeared to respond differently at low population size, indicate the possible presence of a demographic Allee effect for the CPNM.

Evidence of both positive and negative density-dependent feedback was detected. Although the multi-model inference was not conclusive overall due to the relatively low sample size and AIC penalty on fitting parameters, this modeling method would be useful for future research on demographics of pronghorn and other ungulate species. For this study, the ability to further resolve patterns in model results was limited by the size of the data set, and future research on the CPNM and CV populations would require additional years of information. Accordingly, studies which aim to examine density-dependency in small populations will require long-term data sets with more sampling and replication to reach the best possible conclusions.

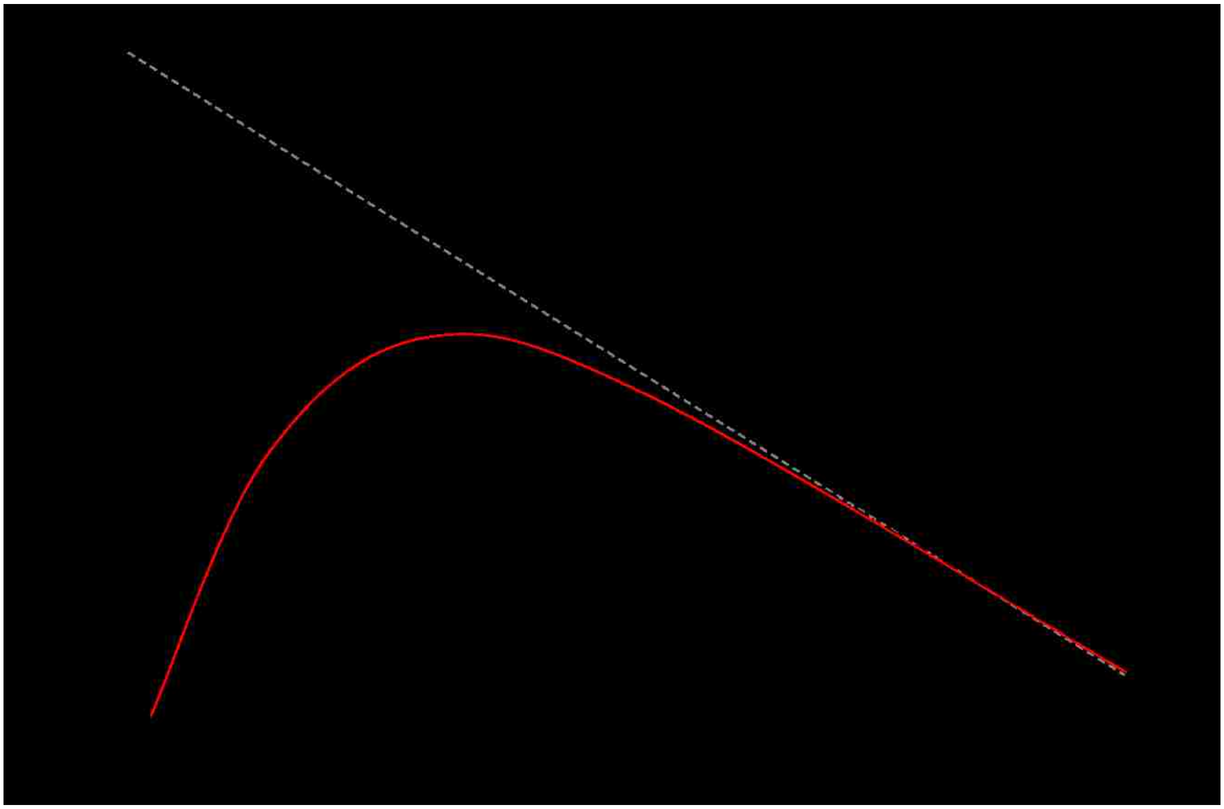
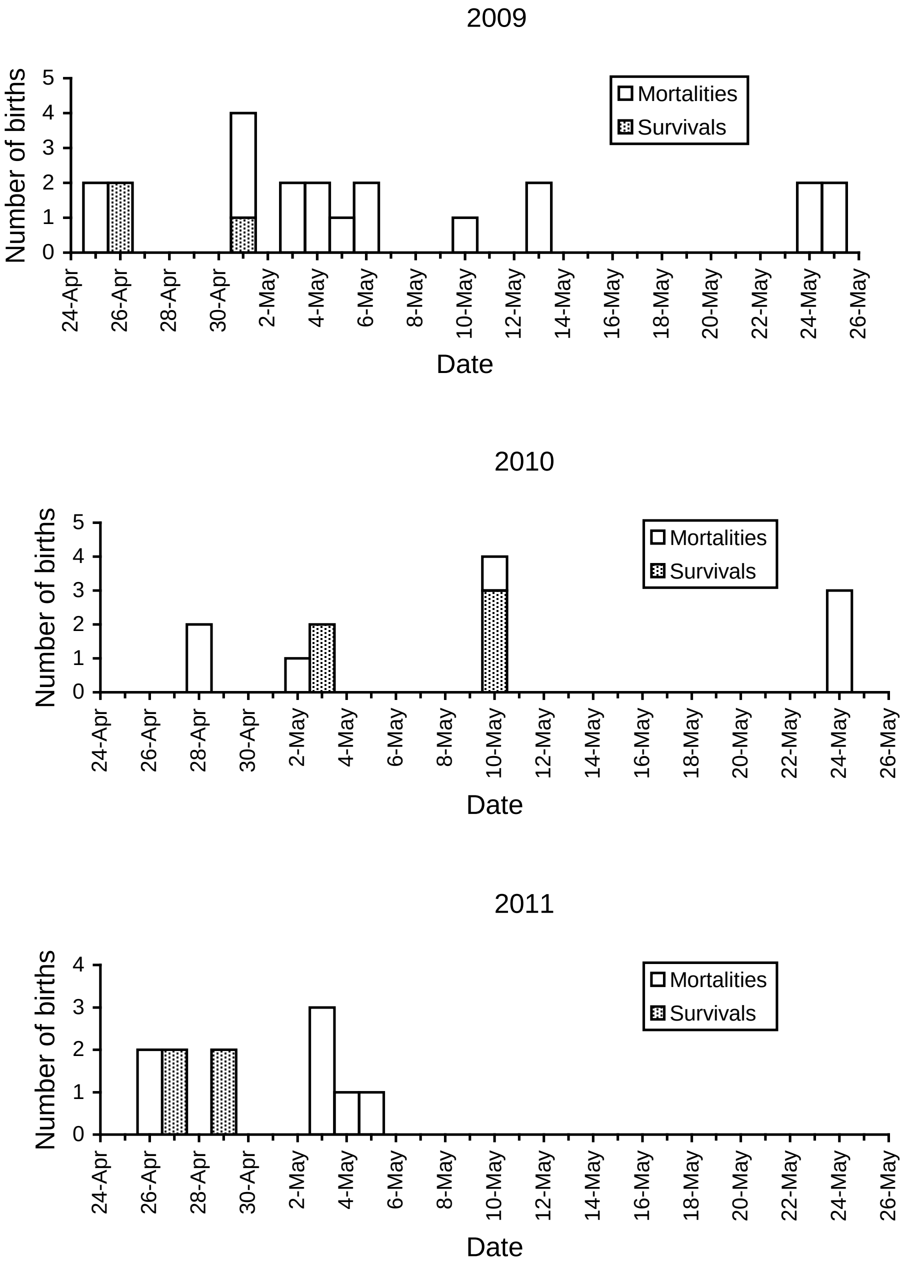


Figure 2.1. Relationship between population size or density and the per capita population growth rate (adapted from Berec et al. 2007). At low population size or density, the relationship is positive for weak (dashed and dotted line) and strong (solid line) Allee effects. For negative or “classical” density dependence (dashed line) the relationship is negative despite population size or density.



2009

2010

2011

Figure 2.2. Pronghorn fawn survival relative to annual birth distribution, for 2009, 2010 and 2011 on the Carrizo Plain National Monument, CA. Survivals (shaded bars) and mortalities (open bars) of individuals are indicated. Birth synchrony was detected for 2009 and 2010, but not for 2011 (*see* Results).

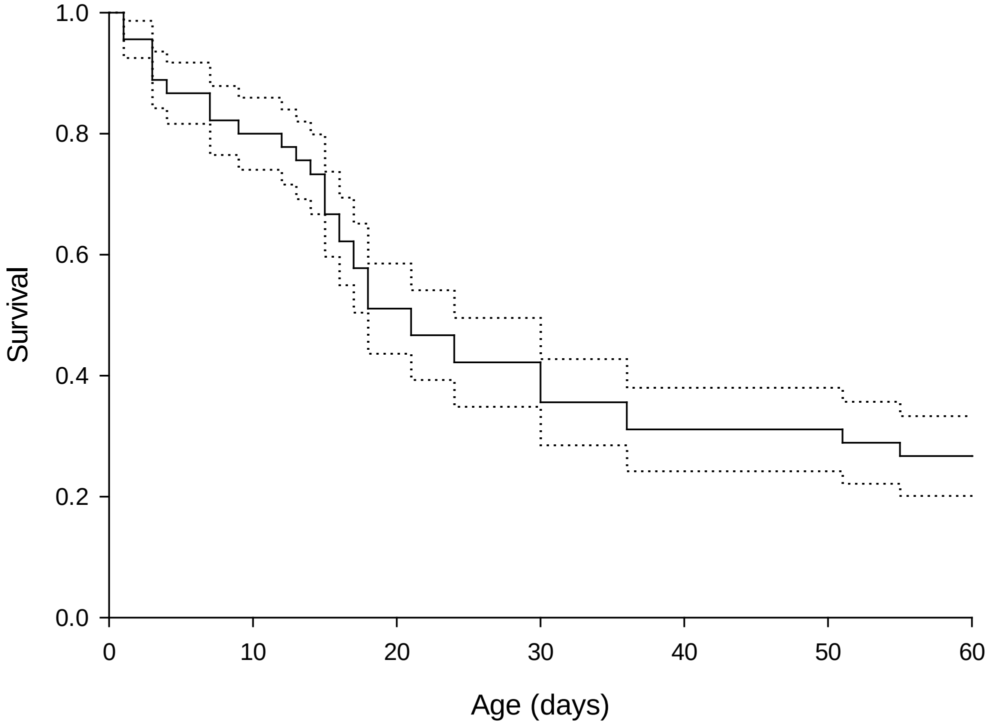


Fig 2.3. Survival curve for pronghorn fawns, born on the Carrizo Plain National Monument, CA during 2009, 2010 and 2011. Survival rate was calculated as proportion of fawns alive at each age class. Upper and lower confidence intervals (dotted lines) were calculated using Kaplan-Meir standard errors.

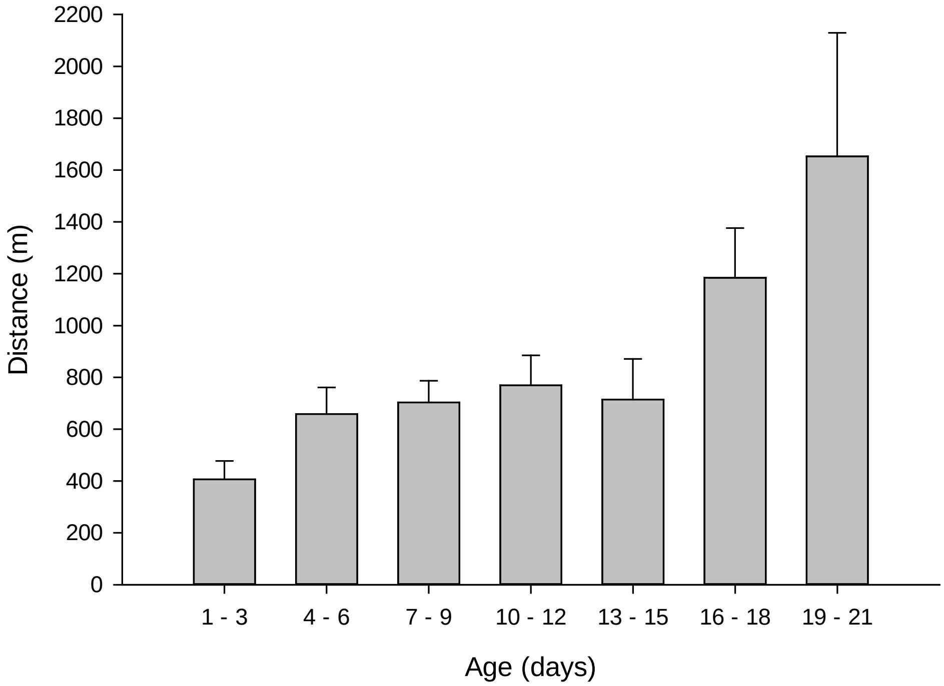


Figure 2.4. Daily distance traveled by GPS collared fawns relative to age, on the Carrizo Plain National Monument, CA from 2009-2011. Distances represent the mean number of meters moved per day, in two hour intervals, by fawns in each respective age class. Distances differed across age classes ($H = 17.77$, $df = 6$, $p = 0.007$) with significance detected between age 1 – 3 days and 19 – 21 days ($p < 0.05$).

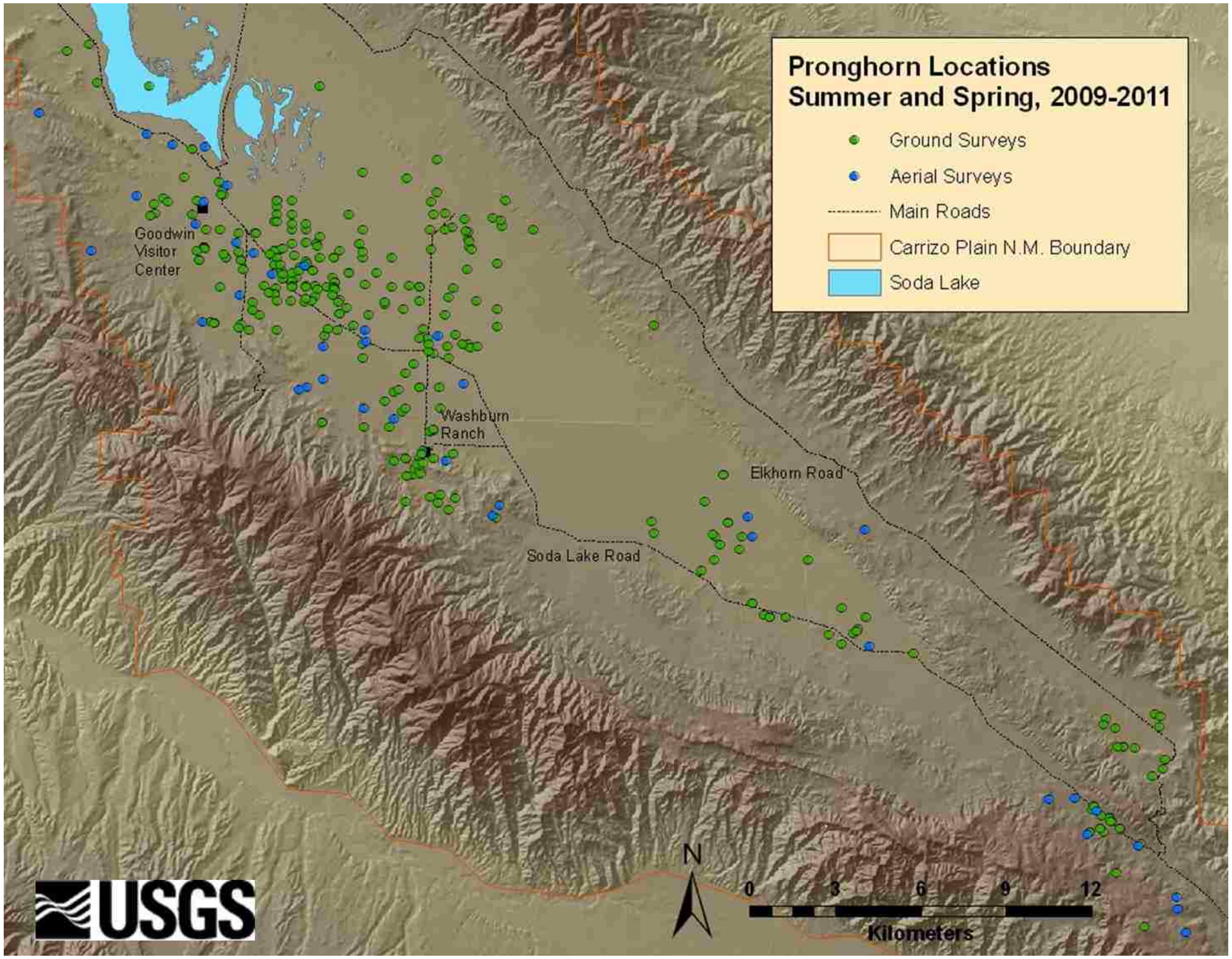


Figure 2.5. Pronghorn locations detected during aerial surveys and road surveys, (blue and green circles, respectively) during spring and summer 2009-2011. Points represent single observations of one or more animals (mean = 3.60 individuals per location, range = 1-16 individuals per location.

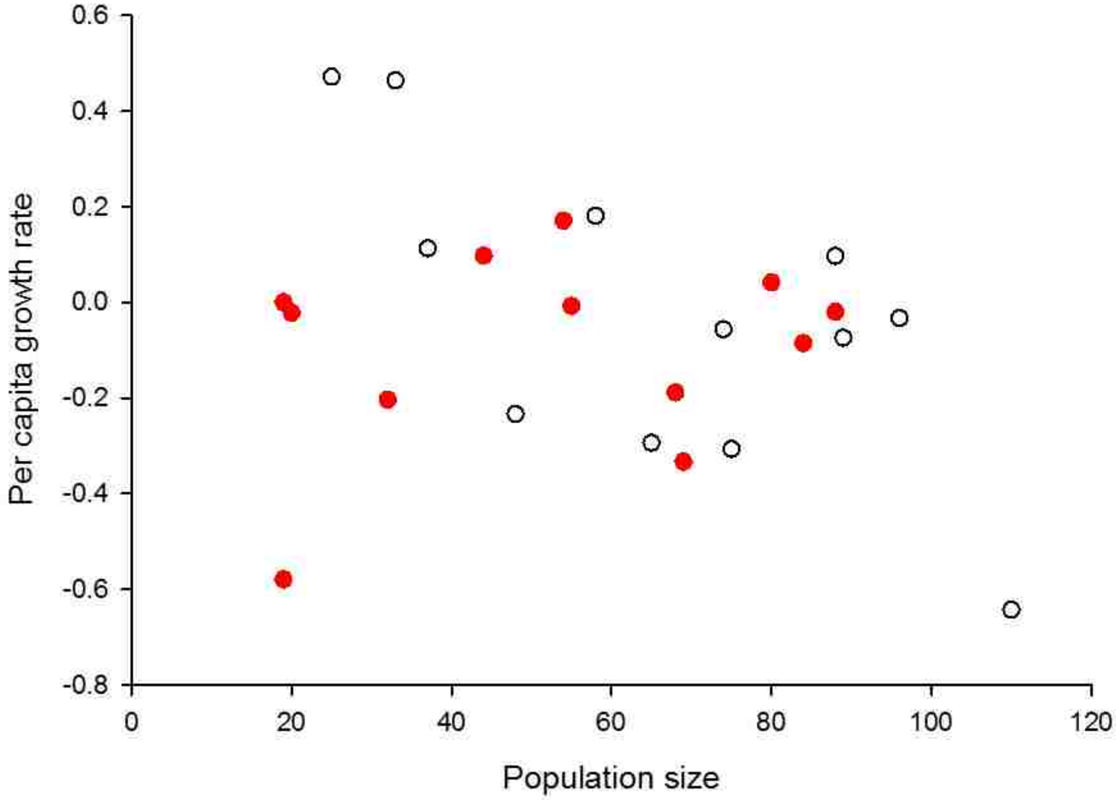


Figure 2.6. Relationship between population size and logarithmic per capita growth rate for pronghorn on the CPNM and in California Valley, (closed circles and open circles, respectively). Information reflects winter count totals from aerial surveys conducted by the California Department of Fish from 2000-2011.

Table 2.1. Comparison and relative ranking of candidate models for analysis of density-dependent feedback between population size and per-capita growth, for pronghorn on the Carrizo Plain National Monument (CPNM) and in California Valley (CV) from 2000 to 2012. Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c) was used for model selection. Included for each candidate model are values for sum of squares (SS), number of parameters (k), AIC_c values, Δ AIC_c values, and Akaike weights (w_i). Relative ranking of models was determined using $\Delta\ \text{AIC}_c \leq 2.5$.

	Model	SS	k	AIC_c	ΔAIC_c	w_i
1	popsize	1.50	1	2.29	0	0.40
2	poptype	1.61	1	3.04	0.75	0.27
3	popsize+popsize2	1.38	2	4.34	2.06	0.14
4	poptype+popsize	1.42	2	4.65	2.36	0.12
5	poptype+popsize+popsize2	1.30	3	6.90	4.62	0.04
6	poptype+popsize+int1	1.50	3	8.42	6.13	0.02
7	poptype+popsize+popsize2+int1	1.50	4	12.03	9.74	0.003
8	Global model	1.20	5	13.80	11.50	0.001

[a]Global model included population type (poptype) (i.e., CPNM and CV), population size (popsize), population size squared (popsize2), interaction between population type and population size (int1), and interaction between population type and population size squared (int2).

Table 2.2. Number of survivals and mortalities for fawns born during peak and non-peak periods on the Carrizo Plain National monument, CA.

	Survivals		Mortalities		
Year	*Peak*	*Non-peak*	*Peak*	*Non-peak*	Total born
2009	3	0	12.5	6.5	22
2010	5	0	4	3	12
2011	4	0	2	5	11
Total	12	0	18.5	14.5	45

Literature Cited

Allen, A. W., J. G. Cook, and M. J. Armbruster. 1984. Habitat suitability index models: Pronghorn. U. S. Fish and Wildlife Service. FWS/OBS-82/10.65.

Angulo E., Roemer G.W., Berec L., Gascoigne J., Courchamp F. 2007. Double Allee effects and extinction in the island fox. Conservation Biology 21:1082-1091.

Bailey, J. A. 1986. Weather and climate. Pages 711-721 *in* A. Y. Cooperrider, R. J. Boyd and H. R. Stuart, eds., Inventory and monitoring of wildlife habitat service center, U.S. Bureau of Land Management. Denver, Co. 858 pp.

Barrett, M. W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. Journal of Wildlife Management. 48(2):542-550.

Buechner, H. K. 1950. Life history, ecology, and range use of the pronghorn antelope in Trans-Pecos, Texas. Am. Midl. Nat. 43(2):257-354.

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

Byers, J. A. and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn and the question of a limit on differential provisioning in ungulates. Behavioral Ecology and Sociobiology. 26:157-164.

Byers, J.A. 1997a. Methods and Materials. Pages 15-22. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Byers, J. A. 1997b. Birth and the Hiding Strategy. Pages 52-78. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Cancino, J. 1994. Food habits of the peninsular pronghorn. Pronghorn Antelope Workshop Proceedings. 16:176-185.

Canon, S. K. and F. Bryant. 1997. Bed site characteristics of pronghorn fawns. Journal of Wildlife Management. 61(4):1134-1141.

Cantrell, R., C. Cosner, W. F. Fagan. 2001. How predator incursions affect critical patch size: the role of functional response. The American Naturalist 158: 368-375.

Clutton-Brock, T. H., Major, M. & Guinness, F. E. 1985. Population regulation in male and female red deer. Journal of Animal Ecology 54: 831-846.

Clutton-Brock, T. H., M. Major, S. D. Albon, F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density dependent effects in juvenile survival. Journal of Animal Ecology 56: 53-67.

Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. 1991. Persistant instability and population regulation in Soay sheep. Journal of Animal Ecology 60: 593-608.

Clutton-Brock T., Gaynor D., McIlrath G. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology 68: 672-683.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the allee effect. Trends in Ecology and Evolution 14:405-410.

Courchamp F. and D. W. Macdonald. 2001. Crucial importance of pack size in the African wild dog *Lycaon pictus*. Animal conservation 4:169-174.

Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in ecology and conservation. Oxford University Press. Oxford, New York. 256 pp.

Danvir, R. E. 2000. Environmental and density-dependent effects on a northern Utah pronghorn population. Pronghorn Antelope Workshop Proceedings 17:36-41.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling. 3, 481-538.

Einarsen. 1948. The pronghorn antelope and its management. Monumental Printing Co., Baltimore, Maryland. 238 pp.

Ellis, J. E. 1970. A computer analysis of fawn survival in the pronghorn antelope. Ph.D. thesis, Univ. California, Davis. 70 pp.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62 (3): 602-610.

Fowler, C.W. and J.D. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. Report to the International Whaling Commission 41: 545-554.

Gaillard, J.M., M. Festa-Bianchet, N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution. 13 (2): 58-63.

Gregg, M. A., Bray, M., Kilbride, K. M., and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management. 65(1):19-24.

Guenzel, R. J., L. L. Irwin and T. J. Ryder. 1982. A comparison of pronghorn movements and distribution during a normal and a mild winter in the Red Rim area, Wyoming. Pronghorn Antelope Workshop Proceedings. 10:156-172.

Hess, M. L. 1986. Density-dependent summer pronghorn fawn survival rates in the interstate antelope population. Pronghorn Antelope Workshop Proceedings. 12:53-54.

Hess, M. L. 1999. Density dependent summer pronghorn survival rates in the northwestern Great Basin-revisited. Pronghorn Antelope Workshop (1998) Proceedings. 19:107.

Hoover, R. L. and S. Ogilvie. 1954. P-R Quart. Rept. Colorado Dept. Game and Fish, Denver. Pp. 33-38.

Hughes, K. S. and N. S. Smith. 1990. Sonoran pronghorn use of habitat in southwest Arizona. Research Report 146-0091564. Arizona Cooperative Fish and Wildlife Research Unit. University of Arizona, Tucson. 58 pp.

Hylander, C. J. 1966. Wildlife communities: From the tundra to the tropics in North America. Houghton Mifflin Co., Boston, Massachusetts. 342 pp.

Jatnieks, S. A. 1983. A study of pronghorn range in southwestern North Dakota. M.S. thesis, University of North Dakota, Grand Forks. 83 pp.

Kindschy, R. R., C. Sundstrom and J. D. Yoakum. 1982. Wildlife habitats in managed rangelands – The Great Basin of southeastern Oregon: Pronghorns. General Technical Report. PNW-145. Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service. Portland, Oregon. 18 pp.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildl. Monogr. 38. 96 pp.

Koch, A. J. and J. D. Yoakum. 2002. Reintroduction and status of pronghorn on the Carrizo Plain National Monument and surrounding areas in southern California. Proceeding of the 20th Biennial Pronghorn Workshop.

Kohlmann, S. G. 2004. Population dynamics and modeling. Pages 645-674. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Lehman, V. W. and J. B. Davis. 1942. Experimental wildlife management in the south Texas chaparral. P-R Quart. Prog.Rept., Proj. 1-R, Unit C, Sect. 1. Texas Game, Fish and Oyster Commiss., Austin. 14 pp.

Leirs, H., N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, W. Verheyen. 1997. Stochastic seasonality and nonlinear density dependent factors regulate population size in an African rodent. Nature 389: 176-180.

Longshore, K. and C. Lowrey. 2008. Habitat analysis and food habits of pronghorn antelope in the Carrizo Plain National Monument, California. Final Report prepared for the Bureau of Land Management, Bakersfield, California. 43 pp. U.S. Geological Survey, Western Ecological Research Center, Henderson, Nevada, USA.

Macarthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39.599-619.

Maher, C. R. 1994. Pronghorn male spatial organization: population differences in degree of non-territoriality. Canadian Journal of zoology. 72:455.

McCarthy, M.A. 1997. The Allee effect, finding mates and theoretical models. Ecological Modeling. 103, 99-102.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130-1146.

McKean, W. T. 1954. Preliminary obersvations of ovulation incidence in North Dakota deer and antelope. P-R Proj. W-7-R-9 to 13. North Dakota Dept. Game and Fish, Bismarck. 3pp.

McKean, W. T. 1951. Sex, age and physical characteristics of North Dakota antelope as obtained by field checking. P-R Proj. 7R. North Dakota Dept. Game and Fish, Bismarck. 5 pp.

Mitchell, G. J. 1965. Natality, mortality, and related phenomena in two populations of pronghorn antelope in Alberta, Canada. Ph.D. thesis, Washington St. Univ., Pullman. 221 pp.

Mitchell, G. J. 1967. Minimum breeding age of female pronghorn antelope. J. Mammal. 48(3):489-490.

Mooring M.S., T.A. Fitzpatrick, T.T. Nishihira, D.D. Reisig. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. Journal of Wildlife Management. 68(3):519-532.

Nelson, E. W. 1925. Status of the pronghorned antelope, 1922-1924. Bull. 1,346. U.S. Department of Agriculture. Washington, D.C. 64 pp.

Ockenfels, R. A. and J. A. Wennerlund. 1994. Analyzing pronghorn habitat use patterns with GIS technology. Pronghorn Antelope Workshop Proceedings. 16:55-63.

Ockenfels, R. A., C. L. Ticer, A. Alexander, and J. A. Wennerlund. 1996. A landscape level pronghorn habitat evaluation model for Arizona. Arizona Game and Fish Technical Report #19. Project W-78-R.

O'Gara, B. W. and J. D. Yoakum.1992. Pronghorn management guides. Proceedings of the 15th biennial pronghorn antelope workshop. 101 pp.

O'Gara, B. W. and J. D. Yoakum. 2004. Forward. Page xxv. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. 2004. Mortality Factors. Pages 379-408. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. and H.G. Shaw. 2004. Predation. Pages 337-377. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W., C. J. Knowles, P.R. Knowles, and J. D. Yoakum. 2004. Capture, translocation and handling. Pages 705-764. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

Poggiale, J.C. 1998. From behavioural to population level: growth and competition. Mathematical and Computer Modeling. 27, 41-49.

Pojar, T. M. 1997. Habitat selection and population performance of a pioneering pronghorn population. P-R Job Final Report. Project W-153-R-4, Work Plan 3A, Job 2. Colorado Division of Wildlife. Fort Collins. 6 pp.

Prenzlow, E. J., D. L. Gilbert and F. A. Glover. 1968. Some behavior patterns of the pronghorn. Spec. Rept.17. Colorado Dept. Game, Fish and Parks, Denver. 16 pp.

Pryah, D. B. 1987. American pronghorn antelope in the Yellow Water Triangle, Montana. Montana Dept. Fish, Wildl. and Parks, Helena, in cooperation with the U.S. Bur. Land Manage. 121 pp.

Roseland, K. 1977. Morphology of the pronghorn ovary (*Antilocapra americana* Ord). M.S. thesis, Univ. Montana, Missoula. 45 pp.

Rothchild, S. L., E. J. Finck and K. E. Sexson. 1994. Mortality and bedding site selection of pronghorn fawns in tallgrass prairie. Pronghorn Antelope Workshop Proceedings. 16:104-116.

Rouse, C. H. 1959. Antelope-range relationships. Interstate Antelope Conf. Trans. 2:4-9.

Rutberg, A. T. 1987. Adaptive hypothesis of birth synchrony in ruminants. The American Naturalist 130: 692-710.

Saether, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trnds in Ecology & Evolution 12:143-149.

Salwasser, H. 1980. Pronghorn antelope population and habitat management in the northwestern Great Basin environments. USDA, Forest Service, Pacific Southwest Region.

Schwartz, C. C., J. G. Nagy and R. W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. Journal of Wildlife Management 41(2):161-168.

Seber, G. A. 1973. Estimation of animal populations and related parameters. Griffin. London, England. 506 pp.

Sinclair A., Pech R., Dickman C., Kik D., Mahon P., and Newsome A. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12: 564-75.

Sommer, M. L. 2012. California pronghorn antelope status report and management update. State of California Natural Resources Agency. California Department of Fish and Game.

Stephens, P. A. and W. J. Sutherland. 1999. Consequences of the allee effect for behavior, ecology, and conservation. Trends in Ecology and Evolution 14:401-405.

Sundstrom, C. 1970. Ecology of the pronghorn antelope in the Red Desert of Wyoming. Species Report. Wyoming Department of Game and Fish. Cheyenne. 227 pp.

Vriend, H. G. and M. W. Barrett. 1978. Low pronghorn recruitment-is it an issue? Pronghorn Antelope Workshop Proceedings. 8:360-379.

Wittmer H., A. Sinclair, and B. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia. 144. 257-267.

Wright, P. L. and S. A. Dow, Jr. 1962. Minimum breeding age in pronghorn antelope. Journal of Wildlife Management 26(1):100-101.

Yoakum, J. D. 1972. Antelope-vegetative relationships. Antelope States Workshop Proceedings. 5:171-177.

Yoakum, J. D. 1974. Pronghorn habitat requirements for sagebrush-grasslands. Proceedings 6th Antelope States Workshop 5:171-177.

Yoakum, J. D. 1979. Managing rangelands for pronghorn. Rangelands. 1(4)146-148.

Yoakum, J. D. 1980. Habitat management guides for the American Pronghorn Antelope. S. Dept. of Interior, Bureau of Land Management, Denver Service Center, University of Denver, Colorado.

Yoakum, J. D. 2004a. Habitat characteristics and requirements. Pages 409-446. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. 2004b. Distribution and Abundance. Pages 75-108. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. 2004c. Foraging Ecology, diet Studies and Nutrient Values. Pages 447-502. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. and B. W. O'Gara. 2000. Pronghorn. Pages 559-577. *In:* S. Demarais and P. Krausman (Eds.). Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey. 778 pp.

CHAPTER 3

PRONGHORN (ANTILOCAPRA AMERICANA) FAWN SPATIOTEMPORAL MICRO- AND MACRO-HABITAT SELECTION AND SURVIVAL

Introduction

Population sizes of large mammalian herbivores are highly influenced by habitat quality, availability, and distribution (Ogutu et al 2008, Gaillard et al. 1998). Marginal or sub-marginal habitats tend to produce fitness costs, such as low rates of recruitment, which cause population size to become unstable and/or decline (Vriend and Barrett 1978). Recruitment rates have been demonstrated to drive population dynamics of temperate herbivores (Coulson et al. 1997, Saether 1997), particularly for polytocous species such as pronghorn (Antilocapra americana) (Gaillard et al. 2000,). Although pronghorn produce large numbers of offspring annually, survival of juveniles in comparison to adults is consistently lower and more sensitive to environmental variability (Gaillard et al. 2000, Eberhardt 2002, Gaillard & Yoccoz 2003). The effect of predators on recruitment and population limitation for pronghorn has been shown to covary with habitat quality, where predation of neonatal fawns is high when environmental conditions are poor (Kohlman 2004). Understanding how predator induced mortality is affected by habitat conditions is a fundamental consideration for the ecology and management of pronghorn populations.

The biotic and abiotic environmental variables which influence fawn survival and ultimately recruitment have been relatively well documented within the three primary biome types commonly used to describe pronghorn habitat (i.e., grassland, shrub-steppe, and desert biomes) (Yoakum 2004, O'Gara 2004). Vegetative attributes appear to influence recruitment through the effects of plant type, density, height, and diversity on fawn concealment from predators and survival during the early hiding phase of fawn development (Bromley 1978, Mitchell 1980, Alldredge et al. 1991). Indirectly, these same vegetative characteristics affect fawn survival by influencing the initial birth site selection by preparturient adult females (e.g., forage conditions, long-range visibility of predators), as well as nutritional quality during lactation (Canon and Bryant 1997, Yoakum 2001, 2003, Johnson et al. 2007). Accordingly, habitat requirements for both fawns and does must be met simultaneously at different spatial scales. At the micro-habitat scale, selection is based on the hiding requirements of a fawn; and at the macro-habitat scale selection depends on the dietary requirements of the doe balanced with the needs of her offspring.

Although information for the influence of habitat on recruitment may be readily available, research has largely focused on specific biome types, without much consideration for biome overlap or for habitats which have undergone significant alterations and no longer reflect standard biome classifications (Yoakum 2004). Conservation efforts to reestablish pronghorn populations within historic ranges often involve the translocation of individuals to areas which have been dramatically altered since extirpation (e.g., anthropogenic effects). Releases of pronghorn into such habitats may hinder the success of relocation programs. On the Carrizo Plain National Monument (CPNM), located along the southwest edge of California's Central Valley, a translocated population of pronghorn has been reduced by approximately 75% since original reintroduction efforts 20 years prior (Sommer 2012). Although pronghorn were once considered abundant in this area of the state (Pyshora 1977, Yoakum 2004b), the species became regionally extinct by the mid 1900's due to overhunting and habitat loss (Koch and Yoakum 2001). Today, the environment on the CPNM differs greatly from historic conditions. Native plants, such as perennial bunchgrasses, have been replaced by non-native annual species (Schiffman 1994, Meyer 1997), an ecological transformation most likely caused by the grazing of domestic livestock (Malo & Suarez 1995, Yoakum 2001). Where perennial plants once offered year round forage and concealment opportunities for pronghorn, the site is now dominated with annual vegetation which dies off seasonally (Longshore and Lowrey 2008). In an effort to assess the quality of habitat on the CPNM, several small-scale studies have been conducted. Longshore and Lowrey (2008) ranked habitat quality within the CPNM as moderate to poor for pronghorn. Their results were based on limited shrub cover and diversity and were supported by similar findings from Koch and Yoakum (2001). Longshore and Lowrey speculated that current habitat conditions on the monument may not be adequate to sustain a viable population of pronghorn, however information on recruitment was not available at that time.

Because the CPNM has undergone a substantial ecological transformation, and contains habitat characteristics found in all three biome types, traditional management techniques (e.g., rangeland manipulation) may not be suitable without site-specific information. Here, I evaluate the relationship between habitat, predation, and recruitment on the CPNM. First, I measured fawn survival and determined causes of mortality. Then, I measured micro- and macro-habitat conditions and used the information to create two independent models: 1.) a habitat selection model and 2.) a fawn survival model. Lastly, to aid in the assessment of general habitat conditions for pronghorn on the CPNM, I evaluated the effect of diet and forage quality on fawn recruitment and measured forage availability of known plant types.

Methods

Methods for pronghorn fawn survival and causes of mortality are described in Chapter 2. Two separate binary logistic regression models were developed to explore the best combination of biotic and abiotic environmental parameters for predicting 1) fawn habitat selection and 2) fawn survival (Hosmer and Lemeshow 2000). Akaike's information criterion adjusted for small sample size (AIC_c) was used for model selection (Burnham and Anderson 2002). The log-likelihood estimates from each of the alternative logistic regression models were used to determine AIC_c and ΔAIC_c values. I used the AIC_c differences to rank the set of candidate models. I considered approximating models with ΔAIC_c of ≤ 2 as possible competing models. I used Akaike weights (w_i) and evidence ratios to assess the relative strength of evidence for each model. For both models, I performed all geographical information system (GIS) analyses using ArcMap 9.3 (ESRI 2008).

The fawn habitat selection model compared the relationship between fawn and random locations (dichotomous response/dependent variables) and a suite of macro- and microhabitat parameters (explanatory/independent variables). I considered microhabitat characteristics to be located within a spatial scale small enough to elicit a response by individual fawns. Microhabitat was defined exclusively as the area within a 100 meter radius of a fawn and included measurements of vegetation height and composition (i.e., forb, grass, shrub, bare ground), as well as adult and fawn visibility. Measurements were made at fawn and random locations, along four equidistant compass directions at 10 meter intervals to 50 meters and then again at 100 meters (modified from Canon and Bryant 1997). Visibility was defined as the proportion of a 1 meter measuring stick (located at the center of each plot) visible at fawn height (0.5 m) and adult height (1 m). Macrohabitat characteristics were considered to be landscape-scale features which would potentially influence doe habitat selection but not necessarily fawn habitat selection. Macrohabitat explanatory variables were generated from six spatially explicit environmental GIS data layers and included slope of terrain and linear distances to active water sources, fences, saltbush (*Atriplex* spp.), high-use main roads (Soda Lake Rd., Panorama Rd., Selby Rd. and Elkhorn Rd) and all roads (small roads as well as main roads.)

The fawn survival model compared the relationship between locations of fawns ≤ or > 17 days of age (dichotomous response/dependent variable) and the same spatially explicit, landscape scale macrohabitat features used in the fawn habitat survival model (explanatory/independent variables). Based on information from Gregg et al. 2001, that the majority (95%) of fawn mortalities take place ≤ 17 days of age, as well as corresponding evidence from this study's survival data (see *Results*), I considered that fawns >17 days of age would have a higher expectancy for survival than fawns < 17 days of age; and that habitat selection between these two groups would vary accordingly to influence survival.

Weather information, consisting of annual and seasonal precipitation and temperature, was collected from the Carrizo Remote Automated Weather Station (RAWS) and compared to annual offspring production and survival observed on the

CPNM from 2009 to 2011. Climatic parameters were not included in the fawn survival model because the study period was not long enough to produce adequate variability in the data (i.e., data could not converge algorithmically).

Pronghorn diets were estimated using micro-histological identification of plant epidermal fragments in fecal material. Fecal samples were collected from ten individuals monthly, oven-dried and ground in a Wiley mill through a 1 mm mesh screen. A one-gram subsample was then taken from each fecal sample and composited for analysis by Wildlife Habitat Nutrition Laboratory, Washington State University. Percent fecal nitrogen (FN) and fecal diaminopimelic acid (DAPA) were used as indicators of diet quality (Goldsmith 1988, Wehausen 1995). Percent diet composition was calculated from the amount of each forage item detected in the diet. I used diet composition results to collect above ground samples of forage species consumed by pronghorn.

Plant biomass and forage availability within the CPNM were measured along 23, 50-meter random transects during spring, summer and winter 2008-2011. Plant composition of above-ground annual vegetation was documented and collected within ten 0.5 meter plots evenly distributed along each transect. Plants were sorted by forage class (i.e., grasses, forbs and shrubs). Forbs (i.e., forbaceous plants) are considered to be herbaceous plants that are not grasses (Yoakum 2004b). Plant samples were weighed immediately after collection, dried, and then reweighed to obtain dry biomass weight and preformed water content (i.e., water contained in forage plants). Nutritional analyses of plant samples were conducted by the Washington State University Wildlife Habitat Nutrition Laboratory. Analyses for nutritional content of forage included, in vitro digestible dry matter (IVDDM), gross energy (cal/g), percent crude protein, percent crude fat, percent neutral detergent fiber, percent acid detergent fiber, percent acid detergent lignin, percent total ash, and percent acid insoluble ash. Available vegetative composition, diet composition, and preference ratings (diet composition divided by available vegetative composition) for forbs, grasses and shrubs were calculated and compared to that for North American grassland and shrubsteppe biomes as reported by Yoakum (2004c).

Results

To model fawn habitat selection, eight candidate models were developed using 70 locations from collared individuals and 61 random locations (Table 3). The habitat parameters used in the global model are indicated at the bottom of Table 3. Two candidate models, Model 1 ($w_i = 0.56$) and Model 2 ($w_i = 0.36$), showed substantial support as the best approximating models ($\Delta AIC_c < 2$). Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 4. Model 1 showed that fawn locations were negatively associated with increased vegetation height at 5m, fawn visibility at 5 m and 50 m, slope of terrain, and distance to saltbush and water, yet positively associated with increased forb composition and fawn visibility (height 0.5 m) at 100 m. The negative associations for variables measured close to fawn locations and the positive associations for similar variables measured 100 m from fawns reveal that the relationship between these variables and choice of bedding locations is scale-dependent. Model 2, consisted of the same parameters and respective negative and positive associations as Model 1 for all variables excluding forb composition and fawn visibility at 50 m. Model 1 and Model 2 variables which could be measured using standard GIS layers (e.g., slope of terrain, distance to water, and distance to saltbush) were used to create a generalized map of fawn habitat selection within CPNM (Fig. 3.1).

The two best approximating models for fawn habitat selection, interpreted in the discussion, are as follows:

Model 1: Fawn habitat = 7.802 - (0.002) Distance to saltbush - (0.001) Distance to water - (0.424) Percent slope of terrain - (0.04) Fawn visibility at 5 meter distance - (0.027) Fawn visibility at 50 meter distance + (0.053) Fawn visibility at 100 meter distance + (0.02) Forb cover at fawn location - (0.045) Vegetation height at 5 meter distance.

Model 2: Fawn habitat = 7.892 - (0.002) Distance to saltbush - (0.001) Distance to water - (0.225) Percent slope of terrain - (0.046) Fawn visibility at 5 meter distance + (0.031) Fawn visibility at 100 meter distance - (0.041) Vegetation height at 5 meter distance.

To model fawn survival, six candidate models were developed (Table 5) using 1,417 locations from 10 GPS collared individuals. The parameters used in the global model of fawn survival are located at the bottom of Table 5. Two candidate models, Model 1 ($w_i = 0.55$) and Model 2 (global model; $w_i = 0.32$), showed support as the best approximating models ($\Delta AIC_c < 2$). Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 6. Model 1 showed that locations of individuals which lived greater than 17 days were positively associated with increased slope and distance to main roads; and negatively associated with increased linear distance to water, fences, and all roads. Model 2, in addition to the same parameters and respective positive/negative associations as Model 1, showed a negative association with linear distance to saltbush. The global model was mapped to include the effect of saltbush on fawn survival (Fig. 3.2). Locations of both collared and uncollared fawns were dispersed throughout the CPNM; located on both the north and south ends of the plain, as well as on the east and west sides of the plain. Locations for the 10 GPS collared fawns used in the models are indicated in Fig. 3.3. The mean fawning area for these collared fawns was 0.05 km^2 (SE = 0.01 km^2).

The two best approximating models for fawn survival included:

Model 1: Survival = 1.235 + (0.0009) Distance to main roads - (0.0028) Distance to all roads - (0.0016) Distance to fences - (0.0004) Distance to water + (0.0403) Percent slope of terrain

Model 2: Survival = 1.530 + (0.0008) Distance to main roads - (0.0028) Distance to all roads) - (0.0018) Distance to fences - (0.0002) Distance to saltbush - (0.0004) Distance to water) + (0.0509) Percent slope of terrain.

Seasonal precipitation and temperature, as well as annual fawn productivity and survival, varied considerably during the study (Table 7). Of the three study years, 2009 had the lowest total seasonal precipitation (6.22 inches) and the greatest summer average high temperature. Although annual fawn production was highest during 2009 (22 fawns), annual survival of fawns was lowest (14%). Measurements of seasonal precipitation and summer high temperature, as well as fawn productivity and survival were similar for 2010 and 2011 (Table 7). Mean annual precipitation during the study (10.58 inches; SE = 5.75 in) exceeded the mean annual precipitation during the past 20 years (9.67 inches; SE = 4.17 in). However, rainfall in 2010 (19.05 inches), was exceptionally high and represented the wettest year on record since 1998 (19.88 inches). In contrast, annual rainfall for 2008, 2009, and 2011 (7.09, 6.92 and 9.26 inches, respectively), were all lower than the mean annual rainfall for the past 20 years.

Pronghorn consumed more than 50 different individual forage items (Appendix C). At least 42 different plant taxa were identified in the diet, including 26 species of forbs, 9 species of grasses and 8 species of shrubs. Principle forage items (Table 8) comprised ≥ 5% of the dietary composition for any one season. Principle forage items among forbs included *Astragalus* spp., *Camissonia* spp., *Erodium* spp., *Lotus* spp., Aster family flower, Borage family, and legume pod; among grasses were *Avena* spp. and *Bromus* spp.; and for shrubs was *Atriplex* spp. Among principle forage items, *Erodium* spp. comprised >20% of the diet for all seasons; and *Astragalus* spp., Aster family flower, and *Atriplex* spp. represented ≥ 10% of the dietary composition for at least one season.

Annual diet composition consisted of 76.19% (1.83% SE) forbs, 14.58% (0.95% SE) grasses, 6.10% (0.98% SE) shrubs, and 3.13% (0.26% SE) other forage items (seeds, lichens and unidentified flowers). Annual composition of forage available for pronghorn consumption on the CPNM consisted of 35.46% (16.43% SE) forbs and 64.54% (16.43% SE) grasses. Shrubs were not detected within vegetation transects. In comparison to pronghorn occupying grassland, shrubsteppe and desert biomes, pronghorn on the CPNM appeared to have consumed a comparable amount of grasses, but a greater percentage of forbs and a fewer percentage of shrubs (Table 9). Preference ratings, a function of forage use (i.e., diet) in relation to availability (Yoakum 2004c), for forbs (2.2) and grasses (0.2) were similar between the CPNM and grassland and shrubsteppe biomes (Table 9).

Seasonal diet composition of forage classes (i.e., forb, grass, and shrub) was consistent throughout the year (Table 11). During all seasons, forbs made up the majority of pronghorn diet, followed by grasses and then by shrubs. In contrast, forage availability varied among seasons (Table 11). During spring, available forb composition (54.40%; SE = 3.29%) was greater than available grass composition (45.60%; SE = (3.29%). However, available forb composition during summer (27.01%; SE = 5.94%) and winter (24.98%; SE = 11.56%) were nearly one-third of available grass composition during summer (72.99%; SE = 5.94%) and winter (75.02%; SE = 11.56%). The seasonal preference rating for forbs was higher during summer (2.78) and winter (2.95) than during spring (1.31). For grasses, the seasonal preference rating was highest during spring (0.36) and lower during summer (0.19) and winter (0.23).

Monthly diet composition (Fig. 3.4) was highest for forbs, followed by grasses and then by shrubs. Consumption of other miscellaneous forage items (i.e., seeds, lichens and unidentified flowers) did not exceeded 10% of the diet for any month. Forb consumption generally increased during the year (from January to December), while monthly consumption of grasses and shrubs declined.

Seasonal vegetative cover of forbs and grasses (Table 12) was highest during spring (25.89%; SE = 0.87% and 43.45%; SE = 1.12%, respectively). Forb and Grass cover declined during summer (19.52%; SE = 0.89 and 29.18%; SE = 1.13, respectively) and again during winter (17.24%; SE = 0.85 and 21.90%; SE = 1.01, respectively). The rate of decline between seasons was higher for grass cover than forb cover. From spring to summer and from summer to winter, grass cover declined by 33% and 25%, respectively; and forb cover declined by 25% and 12%, respectively. The percentage of exposed bare ground (i.e., without vegetation) was < 50% for Summer and Winter (Table 12).

I analyzed nutritional composition of available grasses and forbs at peak biomass production during the fawning season to establish baseline data for available nutrients. Comparison of the nutritional quality of grasses and forbs during spring (Table 13) indicated that grasses contained more gross energy (4426.20 calories/gram; SE = 35.04 calories/gram) than forbs (4259.77 calories/gram; SE = 23.80 calories/gram). Additionally, grasses contained a higher percentage of neutral detergent fiber (58.95%; SE = 1.73%) and acid detergent fiber (29.37%; SE = 1.77 %) than forbs (38.82%; SE = 1.47% and 27.24%; SE = 1.00%, respectively). However, forbs contained a higher percentage of crude fat (2.89%; SE = 0.27) and acid detergent lignin (5.19%; SE = 0.28%) than grasses (1.84%; SE = 0.12% and 1.89%; SE = 0.08%, respectively).

Monthly fecal nitrogen (FN) values (Fig. 3.5a) were highest in March 2009 (3.06%) and April 2008 (3.09%) and lowest during January 2008 (2.01%), January 2009 (2.33%) and August 2009 (2.29%). Monthly fecal diaminopimelic acid (FDAPA) values

(Fig. 3.5b) ranged from a high of 1.15 mg/g during March 2009 to a low of 0.27 mg/g during January of 2008.

Mean preformed water content of available forbs and grasses was 33.1% (SE = 0.01%). Although preformed water content was similar between forbs (38.0%; SE = 0.01%) and grasses (30.3%; SE = 0.01%), seasonal preformed water content was variable. Winter had the highest preformed water content (51.7%; SE = 0.01%), followed by spring (42.8%; SE = 0.01%). Summer preformed water content was considerably lower (5.58%; SE = 0.01%). Preformed water content between foraged plant species (45.58%; SE = 3.11) and non-foraged plant species (51.69%; SE = 3.82) did not differ (z = 0.30, p = 0.77).

Discussion

Results from the fawn habitat selection model indicate that both pronghorn does and their fawns selected for a combination of environmental parameters at both macro- and micro-habitat scales. Fawn locations had taller vegetation and lower visibility at close distances compared to random locations. However, fawn locations within low visibility vegetation patches were on average located on a larger scale in open, more visible areas compared to random locations. Fawns (or does) on the CPNM appear to choose sites in isolated patches of cover located within larger areas containing less concealment from predators rather than in continuous habitat with dense cover. This pattern is apparent in the negative association with 5 meter visibility and the positive association with 100 m visibility for fawn locations. Movement between such dispersed patches of cover is likely to increase the risk of detection by predators. However, pronghorn does may choose areas with higher visibility surrounding hidden fawns as a means of gaining more visibility themselves to detect predators. Does with fawns exhibit increased vigilance and aggressive defensive behavior against predators (Byers 1997b), and fawn survival can be higher in habitat containing open areas with shorter vegetation height (Bodie 1979, Autenrieth 1982). Additionally, model results show that forb cover was higher at 100 meters from fawns than at random locations; fawns may simply be selecting bed sites within areas that also meet the dietary needs of does.

At the macrohabitat scale, fawn locations were in areas with lower slope and in closer proximity to water sources and saltbush shrub communities than available random locations. Flat terrain increases the ability of adult pronghorn to detect and avoid predators. In addition, the availability of open drinking water for adult pronghorn can be important in arid environments, particularly for females providing water to fawns through lactation (Yoakum 2001). Ockenfels et al. (1992) suggested that water on arid grasslands may be an important, if not critical, factor in determining the location of fawn bed sites (Yoakum 2004b). I did not anticipate that proximity to saltbush would be an important habitat variable for fawns because saltbush communities on the CPNM tend to be clustered in dense stands with heights that are indicative of low quality habitat (> 50 cm; Longshore and Lowrey 2008). Although moderate dispersion of shrubs in grassland habitats can increase fawn survival (Autenrieth 1982), sites with taller shrub height (76 to 137 centimeters [30 – 54 in]) can have significantly higher predator related mortality (Bodie 1979). If pronghorn on the CPNM are selecting for saltbush based on the need for concealment, then predation risk due to tall shrub height may be high.

Results from the fawn survival model indicate that locations of individuals who lived beyond 17 days of age were closer to water sources, farther from high-use main roads (i.e., Soda Lake Rd, Selby Rd, Panorama Rd, and Elkhorn Rd.) and on steeper terrain. Model results also indicated that these individuals were located in closer proximity to fences and all roads (small dirt roads as well as main roads), however this association is most likely due to the fact that fences and dirt roads are abundant and well dispersed throughout the monument; not because they increased survival times. The positive association between survival and distance from high-use main roads may indicate that anthropogenic disturbance during the fawning season could influence survival. Proximity to water sources appeared to increase survival times of fawns on the CPNM. Although postnatal fawns acquire water strictly from nursing, and does typically meet most of their water requirements through the consumption of succulent forage items, pronghorn on the CPNM may require supplemental water sources for drinking. The availability and dispersion of open water sources on arid ranges directly affects adult health and reproduction, as well as fawn productivity and survival (L. McKee and Wolf 1963, Beale and Smith 1970, Whisler 1984, Ockenfels et al. 1992). It was unexpected that survival would be positively influenced by steeper terrain because pronghorn typically select habitat with the lowest slope (Ockenfels et al. 1994). However, Einarsen (1948) found that the best physiography for fawning sites was among basins surrounded by low ridges or hills. On the CPNM, environmental conditions in areas with steeper terrain, including vegetation structure, forage quality and availability, or even the absence of human disturbance, may offer benefits which increase fawn survival and outweigh the costs of increased slope.

Fawn birth sites were not restricted to traditional fawning areas (i.e., areas where fawns were observed during years prior to the study) (Longshore and Lowrey 2008). Observed birth sites varied between years and were spatially dispersed throughout the monument, located along both the east and west sides as well as on the north and south ends of the plain. Selection of traditional fawning areas is dependent on pronghorn seasonal rangeland use (Yoakum 2004b). Herds that are required to travel long distances between summer and winter rangelands due to harsh winter conditions tend to have high site-specific fidelity for traditional fawning locations. In contrast, herds occupying ranges with mild winter conditions, such as on the CPNM, are not forced to travel far between seasonal rangelands and tend to fawn throughout their small home ranges (Yoakum 2004b).

Trend information for the correlative effects of climate on offspring productivity and survival are difficult to evaluate for short-term studies. However, available information suggests that fawn survival was influenced by low seasonal precipitation and high summer temperatures. Adverse weather conditions on pronghorn ranges, including droughts and severe winters, reduce the availability of nutritious forage, increase predation on fawns, and limit survival overall (O'Gara 2004). On the CPNM, mean annual rainfall is within the range of precipitation required to sustain a moderately high density pronghorn population (8 to 15 inches; Yoakum 2004b). However, both annual and seasonal rainfall are highly variable, creating stochastic environment in which small populations are likely to suffer, especially during sustained drought or temperature extremes. Additionally, habitat quality at this cite has been significantly altered by over one hundred years of dry-land wheat farming and domestic livestock grazing, as well as by inundation of non-native annual grasses (Longshore and Lowrey 2009). Native perennial plant communities provide important forage opportunities for pronghorn during dry summer months, however non-native annual plants become desiccated and vegetative cover is greatly reduced. While the amount of total annual precipitation may be adequate to support a viable pronghorn population on the CPNM, offspring survival and population density are likely limited by poor seasonal forage conditions during summer and fall.

The abundance, diversity and quality of forage available to, and consumed by, pronghorn directly influence fitness and population density (Yoakum 2004c). On the CPNM, total vegetative cover was within the range typically found on arid rangelands (40% to 60%; Yoakum 1972, Ockenfels et al. 1994). However, the composition of vegetative cover reflected characteristics found in both high and low quality habitats according to criteria developed by Longshore and Lowrey (2009) and modified from Allen et al. (1984), O'Gara and Yoakum (1992), Okenfels et al. (1996), and Yoakum (2004c). Forb and grass cover were representative of high quality grassland-scrub habitat. Shrubs however, were scarce and undetected within vegetation transects; and shrub cover was indicative of low quality grassland-scrub habitat. This information is consistent with other reports for the CPNM, including Koch and Yoakum (2002) who also reported zero shrub cover within transects and Longshore and Lowrey (2008) who reported low shrub cover and diversity. Habitat with greater forb and grass cover and relatively lesser shrub cover is considered optimal for foraging and predator avoidance (Yoakum 2004b). However, the importance of shrubs increases during summer and fall, when late season annual forbs and grasses are not available (O’Gara and Yoakum 1992). While the amount of forage available to pronghorn on the CPNM may be adequate during late gestation and early postnatal development (i.e., during spring), low forage availability during summer and fall likely affect fawn survival and adult reproduction. Increased shrub cover on the CPNM would likely offer a critical nutrient source for pronghorn during summer and fall, and may be required to increase offspring production and survival, as well as population density.

In comparison to pronghorn occupying grassland, shrubsteppe and desert biomes, pronghorn on the CPNM consumed large amounts of forbs, moderate amounts of grasses, and low amounts of shrubs. Regardless of habitat type, forbs comprise the majority of pronghorn diet and shrub composition is generally equal to, or far greater than, grass composition. Grasses are consumed increasingly, however, where shrubs are not plentiful (Yoakum 2004c). On the CPNM, shrub consumption was atypical and comprised less than half the composition of grasses. Pronghorn are highly selective foragers, and although forage availability may vary among different habitats, the preference for certain forage classes is remarkably consistent (Yoakum 2004c). This was supported by results from this study, where preference ratings for forage classes on the CPNM were the same as other populations. The strong preference for certain forage classes across habitat types indicates that pronghorn are highly restricted by forage availability on rangelands, especially during certain times of year. Pronghorn can make seasonal adjustments to their diet according to nutrient availability associated with plant phenology. Forbs are most nutritious during spring and summer, and consumption of forbs during these periods has been linked to offspring production and survival (Yoakum 2004c). Shrubs have comparatively high nutrient levels in fall and winter and can be important for adult body condition during breeding and pregnancy (Yoakum 2004c). Maternal condition during late gestation can affect offspring birth weights (Thorne et al. 1976) and low birth weight can decrease survival (Thorne et al. 1976, Clutton-Brock et al. 1982, Fairbanks 1993). Grasses can offer important digestible energy during winter. On the CPNM however, pronghorn did not appear to adjust their diet to account for seasonal changes in forage availability. Even when late season forbs and grasses were largely desiccated and vegetative cover was greatly reduced, pronghorn on the CPNM continued to consume forage classes in the same proportion throughout the year. Pronghorn occupying arid lands, such as the CPNM, can exhibit less pronounced shifts in seasonal diet (Cancino 1994c, Miranda 2000) compared to pronghorn in northern grassland and shrubsteppe habitat (Salwasser 1980, Yoakum 1990). Although shrub availability was not well measured, the relatively high consumption of grasses and the low consumption of shrubs throughout the year, indicate that shrub availability is likely limited on the CPNM. Limited availability of preferred forage items during different seasons is likely to have a negative influence on individual fitness and restrict population growth on the CPNM.

Plant taxa in pronghorn diets during this study were similar to results from 2003-2004 for shrubs and grasses (Longshore and Lowrey 2008). However, the number of forb species in the diets during this study was lower than in 2003-2004. Pronghorn did consume other miscellaneous forage items including seeds, lichens and unidentified flowers, however mean percent composition of these items was small (< 3.5%) and their relative importance in the diet is likely insignificant.

Nutrient quality of pronghorn diets can be evaluated by measuring fecal nitrogen (FN) and fecal diaminopimelic acid (FDAPA) content (Leslie and Starkey 1987). On the CPNM, FN values were highest during March and April and lowest during January and August; and FDAPA values were highest during March and lowest during January. Although seasonal differences in percent FN and percent FDAPA were not statistically significant, and some variability occurred between years, seasonal trends overall matched those found for other pronghorn populations (Hansen et al. 2001).

Pronghorn often make use of preformed water (i.e., water contained in forage) because surface water typically occurs sparsely in most pronghorn habitats (Sundstrom 1968, Boyle and Alldredge 1984, Kindschy et al. 1982). When moisture content in plants exceeds 75%, pronghorn may cease drinking, even if surface water is readily available (Beale and Smith 1970). On the CPNM, performed water content was low and pronghorn were frequently observed making use of drinking water. Seasonally, performed water content was particularly low during summer and was likely lower during fall. The abundance of forage with high moisture content during spring and summer can influence fawn survival (Beale and Smith 1966) and moisture content during fall likely influences adult body condition. Studies indicate that plants foraged by pronghorn have higher moisture content than non-foraged plants (Fox 1997, Beale and Smith 1970, Deblinger and Alldredge 1991, Hughes 1991) and selection of plant species with higher preformed water content can be important for offspring production and survival (Yoakum 2004c). On the CPNM, no difference was detected between preformed water content of foraged and non-foraged plant species. In certain arid environments preformed water content alone may not be enough to support viable populations, especially during particularly dry seasons (Fox 1997). Water on arid grasslands may be an important factor influencing fawn bedsites (Ockenfels et al. 1992) and will likely continue to be critical for pronghorn on the CPNM.

Summary

Collectively, these findings highlight the importance of both micro- and macro-habitat scale environmental attributes for recruitment in pronghorn. Results from this study indicate that fawns select the best available bed sites within larger scale areas preselected by does. Thus, ecological studies on recruitment, as well as conservation strategies aimed at increasing rates of recruitment, should consider the habitat requirements of both does and fawns simultaneously.

On the CPNM, it appears that increased shrub cover, diversity, and moderate spatial dispersal are needed to improve concealment of fawns from predators and to provide important late-season nutrients during adult breeding and reproduction. Presently, available shrubs on the CPNM tend to be dominated by large, dense saltbush (*Atriplex* spp.) stands which may reduce visibility of predators and offer limited seasonal nutrition. Pronghorn prefer a mosaic of vegetative structure rather than extensive monotypic plant communities (Yoakum 2004d).

Forb and grass cover on the CPNM is adequate during spring. However, late-season annual forb and grass species on the CPNM are largely desiccated or dead during summer and fall and offer limited nutrients and preformed water content during late fawning. Promoting perennial plant growth is likely important for reproduction and recruitment.

The availability of open drinking water on the CPNM was a significant factor for fawn survival. Although drinking water is not generally considered essential for pronghorn throughout many parts of their range, drinking water becomes increasingly important in arid habitats with variable precipitation and low forage succulence (Yoakum 2004b).

The results of this study hold broad implications for conservation and management of pronghorn. Understanding how fawn habitat is selected for and which specific environmental features affect survival is an important component of pronghorn ecology. Research on fawn survival is relatively ubiquitous, however few studies aim to distinguish between micro- and macro-habitat scale parameters. Methods and results contained in this thesis may be used as guidelines for continued research on pronghorn within the CPNM and across the species' range.

Literature Cited

Allen, A. W., J. G. Cook, and M. J. Armbruster. 1984. Habitat suitability index models: Pronghorn. U. S. Fish and Wildlife Service. FWS/OBS-82/10.65.

Bailey, J. A. 1986. Weather and climate. Pages 711-721 *in* A. Y. Cooperrider, R. J. Boyd and H. R. Stuart, eds., Inventory and monitoring of wildlife habitat service center, U.S. Bureau of Land Management. Denver, Co. 858 pp.

Barrett, M. W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. Journal of Wildlife Management. 48(2):542-550.

Bourbeau-Lemieux, A., M. Festa-Bianchet, J.M. Gaillard, F. Pelletier. 2011. Predator-driven component Allee effects in a wild ungulate. Ecology. 14: 358-363.

Buechner, H. K. 1950. Life history, ecology, and range use of the pronghorn antelope in Trans-Pecos, Texas. The american Midland Naturalist Journal. 43(2):257-354.

Byers, J. A. and J. D. Moodie. 1990. Sex-specific maternal investment in pronghorn and the question of a limit on differential provisioning in ungulates. Behavioral Ecology and Sociobiology. 26:157-164.

Byers, J.A. 1997a. Methods and Materials. Pages 15-22. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Byers, J.A. 1997b. Birth and the hiding Strategy. Pages 52-78. *In*: American Pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press. Chicago, IL. 300 pp.

Cancino, J. 1994. Food habits of the peninsular pronghorn. Pronghorn Antelope Workshop Proceedings. 16:176-185.

Canon, S. K. and F. Bryant. 1997. Bed site characteristics of pronghorn fawns. Journal of Wildlife Management. 61(4):1134-1141.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Applied Biology 1:183-246.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the allee effect. Trends in Ecology and Evolution 14:405-410.

Danvir, R. E. 2000. Environmental and density-dependent effects on a northern Utah pronghorn population. Pronghorn Antelope Workshop Proceedings 17:36-41.

DeAngelis, D. W., and J. C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. Ecological Monographs 57:1-21.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling. 3, 481-538.

Einarsen. 1948. The pronghorn antelope and its management. Monumental Printing Co., Baltimore, Maryland. 238 pp.

Ellis, J. E. 1970. A computer analysis of fawn survival in the pronghorn antelope. Ph.D. thesis, Univ. California, Davis. 70 pp.

Ellis, J. E., and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. Journal of Range Management 41:450-459.

Fowler, C.W. and J.D. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. Report to the International Whaling Commission 41, 545-554.

Gaillard, J. M., Bianchet M. F., Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58-63.

Gregg, M. A., Bray, M., Kilbride, K. M., and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management. 65(1):19-24.

Guenzel, R. J., L. L. Irwin and T. J. Ryder. 1982. A comparison of pronghorn movements and distribution during a normal and a mild winter in the Red Rim area, Wyoming. Pronghorn Antelope Workshop Proceedings. 10:156-172.

Hess, M. L. 1986. Density-dependent summer pronghorn fawn survival rates in the interstate antelope population. Pronghorn Antelope Workshop Proceedings. 12:53-54.

Hess, M. L. 1999. Density dependent summer pronghorn survival rates in the northwestern Great Basin-revisited. Pronghorn Antelope Workshop (1998) Proceedings. 19:107.

Hoover, R. L. and S. Ogilvie. 1954. P-R Quart. Rept. Colorado Dept. Game and Fish, Denver. Pp. 33-38.

Hughes, K. S. and N. S. Smith. 1990. Sonoran pronghorn use of habitat in southwest Arizona. Research Report 146-0091564. Arizona Cooperative Fish and Wildlife Research Unit. University of Arizona, Tucson. 58 pp.

Hylander, C. J. 1966. Wildlife communities: From the tundra to the tropics in North America. Houghton Mifflin Co., Boston, Massachusetts. 342 pp.

Jatnieks, S. A. 1983. A study of pronghorn range in southwestern North Dakota. M.S. thesis, University of North Dakota, Grand Forks. 83 pp.

Johnson, H. E. V. C. Bleich, P. R. Krausman. 2007. Mineral deficiencies in Tule elk, Owens Valley, California. Journal of Wildlife Diseases. 43(1): 61-74.

Kindschy, R. R., C. Sundstrom and J. D. Yoakum. 1982. Wildlife habitats in managed rangelands – The Great Basin of southeastern Oregon: Pronghorns. General Technical Report. PNW-145. Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service. Portland, Oregon. 18 pp.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildl. Monogr. 38. 96 pp.

Koch, A. J. and J. D. Yoakum. 2002. Reintroduction and status of pronghorn on the Carrizo Plain National Monument and surrounding areas in southern California. Proceeding of the 20th Biennial Pronghorn Workshop.

Kohlmann, S. G. 2004. Population dynamics and modeling. Pages 645-674. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Lehman, V. W. and J. B. Davis. 1942. Experimental wildlife management in the south Texas chaparral. P-R Quart. Prog.Rept., Proj. 1-R, Unit C, Sect. 1. Texas Game, Fish and Oyster Commiss., Austin. 14 pp.

Longshore, K. and C. Lowrey. 2008. Habitat analysis and food habits of pronghorn antelope in the Carrizo Plain National Monument, California. Final Report prepared for the Bureau of Land Management, Bakersfield, California. 43 pp. U.S. Geological Survey, Western Ecological Research Center, Henderson, Nevada, USA.

Macarthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39.599-619.

Maher, C. R. 1994. Pronghorn male spatial organization: population differences in degree of non-territoriality. Canadian Journal of zoology. 72:455.

Malo, F., and T. Suarez. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehasa. Oecologia 104:246-255.

McCarthy, M.A. 1997. The Allee effect, finding mates and theoretical models. Ecological Modeling. 103, 99-102.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130-1146.

McKean, W. T. 1954. Preliminary obersvations of ovulation incidence in North Dakota deer and antelope. P-R Proj. W-7-R-9 to 13. North Dakota Dept. Game and Fish, Bismarck. 3pp.

McKean, W. T. 1951. Sex, age and physical characteristics of North Dakota antelope as obtained by field checking. P-R Proj. 7R. North Dakota Dept. Game and Fish, Bismarck. 5 pp.

Mitchell, G. J. 1965. Natality, mortality, and related phenomena in two populations of pronghorn antelope in Alberta, Canada. Ph.D. thesis, Washington St. Univ., Pullman. 221 pp.

Mitchell, G. J. 1967. Minimum breeding age of female pronghorn antelope. J. Mammal. 48(3):489-490.

Mooring M.S., T.A. Fitzpatrick, T.T. Nishihira, D.D. Reisig. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. Journal of Wildlife Management. 68(3):519-532.

Nelson, E. W. 1925. Status of the pronghorned antelope, 1922-1924. Bull. 1,346. U.S. Department of Agriculture. Washington, D.C. 64 pp.

Ockenfels, R. A. and J. A. Wennerlund. 1994. Analyzing pronghorn habitat use patterns with GIS technology. Pronghorn Antelope Workshop Proceedings. 16:55-63.

Ockenfels, R. A., C. L. Ticer, A. Alexander, and J. A. Wennerlund. 1996. A landscape level pronghorn habitat evaluation model for Arizona. Arizona Game and Fish Technical Report #19. Project W 78-R.

O'Gara, B. W. and J. D. Yoakum.1992. Pronghorn management guides. Proceedings of the 15th biennial pronghorn antelope workshop. 101 pp.

O'Gara, B. W. and J. D. Yoakum. 2004. Forward. Page xxv. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. 2004. Mortality Factors. Pages 379-408. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W. and H.G. Shaw. 2004. Predation. Pages 337-377. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

O'Gara, B. W., C. J. Knowles, P.R. Knowles, and J. D. Yoakum. 2004. Capture, translocation and handling. Pages 705-764. *In:* O'Gara, B. W. and J. D. Yoakum. Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado. 903pp.

Ogutu, J. O., Piepho H. P., Dublin H. T., Bhola N., Reid R.S. 2008. Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. Journal of Animal Ecology 77:814-829.

Painter, E. L. 1995. Threats to the California flora: ungulate grazers and browsers. Madrono 42:180-188. Heady, H. F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37:798-812.

Poggiale, J.C. 1998. From behavioral to population level: growth and competition. Mathematical and Computer Modeling. 27, 41-49.

Pojar, T. M. 1997. Habitat selection and population performance of a pioneering pronghorn population. P-R Job Final Report. Project W-153-R-4, Work Plan 3A, Job 2. Colorado Division of Wildlife. Fort Collins. 6 pp.

Prenzlow, E. J., D. L. Gilbert and F. A. Glover. 1968. Some behavior patterns of the pronghorn. Spec. Rept.17. Colorado Dept. Game, Fish and Parks, Denver. 16 pp.

Pryah, D. B. 1987. American pronghorn antelope in the Yellow Water Triangle, Montana. Montana Dept. Fish, Wildl. and Parks, Helena, in cooperation with the U.S. Bur. Land Manage. 121 pp.

Roseland, K. 1977. Morphology of the pronghorn ovary (*Antilocapra americana* Ord). M.S. thesis, Univ. Montana, Missoula. 45 pp.

Rothchild, S. L., E. J. Finck and K. E. Sexson. 1994. Mortality and bedding site selection of pronghorn fawns in tallgrass prairie. Pronghorn Antelope Workshop Proceedings. 16:104-116.

Rouse, C. H. 1959. Antelope-range relationships. Interstate Antelope Conf. Trans. 2:4-9.

Rutberg, A. T. 1987. Adaptive hypothesis of birth synchrony in ruminants. The American Naturalist 130:692-710.

Salwasser, H. 1980. Pronghorn antelope population and habitat management in the northwestern Great Basin environments. USDA, Forest Service, Pacific Southwest Region.

Schwartz, C. C., J. G. Nagy and R. W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. Journal of Wildlife Management. 41(2):161-168.

Seber, G. A. 1973. Estimation of animal populations and related parameters. Griffin. London, England. 506 pp.

Sommer, M. L. 2012. California pronghorn antelope status report and management update. State of California Natural Resources Agency. California Department of Fish and Game.

Stenseth, N. C., Bjornstad, O. N. & Saitoh, T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. Proc. R. Soc. Lond. B 263: 1117-1126.

Stephens, P. A. and W. J. Sutherland. 1999. Consequences of the allee effect for behavior, ecology, and conservation. Trends in Ecology and Evolution 14:401-405.

Sundstrom, C. 1970. Ecology of the pronghorn antelope in the Red Desert of Wyoming. Species Report. Wyoming Department of Game and Fish. Cheyenne. 227 pp.

Vriend, H. G. and M. W. Barrett. 1978. Low pronghorn recruitment-is it an issue? Pronghorn Antelope Workshop Proceedings. 8:360-379.

Yoakum, J. D. 1972. Antelope-vegetative relationships. Antelope States Workshop Proceedings. 5:171-177.

Yoakum, J. D. 1974. Pronghorn habitat requirements for sagebrush-grasslands. Proceedings 6th Antelope States Workshop 5:171-177.

Yoakum, J. D. 1979. Managing rangelands for pronghorn. Rangelands. 1(4)146-148.

Yoakum, J. D. 1980. Habitat management guides for the American Pronghorn Antelope. S. Dept. of Interior, Bureau of Land Management, Denver Service Center, University of Denver, Colorado.

Yoakum, J. D. 2004a. Habitat characteristics and requirements. Pages 409-446. *In:* O’Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. 2004b. Distribution and Abundance. Pages 75-108. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. 2004c. Foraging Ecology, diet Studies and Nutrient Values. Pages 447-502. *In:* O'Gara, B. W. and J. D. Yoakum, (Eds.). Pronghorn: ecology and management. University Press of Colorado. Boulder, Colorado. 903 pp.

Yoakum, J. D. and B. W. O'Gara. 2000. Pronghorn. Pages 559-577. *In:* S. Demarais and P. Krausman (Eds.). Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey. 778 pp.

Wagner, F. H. 1989. Grazers, past and present. Pages 151-162 in L. F. Huenneke and H. A. Mooney, editors. Grasslands structure and function: California annual grassland. Kluwer Academic Publishers, Boston.

Wittmer H., A. Sinclair, and B. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia. 144. 257-267.

Wright, P. L. and S. A. Dow, Jr. 1962. Minimum breeding age in pronghorn antelope. Journal of Wildlife Management 26(1):100-101.

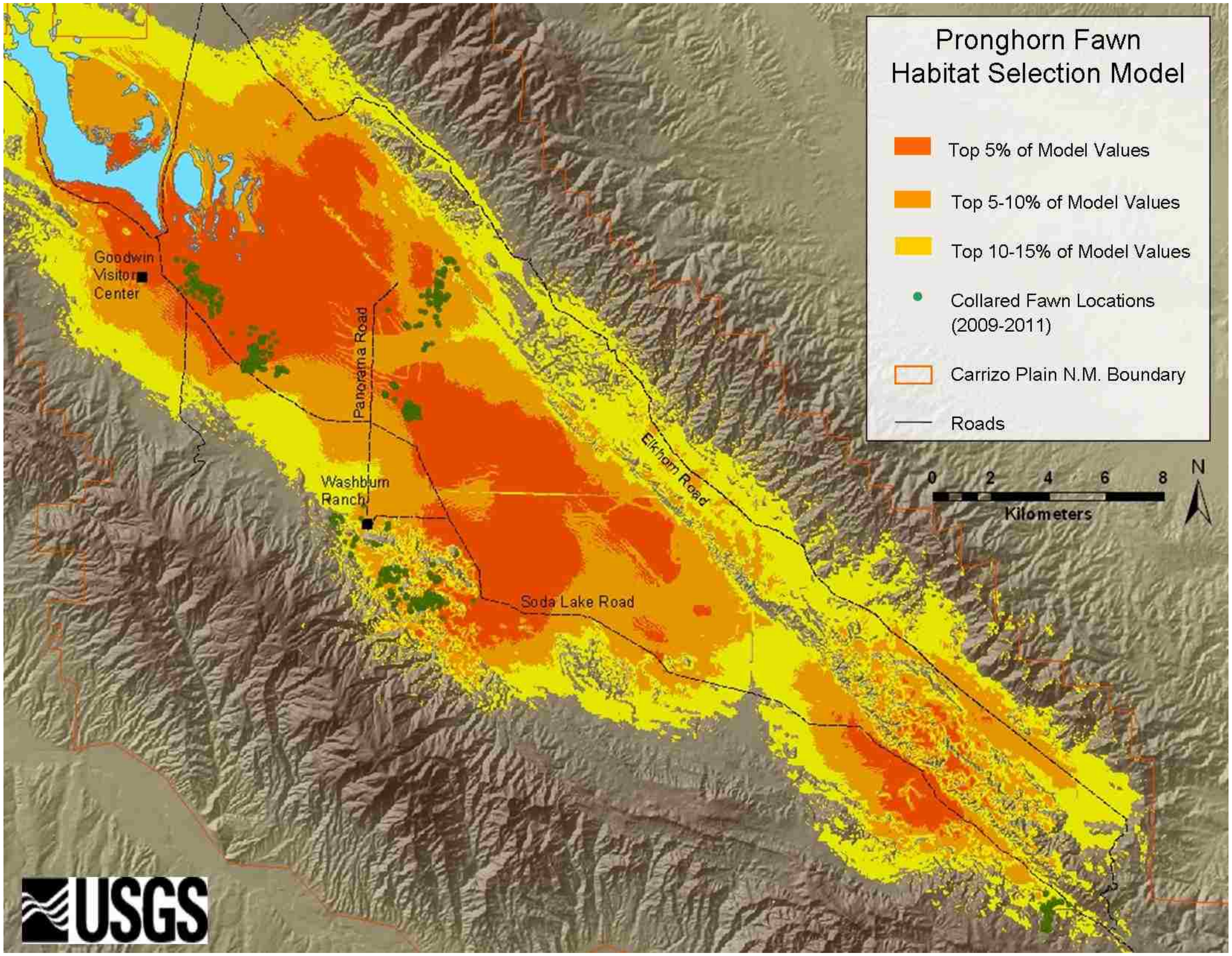


Figure 3.1. Pronghorn fawn habitat selection model, for the Carrizo Plain National Monument, CA. Included are variables from the best approximating binary logistic regression model for predicting fawn habitat and which could be mapped using a GIS (i.e., linear distance to water and saltbush communities and percent slope of terrain). The top 15% of model values are indicated.

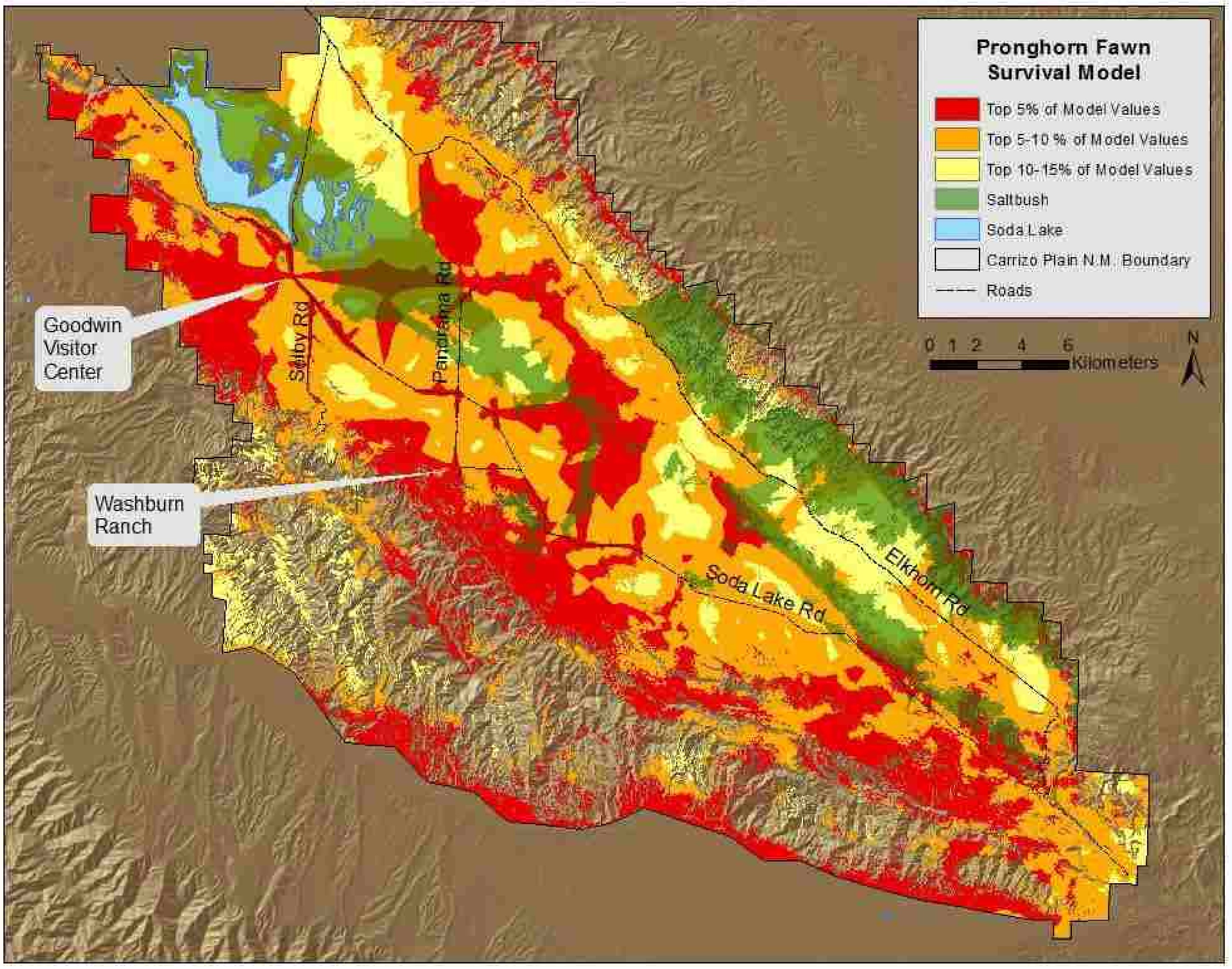


Figure 3.2. Pronghorn fawn survival model, for the Carrizo Plain National Monument, CA. Model parameters include slope of terrain and distances to water sources, saltbush (*Atriplex* spp.), fences, small dirt roads, and high use main roads (Soda Lake Rd., Elkhorn Rd., Panorama Rd. and Selby Rd.). Indicated are the top 15% of model values within the CPNM boundary.

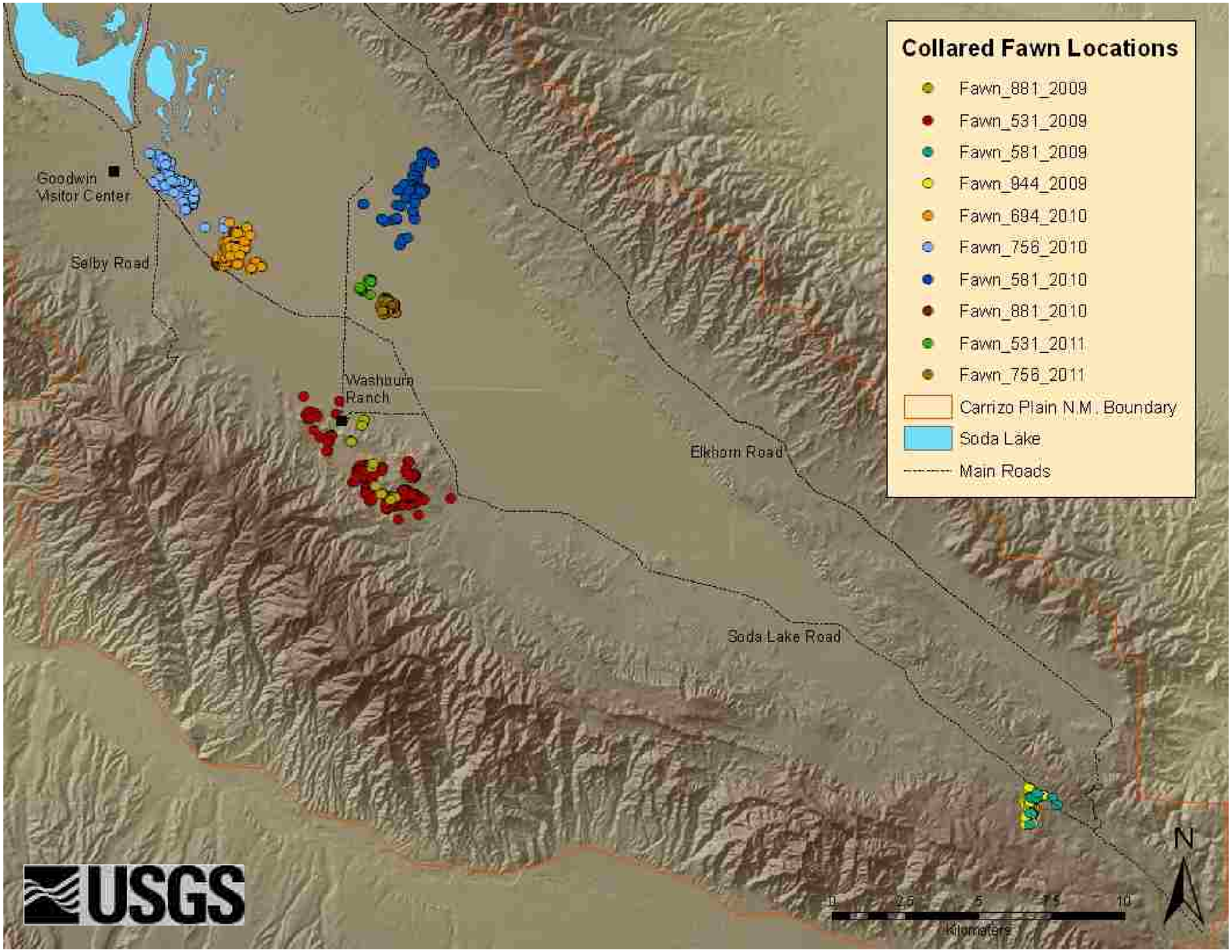


Figure 3.3. Locations of ten GPS collared pronghorn fawns, on the Carrizo Plain National Monument, California from 2009-2011.

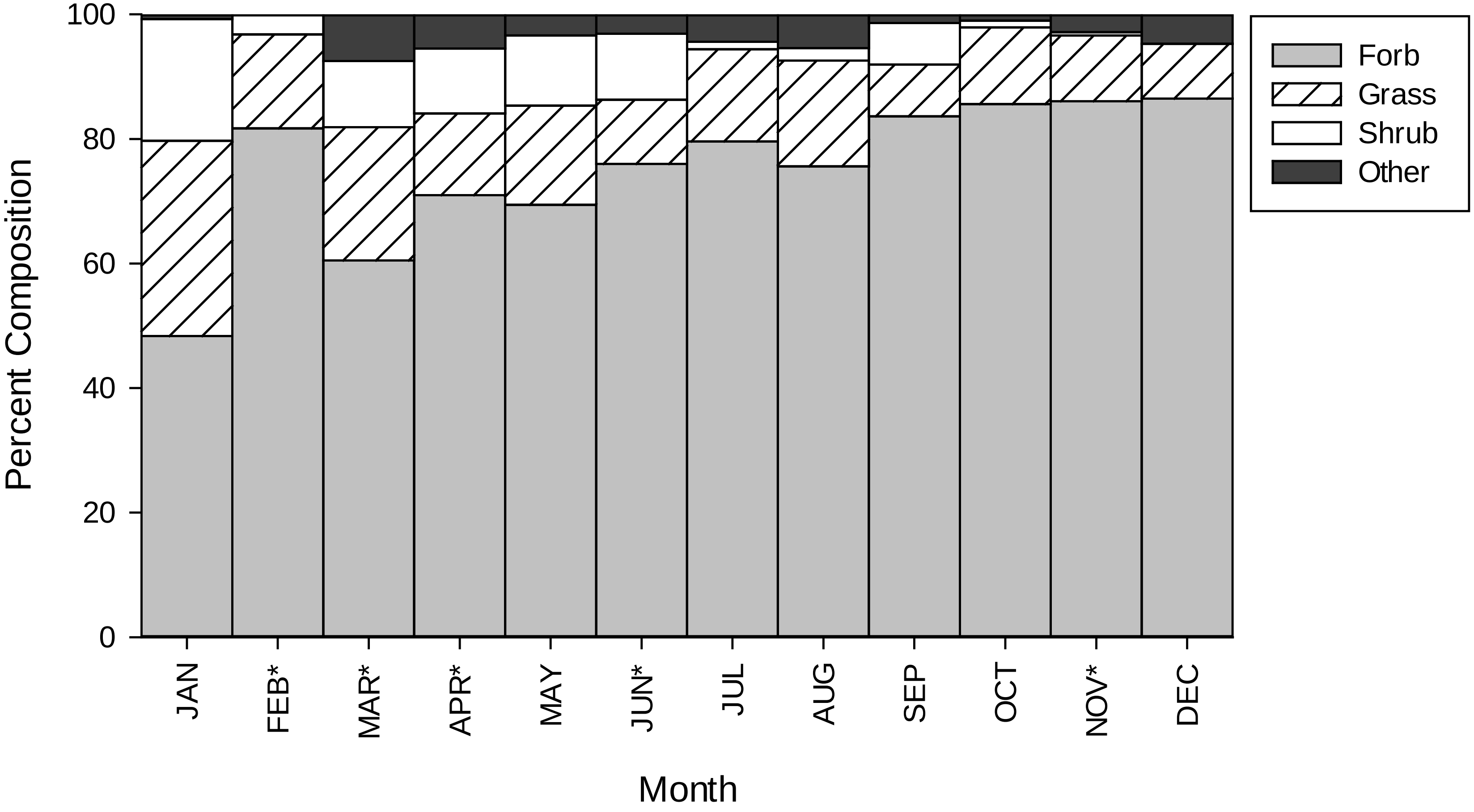


Figure 3.4. Mean monthly percent composition of forage classes consumed by pronghorn, (i.e., forb, grass, shrub) on the Carrizo Plain National Monument, CA during 2008 and 2009. The category labeled “Other” was comprised of seeds, lichens, and unidentified flowers. Diet composition was determined by microhistological analysis of pronghorn fecal samples. Percentages reflect the mean monthly composition for two years except for months for which only one year of information was available (*).

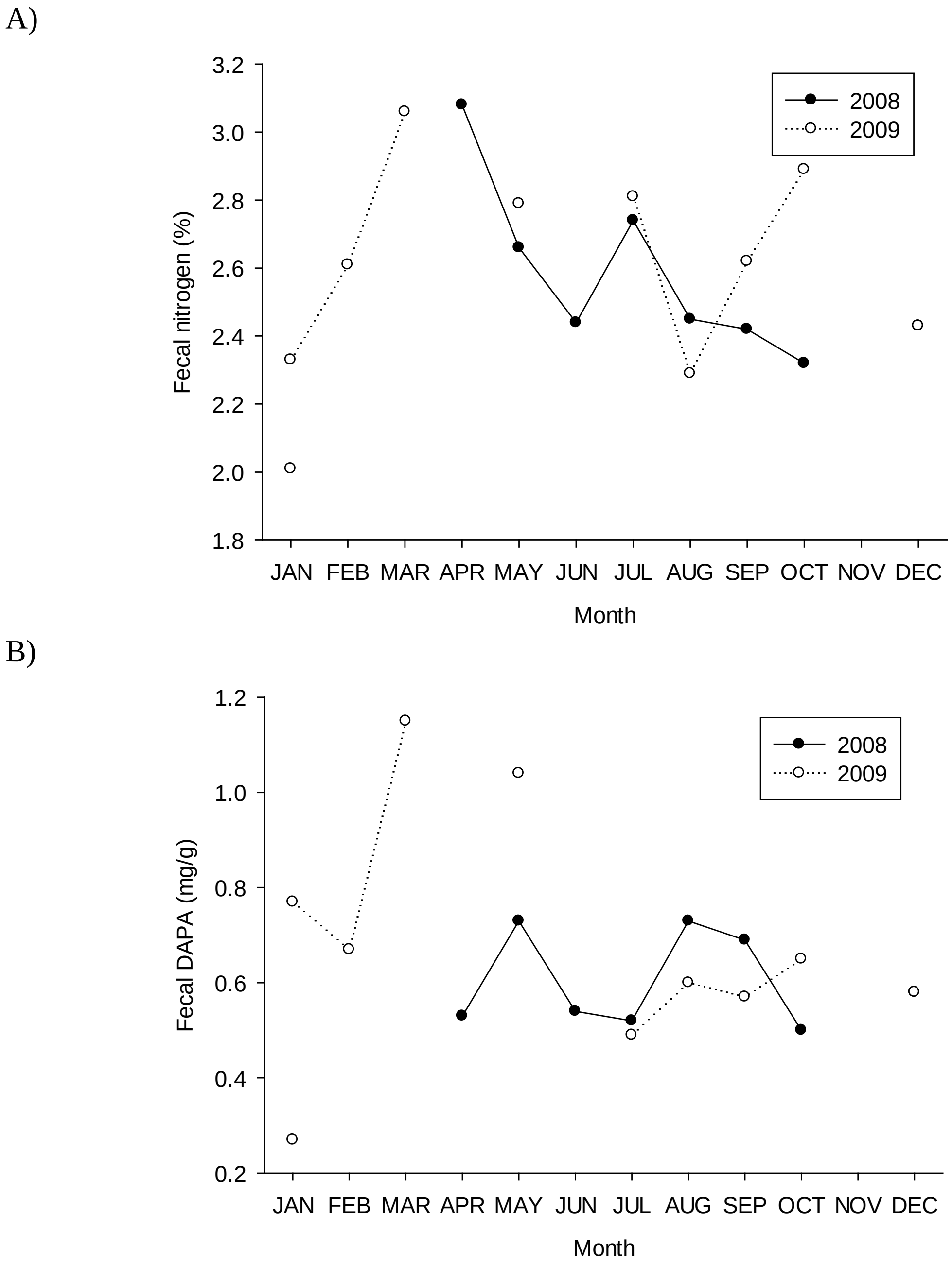


Figure 3.5. Fecal nitrogen and fecal diaminopimelic acid measurements for pronghorn, (A and B, respectively) on the Carrizo Plain National Monument, CA during 2008 (closed circles) and 2009 (open circles). Information for certain months was not available due to inaccessible road conditions following heavy rains or when no fecal samples could be found.

Table 3.1. Comparison and relative ranking of candidate models for pronghorn fawn habitat selection, on the Carrizo Plain National Monument, California from 2009 to 2011. Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c) was used for model selection. Included for each candidate model are values for log-likelihood, number of parameters (k), AIC_c values, Δ AIC_c values, and Akaike weights (w_i). Relative ranking of models was determined using Δ AIC_c.

	Model	-2LogL	k	AIC_c	ΔAIC_c	w_i
1	dsb+dw+ps+fvis5+fvis50+fvis100+f0+ht5	98.33	8	115.51	0	0.5593
2	dsb+dw+ps+fvis5+fvis100+ht5	103.74	6	116.41	0.91	0.3552
3	dsb+dw+fvis5+fvis100+f0	109.57	5	120.05	4.54	0.0578
4	Global model[a]	83.51	17	122.93	7.42	0.0137
5	dsb+dw+fvis100	116.76	3	122.95	7.44	0.0135
6	dsb+dw+f0	123.44	3	129.63	14.12	0.0005
7	dsb+dw	128.57	2	132.66	17.16	0.0001
8	dw+ps+ht5+fvis100+f0	125.73	5	136.21	20.70	0.00002

[a] Global model included distances to saltbush (dsb), water (dw), main roads (dmr), and fences (df); percent slope of terrain (ps); fawn visibility at fawn location (fvis0) and at distances of 5 meters (fvis5), 10 meters (fvis10), 50 meters (fvis50) and 100 meters (fvis100); forb cover at fawn location (f0), grass cover at fawn location (g0), and cover at distances of 5 meters for forbs (f5), grasses (g5) and shrubs (s5); vegetation height at fawn location (ht0) and at 5 meters distance (ht5).

Table 3.2. Parameter estimates, standard errors of the estimates, odds ratios, and 95% confidence intervals for the odds ratios of the variables in the two best approximating models for the occurrence of pronghorn fawns, (β, SE, Odds ratio, 95% CI, respectively) on the Carrizo Plain National Monument, California.

Effect	β	SE	Odds ratio	95% CI
Model 1:				
dsb	-0.002	0.001	0.998	0.996-0.999
dw	-0.001	<0.001	0.999	0.998-1.000
ps	-0.424	0.256	0.654	0.396-1.080
fvis5	-0.040	0.020	0.961	0.924-1.000
fvis50	-0.027	0.026	0.973	0.924-1.025
fvis 100	0.053	0.027	1.054	1.000-1.111
f0	0.020	0.010	1.021	1.001-1.040
ht5	-0.045	0.023	0.956	0.915-0.999
Model 2:				
dsb	-0.002	0.001	0.997	0.997-0.999
dw	-0.001	<0.001	0.998	0.998-0.999
ps	-0.225	0.191	0.550	0.550-1.161
fvis5	-0.046	0.020	0.919	0.919-0.993
fvis 100	0.031	0.012	1.011	1.011-1.054
ht5	-0.041	0.021	0.921	0.921-1.001

Variables include distance to saltbush (dsb), distance to water (dw), percent slope of terrain (ps), fawn visibility at distances of 5 meters (fvis5), 50 meters (fvis50) and 100 meters (fvis100), forb cover at fawn location (f0), and vegetation height at 5 meters (ht5).

Table 3.3. Comparison and relative ranking of candidate models for pronghorn fawn survival, on the Carrizo Plain National Monument, CA from 2009 to 2011. Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c) was used for model selection. Included for each candidate model are values for log-likelihood, number of parameters (*k*), AIC_c values, Δ AIC_c values, and Akaike weights (w_i). Relative ranking of models was determined using Δ AIC_c.

	Model	-2LogL	*k*	AIC_c	ΔAIC_c	w_i
1	dmr+dar+df+dw+ps	478.20	5	488.25	0	0.5540
2	Global model[a]	477.30	6	489.36	1.12	0.3172
3	dmr +dar+df+dw	483.16	4	491.19	2.94	0.1275
4	dmr+ dar+df	494.34	3	500.35	12.11	0.0013
5	dmr + dar	508.19	2	512.19	23.95	< 0.0001
6	dmr +dw+ps	527.97	3	533.98	45.74	< 0.0001

[a] Global model included percent slope of terrain (ps) and distances to saltbush (dsb), water (dw), main roads (dmr), all roads (dar) and fences (df).

Table 3.4. Parameter estimates, standard errors of the estimates, odds ratios, and 95% confidence intervals for the odds ratios of the variables in the two best approximating models of pronghorn fawn survival, (β, SE, Odds ratio, 95% CI, respectively) on the Carrizo Plain National Monument, CA.

Effect	β	SE	Odds ratio	95% CI
Model 1:				
dmr	0.001	<0.001	1.001	1.000-1.001
dar	-0.003	0.001	0.997	0.996-0.998
df	-0.002	<0.001	0.998	0.997-0.999
dw	-0.0004	<0.001	1.000	0.999-1.000
ps	0.0403	0.019	1.041	1.004 -1.080
Model 2:				
dmr	0.001	<0.001	1.001	1.000-1.001
dar	-0.003	0.001	0.997	0.996-0.998
df	-0.002	0.001	0.998	0.997-0.999
dw	-0.0004	<0.001	1.000	0.999-1.000
ps	0.051	0.022	1.052	1.009-1.097
dsb	-0.002	<0.001	1.000	0.999-1.000

Variables include percent slope of terrain (ps) and distances to water (dw), main roads (dmr), all roads (dar), fences (df) and saltbush (dsb).

Table 3.5. Fawn productivity and survival in respect to seasonal precipitation and temperature, (precip.; Centimeters and temp.; Celsius, respectively) from fall 2008 to summer 2011 on the Carrizo Plain National Monument, CA.

Year	Number of fawns born	Number of fawns survived	Fall[1] precip.	Winter[2] precip.	Spring precip.	Summer precip.	Total[3] precip.	Summer avg. high temp.
2009	22	3 (14 %)	0.00	6.68	9.04	0.08	15.80	31.24
2010	12	5 (42%)	0.36	16.97	11.61	0.58	29.51	29.02
2011	11	4 (36%)	4.60	21.97	13.16	2.01	41.73	28.32

[1] Fall = August through October of previous year

[2] Winter = November and December of previous year through January.

[3] Total = fall of previous year through summer.

Table 3.6. Percentage of principle forage items found in the diet of pronghorn, on the Carrizo Plain National Monument, CA during 2008 and 2009. Principle forage items comprised ≥ 5% of the dietary composition for any one season. Diet composition was determined by microhistological analysis of pronghorn fecal samples. Standard error values are indicated within parentheses.

Forage item	Spring (Feb – Apr)	Summer (May – Jul)	Fall (Aug – Oct)	Winter (Nov – Jan)
Forbs				
Astragalus spp.	12.0 (6.6)	4.7 (1.3)	6.1 (1.1)	9.0 (2.5)
Camissonia spp.	4.4 (1.3)	9.6 (2.5)	6.9 (2.1)	5.8 (2.8)
Erodium spp.	20.9 (1.0)	21.0 (2.4)	21.4 (4.3)	21.3 (5.0)
Lotus spp.	5.4 (2.4)	4.3 (1.2)	6.8 (1.6)	5.1 (2.8)
Aster family flower	2.8 (1.2)	9.2 (3.1)	10.0 (8.0)	3.4 (1.8)
Borage family	2.2 (0.1)	7.8 (2.3)	8.1 (3.4)	1.4 (0.7)
Legume pod	1.0 (0.7)	2.1 (0.7)	6.0 (1.7)	0.7 (0.5)
Grasses				
Avena spp.	2.8 (1.2)	2.5 (0.7)	2.1 (0.6)	9.5 (5.7)
Bromus spp.	5.5 (1.9)	4.1 (0.9)	6.6 (1.8)	4.9 (1.9)
Shrubs				
Atriplex spp.	0.4 (0.4)	0.6 (0.2)	0.3 (0.3)	12.2 (11.0)

Table 3.7. Comparison between annual available forage composition, diet composition, and preference ratings by forage class, (i.e., forb, grass, shrub) for pronghorn on the Carrizo Plain National Monument, CA during 2008 and 2009, and pronghorn occupying shrubsteppe, grassland, and desert biomes (modified from Yoakum 2004c.).

	Carrizo Plain N.M			Grassland biome			Shrubsteppe biome			Desert biome		
	F[a]	G	S	F	G	S	F	G	S	F	G	S
Available forage composition (%)	35	65	-	16	74	9	15	37	46	-	-	-
Pronghorn diet composition (%)	76	15	6	62	19	17	30	7	62	58	2	38
Preference Rating	2.2	0.2	-	3.9	0.2	1.9	2.0	0.2	1.3	-	-	-

[a] F = Forbs; G = Grasses; S = Shrubs.

Table 3.8. Comparison between percent available forage composition, percent pronghorn diet composition and preference ratings of forage classes, on the Carrizo Plain National Monument, CA during 2008 and 2009. Percent composition of available forage was calculated using dry biomass weight collected seasonally along vegetation transects. Transect surveys were not conducted during fall and shrubs were not detected within transects. Preference rating is a function of forage use (i.e., diet) in relation to availability. Percent composition of diet was determined by microhistological analysis of pronghorn fecal samples.

Season	Forage class	Available forage composition (SE)	Pronghorn diet composition (SE)	Preference Rating
Spring (Feb – Apr)	*Forb*	54.40 (3.29)	71.07 (6.12)	1.31
	Grass	45.60 (3.29)	16.53 (2.50)	0.36
	Shrub		8.07 (2.43)	
Summer (May – Jul)	*Forb*	27.01 (5.94)	75.02 (2.97)	2.78
	Grass	72.99 (5.94)	13.67 (1.71)	0.19
	Shrub		7.68 (3.25)	
Fall (Aug – Sep)	*Forb*		81.62 (3.06)	
	Grass		12.53 (2.51)	
	Shrub		3.25 (1.72)	
Winter (Nov – Jan)	*Forb*	24.98 (11.56)	73.63 (12.64)	2.95
	Grass	75.02 (11.56)	16.90 (7.24)	0.23
	Shrub		6.70 (6.43)	

Table 3.9. Percent forb cover, grass cover and bare ground during spring, summer, and winter, on the Carrizo Plain National Monument, CA from 2008 to 2011. The standard error is shown in parentheses. Shrubs were not detected within vegetation transects.

Season	Forb cover	Grass cover	Bare ground
Spring (Feb – Apr)	25.89 (0.87)	43.45 (1.12)	30.66 (1.07)
Summer (May – Jul)	19.52 (0.89)	29.18 (1.13)	51.30 (1.26)
Winter (Nov – Jan)	17.24 (0.85)	21.90 (1.01)	60.87 (1.27)
Mean	20.88 (2.59)	31.51 (6.33)	47.61 (8.91)

Table 3.10. Nutritional information for forbs, grasses, and forbs and grasses combined, (in the proportion they were available) on the Carrizo Plain National Monument, CA during spring 2008 and 2009. Forb and grass composition at the time of collection was 67.81% (SE = 1.75%) and 31.97% (SE = 1.74%), respectively. Standard error values are indicated within parentheses.

Nutritional information	Forbs (SE)	Grasses (SE)	Forbs and Grasses (SE)
% CP Crude protein	9.05 (0.57)	11.31 (1.69)	8.21 (0.35)
Gross energy (calories/gram)	4259.77 (35.04)	4426.20 (58.99)	4275.33 (23.80)
Total ash (grams)	12.44 (0.74)	8.16 (0.67)	9.62 (0.43)
% Crude fat	2.89 (0.27)	1.84 (0.12)	2.37 (0.12)
% Neutral detergent fiber	38.82 (1.47)	58.95 (1.73)	50.56 (1.78)
% Acid detergent fiber	27.24 (1.00)	29.37 (1.77)	30.94 (0.80)
% Acid detergent lignin	5.19 (0.28)	1.89 (0.08)	3.89 (0.23)
% Acid insoluble ash	1.55 (0.40)	0.53 (0.07)	0.58 (0.10)
% In-vitro dry matter digestibility	63.41 (2.04)	47.74 (3.14)	54.05 (2.13)

CHAPTER 4

SUMMARY AND CONCLUSIONS

The results from this study provide two lines of evidence for birth synchrony as a mechanism for a component Allee effect in pronghorn inhabiting the CPNM. First, fawn survival was highest during peak productivity and second, the synchrony of seasonal births appeared to degrade with decreasing population size. Birth synchrony may act as a mechanism for producing component Allee effects without necessarily leading to a demographic Allee effect. While the evidence for a demographic Allee effect was not conclusive, there was evidence of both positive and negative density-dependent feedback for the CPNM and CV populations. The effect of population density on per capita growth between these two populations likely does not differ at large population size, but does differ at small population size. The variation in density-dependent feedback at low numbers is likely due to a habitat effect (i.e., a difference in quality of habitat available).

Both micro-and macro-habitat scale environmental attributes were important for fawn habitat selection and survival on the CPNM. Fawns appeared to select the best available bed sites within larger scale areas preselected by does. An apparent cost-benefit relationship existed between separate environmental features important to fawns and does. Thus, ecological studies on recruitment, as well as conservation strategies aimed at increasing rates of recruitment, should consider the habitat requirements of both does and fawns simultaneously.

Population decline on the CPNM is likely due to the compounding effects of both low population density and marginal habitat quality. Pronghorn at this site may be able to exist at low population size, but ultimately, environmental and demographic stochasticity are likely to affect growth, with a high probability of further decline in numbers. The ability to resolve patterns in density dependent feedback, as well as fawn habitat selection and survival, was limited in part by the number of annual population counts and the number of captured fawns.. Accordingly, studies which aim to examine density-dependence and environmental impacts for small populations will require long-term data sets with more sampling and replication to reach more robust conclusions. Collectively, the methods, results, and concepts covered in this thesis offer a good template for future studies on the importance of Allee effects and habitat quality for small ungulate populations.

APPENDIX A. Information for fourteen pronghorn fawns collared on the Carrizo Plain National Monument, CA from 2009-2011.

Fawn ID	**819-2009**	**581-2009**	**944-2009**	**531-2009**	**644-2009**	**756-2009**	**881-2009**	**694-2009**	**700-2009**	**200-2009**	**668-2009**	**800-2009**	**831-2009**	**694-2010**	**881-2010**	**581-2010**	**756-2010**	**881-2011**	**531-2011**	**756-2011**
VHF frequency	165.819	165.581	165.944	165.531	165.644	165.756	165.881	165.694	165.700	165.200	165.668	165.800	165.831	165.694	165.881	165.581	165.756	165.881	165.531	165.756
Sex	Male	Male	Male	Female	Female	Female	Male	Female	Female	Male	Female	Female	Male	Female	Male	Female	Female	Female	Female	Female
Date of birth	04/26/2009	05/01/2009	05/01/2009	05/01/2009	05/01/2009	05/05/2009	05/05/2009	05/06/2009	05/06/2009	05/13/2009	05/25/2009	05/25/2009	05/24/2009	04/28/2010	04/28/2010	05/02/2010	05/10/2010	04/27/2011	04/04/2011	05/05/2011
Survived?	Yes	No	No	No	Yes	No	No	No	No	No	No	No	No	No	No	No	Yes	Yes	No	No
Age at death (days)	-	17	16	36	-	17	7	36	3	3	21	21	16	12	15	18	-	-	13	9
Date of capture	04/30/2009	05/01/2009	05/01/2009	05/01/2009	05/01/2009	05/07/2009	05/08/2009	05/09/2009	05/09/2009	05/16/2009	05/25/2009	05/25/2009	05/26/2009	04/28/2010	04/29/2010	05/05/2010	05/12/2010	05/01/2011	05/08/2011	05/08/2011
Age at capture (days)	4.00	0.17	0.17	0.17	0.17	2.00	4.00	3.00	3.00	3.00	1.00	1.00	1.00	0.29	1.50	3.00	3.00	4.00	4.00	3.00
Easting (UTM)	261800	270875	270875	247996	247996	243885	248263	271470	271283	261370	244041	244041	239786	243821	243192	249250	241904	244001	248797	249031
Northing (UTM)	3882550	3876121	3876121	3887517	3887517	3890498	3887650	3874555	3874506	3882888	3895175	3895175	3893748	3895700	3894522	3897080	3897286	3894944	3892872	3892909
Start time	1900	1205	1205	1700	1700	1655	1152	1135	1325	1204	1906	1906	1408	1600	1105	1730	1500	1407	1400	1830
End time	1915	1220	1220	1720	1720	1715	1215	1159	1349	1225	1944	1944	1425	1630	1130	1745	1520	1425	1430	1845
processing time (minutes)	15	15	15	20	20	60	63	24	24	21	38	38	17	30	25	15	20	18	30	15

Weight (kg)	-	4.20	4.10	4.20	4.10	4.00	4.50	3.75	3.60	4.05	3.50	3.50	3.70	3.95	4.00	4.10	4.00	4.10	4.40	3.95
Body length (cm)	-	-	-	-	-	58.0	63.0	60.7	62.0	67.7	59.4	59.6	53.1	59.8	61.0	62.0	61.0	63.5	61.5	60.9
Tarsus length (cm)	-	-	-	-	-	50.5	22.0	21.2	20.4	20.8	20.5	21.0	21.2	20.9	20.4	21.2	22.3	21.0	21.6	20.5
Neck girth (cm)	-	-	-	-	-	19.0	18.0	17.5	17.0	17.9	18.3	17.7	16.5	17.8	18.7	16.5	17.4	18.2	17.5	17.0
Body girth (cm)	-	-	-	-	-	-	38.0	38.7	37.3	41.7	37.5	37.3	36.5	38.0	38.0	39.1	39.4	39.1	38.0	37.5
Body temperature (Fahrenheit)	-	-	-	-	-	103.2	102.6	104.9	103.8	106.8	103.0	102.7	109.4	102.4	102.9	104.0	105.4	104.8	105.7	104.2
Number of incisors	-	-	-	-	-	2	4	4	6	4	2	2	4	2	2	4	2	2	8	6
Blood sample collected?	No	No	No	No	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes
Number of vials used (lavender, red/black, blue)	0,0,0	0,0,0	0,0,0	0,0,0	0,0,0	1,1,1	1,2,1	1,1,1	1,2,1	0,0,1	1,1,1	1,1,1	1,1,1	1,0,1	1,0,1	1,1,1	1,0,1	1,1,1	0,0,0	1,1,1

Missing information was either not applicable or not collected during capture.

APPENDIX B. Laboratory necropsy results for two pronghorn fawns from the Carrizo Plain National Monument, CA in 2010 and 2011.

California Animal Health & Food Safety Laboratory System
105 W. Central Avenue
San Bernardino, CA
92408-2113

Final
Version 1
This report supersedes all previous reports for this case

CAHFS Case #: S1003930
Referral #: PRONGHORN
Date Collected: 05/14/2010
Date Received: 05/14/2010
Case Coordinator: F.A. Uzal, DVM, MSc, PhD, Dipl ACVP
Electronically Signed and Authorized By: Uzal, Francisco A. on 6/23/2010 1:25:04PM

Email To:
CALIF DEPT OF FISH AND GAME
pswift@dfg.ca.gov

Specimens Received: 1 Carcass;

Case Contacts

Bill To	CALIF DEPT OF FISH AND GAME	916-358-1462	BIO TST VAR/WL P08800011701 NIMBUS ROAD SUITE D RANCHO CORDOVA, CA 95670
Report To	BLAIR, S		
Submitter	GONZALES, BEN JOE	916-358-2790	1701 NIMBUS RD STE D RANCHO CORDOVA, CA 95670

Specimen Details

ID	ID Type	Taxonomy	Gender	Age
	CAHFS Internal ID	Pronghorn Antelope	Female	

Laboratory Findings/Diagnosis

Proghorn, history of acute disease and death:

1-Internal umbilical remnant infection (omphalophlebitis), suppurative, with myriad intralesional coccobacilli, with extension to the liver; etiology Fusobacterium necrophorum, Bibersteinia trehalosi

2-Hepatitis, necrotizing-suppurative, multifocal to coalescing, with myriad intralesional coccobacilli; etiology Fusobacterium necrophorum, Bacteroides sp. and B. trehalosi

Other lab test results
1-No parasite eggs detected in feces
2-Negative Yersinia culture
3-Negative Brucella culture
4-Bluetongue PCR, Negative; spleen.
5-BVDV PCR, Negative; spleen.

Case Summary

5/18/10: This animal had a severe umbilical infection which was the portal of entry for the liver infection. Although I think it is unlikely the case, I have ordered cultures for plague and tularemia, in addition to regular bacterial cultures. All the other tests requested will be performed as soon as these two diseases are ruled out. I will keep you posted with our results, but in the meantime, please do not hesitate to contact me if you would like to discuss any aspects of this report.

5/19/10: Histology confirmed a diagnosis of necro-suppurative hepatitis. Cultures are still pending. Please keep in mind that the Yersinia spp. culture may take up to 4 weeks before this microorganism can be ruled out.

06/18/10 (Dr. Diab on behalf of Dr. Uzal): Fusobacterium necrophorum was isolated from the liver lesions. Bluetongue and BVD PCR were negative and Yersinia sp were not isolated. Additional bacteriology to follow.

6/23/10: Several bacterial organisms were isolated from the umbilicus and liver. This concludes testing in this case.

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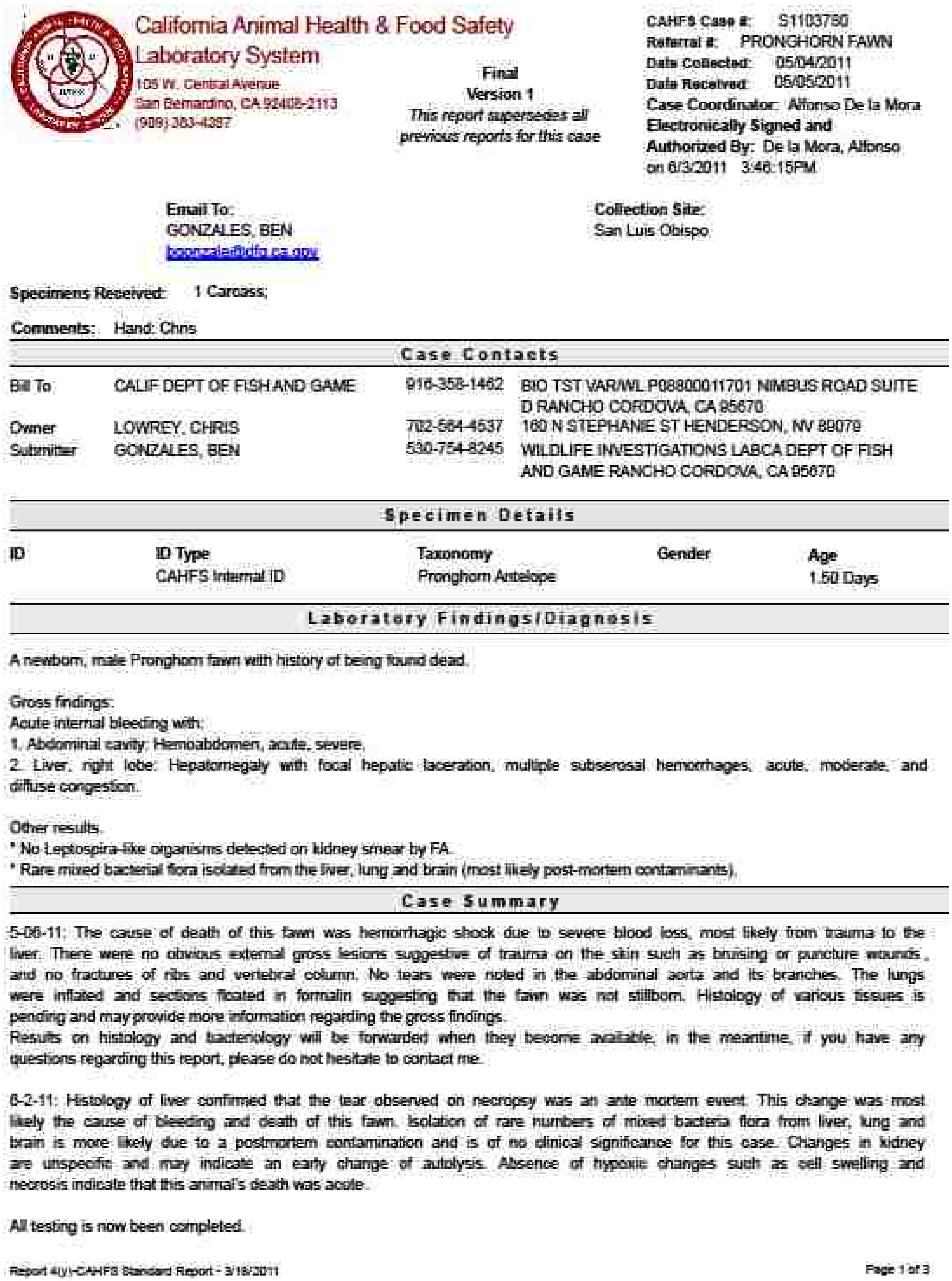

California Animal Health & Food Safety Laboratory System
105 W. Central Avenue
San Bernardino, CA 92408-2113
(909) 383-4287

Final
Version 1
This report supersedes all previous reports for this case

CAHFS Case #: S1103750
Referral #: PRONGHORN FAWN
Date Collected: 05/04/2011
Date Received: 05/05/2011
Case Coordinator: Alfonso De la Mora
Electronically Signed and Authorized By: De la Mora, Alfonso on 6/3/2011 3:46:15PM

Email To:
GONZALES, BEN
bgonzale@dfg.ca.gov

Collection Site:
San Luis Obispo

Specimens Received: 1 Carcass;

Comments: Hand: Chris

Case Contacts

Bill To	CALIF DEPT OF FISH AND GAME	916-358-1462	BIO TST VAR/WL P08800011701 NIMBUS ROAD SUITE D RANCHO CORDOVA, CA 95670
Owner	LOWREY, CHRIS	702-564-4537	160 N STEPHANIE ST HENDERSON, NV 89078
Submitter	GONZALES, BEN	530-754-8245	WILDLIFE INVESTIGATIONS LABCA DEPT OF FISH AND GAME RANCHO CORDOVA, CA 95670

Specimen Details

ID	ID Type	Taxonomy	Gender	Age
	CAHFS Internal ID	Pronghorn Antelope		1.50 Days

Laboratory Findings/Diagnosis

A newborn, male Pronghorn fawn with history of being found dead.

Gross findings:
Acute internal bleeding with:
1. Abdominal cavity: Hemoabdomen, acute, severe.
2. Liver, right lobe: Hepatomegaly with focal hepatic laceration, multiple subserosal hemorrhages, acute, moderate, and diffuse congestion.

Other results.
* No Leptospira-like organisms detected on kidney smear by FA.
* Rare mixed bacterial flora isolated from the liver, lung and brain (most likely post-mortem contaminants).

Case Summary

5-06-11: The cause of death of this fawn was hemorrhagic shock due to severe blood loss, most likely from trauma to the liver. There were no obvious external gross lesions suggestive of trauma on the skin such as bruising or puncture wounds , and no fractures of ribs and vertebral column. No tears were noted in the abdominal aorta and its branches. The lungs were inflated and sections floated in formalin suggesting that the fawn was not stillborn. Histology of various tissues is pending and may provide more information regarding the gross findings.
Results on histology and bacteriology will be forwarded when they become available, in the meantime, if you have any questions regarding this report, please do not hesitate to contact me.

6-2-11: Histology of liver confirmed that the tear observed on necropsy was an ante mortem event. This change was most likely the cause of bleeding and death of this fawn. Isolation of rare numbers of mixed bacteria flora from liver, lung and brain is more likely due to a postmortem contamination and is of no clinical significance for this case. Changes in kidney are unspecific and may indicate an early change of autolysis. Absence of hypoxic changes such as cell swelling and necrosis indicate that this animal's death was acute.

All testing is now been completed.

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APPENDIX C. Percentages of forage items in the diet of pronghorn on the Carrizo Plain National Monument, CA in 2008 and 2009. Percentages are based on microhistological analysis of fecal samples.

	Forage item	2008									2009							
		JAN	APR	MAY	JUN	JUL	AUG	SEP	OCT	DEC	JAN	FEB	MAR	MAY	JUL	AUG	SEP	OCT	Mean annual
FORBS	*Astragalus* spp.	4.0	2.0	1.2	4.9	5.5	2.1	3.4	3.9	11.5	11.6	24.5	9.6	3.7	10.5	6.8	9.1	7.1	7.1
	Camissonia spp.	4.0	5.1	11.8	18.0	14.7	6.5	10.7	13.0	11.3	2.0	6.3	1.8	1.9	4.8	2.7	3.5	4.6	7.2
	Chenopodium								0.8							0.4			0.6
	Cirsium												1.0						1.0
	Clarkia spp.	0.3	0.3	0.8						0.4					0.6				0.5
	Delphinium spp.															0.4			0.4
	Epilobium spp.	5.9											3.2						4.6
	Erodium spp.	11.5	22.2	17.8	13.8	22.1	23.9	5.4	23.6	27.5	25.0	18.9	21.7	17.8	30.6	20.8	27.4	30.0	21.2
	Eriogonum spp.		0.6	3.1							1.5			1.2			0.5		1.4
	Euphorbia (Chamaesyce) spp.		0.9																0.9
	Gilia spp.										0.7	0.5		0.7			0.2	0.2	0.5
	Lactuca serriola		2.9																2.9

	Lepidium spp.	2.3	4.5	4.1	4.2	1.1	1.0	0.3	2.5	1.6	2.2	0.5	0.2	0.6	0.9	0.6	0.5	4.0	1.8
	Lomatium											1.4				0.8			1.1
	Lotus spp.	0.1	6.5	2.5	3.1	9.5	6.3	1.9	4.8	9.7	5.6	8.9	0.8	1.9	2.4	6.6	11.1	9.5	5.4
	Lupinus spp.		0.6	2.7	0.9	2.1	0.6	0.1	3.1	0.8	0.4	4.4	5.5	5.6	1.4	6.6	6.4	2.2	2.7
	Mentzelia spp.		0.3																0.3
	Monarda	3.1	4.9							5.5	2.5	2.3	1.3	1.5			0.9		2.8
	Phacelia spp.		2.2	1.5	0.5	5.0	8.2	1.8	1.7	1.6	0.4	0.9	1.3	6.2	2.9	2.3	0.4	5.7	2.7
	Phlox/ Linanthus									2.0	1.1	0.5		1.5			0.9		1.2
	Plantago spp.		2.2	1.5		1.5					1.8	0.5	5.5	3.5	1.1	0.2			2.0
	Salsola tragus				0.5	1.1	2.5	4.2								2.7			2.2
	Salvia spp.		0.3						1.0	1.6							0.9		1.0
	Trifolium spp.			0.2			0.4	0.3		0.2		0.7		0.7		0.4	0.2	0.2	0.4
	Aster family flower		5.1	7.9	20.7	9.4	14.7	41.7	7.7	5.9	4.4	1.9	1.3	2.7				0.8	9.6
	Aster (Composite) family hair		3.1	2.7	0.9						0.7	0.9		2.1	0.3	0.2	1.3	2.0	1.4
	Borage family		2.1	2.7	0.9	12.6	9.8	2.4	7.0	2.4	1.8	2.3	2.3	14.8	6.0	4.3	5.3	21.4	6.1
	Cruciferae (Mustard family)			0.4	0.4			3.4	0.2	0.2	0.5	0.7	0.3		0.8		0.5	1.8	0.8

	Flower															0.4			0.4
	Lamiaceae (Mint family)		1.8	2.7	0.5		0.4												1.4
	Legume pod		0.6	2.7	3.6		2.1	3.9	5.0	1.6	0.4	2.3			4.1	9.3	10.6	1.2	3.6
	Polygonaceae family												0.6						0.6
	Uknown Forb	1.1	2.8	3.7	3.1	3.1	2.0	3.0	6.2	2.7	1.8	3.3	4.1	2.5	5.1	5.2	5.1		3.4
	Forb Total :	**32.3**	**71.0**	**70.0**	**76.0**	**87.7**	**80.5**	**82.5**	**80.5**	**86.5**	**64.4**	**81.7**	**60.5**	**68.9**	**71.5**	**70.7**	**84.8**	**90.7**	**74.1**
GRASSES	*Avena* spp.	20.2	4.0	1.9	2.7		2.1	3.0	3.7	0.8	7.6	0.5	3.9	5.6	2.5	1.9	0.9	0.8	3.9
	Bromus spp.	6.2	1.8	1.9	4.5	1.5	3.7	2.4	10.3	1.2	7.3	8.0	6.8	7.4	5.7	11.3	3.5	5.3	5.2
	Distichlis spicata		0.9																0.9
	Elymus spp.								0.4										0.4
	Hordeum spp.										5.4		0.3						2.9
	Leymus triticoides	0.6	1.5		0.9			0.6		1.2	0.4	0.5	1.0	4.1	4.8	0.4		1.2	1.4
	Poa spp.	4.0	0.6	0.8	0.9	2.3	3.7		1.7	2.4	4.0	3.3	5.2	1.5	0.6	5.1	1.3		2.5
	Stipa (Nasella) spp.	0.8	4.3	1.5		1.5		1.8		2.4	0.7	0.9	4.2	2.4	4.8	2.3	1.8		2.3
	Vulpia spp.										2.2			1.5					1.9
	Unkown Grass				1.3	2.7			0.8	0.8	3.3	1.9		3.2	3.2	3.5	1.3	0.4	2.0
	Grass Total	**31.8**	**13.1**	**6.1**	**10.3**	**8.0**	**9.5**	**7.8**	**16.9**	**8.8**	**30.9**	**15.1**	**21.4**	**25.7**	**21.6**	**24.5**	**8.8**	**7.7**	**15.8**

Grand Total	**OTHER**				**SHRUBS**									
	Other Total	Lichen	Flower	Seed	**Shrub Total**	Shrub stem	*Quercus* spp.	*Krascheninnikovia lanata*	*Isocoma acradenia*	*Gutierrezia californica*	Ericameria	*Chrysothamnus nauseosus*	*Atriplex* spp.	*Artemisia* spp.
100	**0.0**				**35.9**				0.6	0.6	0.6		34.1	
100	**5.5**			5.5	**10.4**			0.3			9.2	0.9		
100	**6.2**			6.2	**17.7**				1.2	4.2	7.2	3.9	1.2	
100	**3.1**			3.1	**10.6**			0.4			8.0	0.9	1.3	
100	**1.9**			1.9	**2.4**				0.8	0.8	0.4		0.4	
100	**9.6**			9.6	**0.4**								0.4	
100	**1.5**			1.5	**8.2**	0.9				1.8	5.4	0.1		
100	**1.2**			1.2	**1.4**					0.8		0.6		
100	**4.7**			4.7	**0.0**									
100	**1.5**			1.5	**3.2**	0.7							2.5	
100	**0.0**				**3.2**	0.9	0.9		1.4					
100	**7.5**	6.2	1.3		**10.6**					4.9		4.4	1.3	
100	**0.6**	0.6			**4.8**					4.4		0.4		
100	**6.9**	0.9		6.0	**0.0**									
100	**1.2**			1.2	**3.6**	1.2	0.4						1.6	0.4
100	**1.3**			1.3	**5.1**	0.9				0.9		3.3		
100	**0.8**			0.8	**0.8**	0.8								
100	**3.1**	2.6	1.3	3.4	**7.0**	0.9	0.7	0.4	1.0	2.3	5.1	1.8	5.4	0.4

VITA

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Diego Ramirez Johnson

Degrees:
Bachelor of Science, Biology, 2004
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Thesis Title:

Pronghorn (*Antilocapra americana*) offspring recruitment on the carrizo plain national monument: Evaluating the effects of low population density and marginal habitat quality.

Thesis Examination Committee:
Committee Chair, Daniel B. Thompson, Ph. D.
Committee Member, Brett Riddle, Ph. D.
Committee Member, Kathleen Longshore, Ph. D.
Graduate College Representative, Stephen Rowland, Ph. D.