

**SURVIVAL OF WHITE-TAILED DEER AND PREDATOR-PREY
DYNAMICS IN SOUTH TEXAS**

A Thesis

by

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ABSTRACT

Survival of White-tailed Deer and Predator-Prey Dynamics in South Texas

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Understanding drivers of population performance is critical for effective wildlife management. For ungulates, such as white-tailed deer (*Odocoileus virginianus*), adult survival is typically high and stable. Conversely, juvenile survival is highly variable, an important determinant of population growth, and influenced by environmental stochasticity, landscape characteristics, and land management. We assessed population performance of white-tailed deer not exposed to predator control, supplemental feed, or harvest on working rangelands in South Texas, USA. To assess recruitment, we captured deer during autumn from 2011-2025 and identified evidence of lactation ($n = 338$). From 2020-2024, we collared deer at birth, 4-months-old, 8-months-old ($n = 251$), and as adults ($n = 63$) to understand survival. We found lactation rates decreased with the presence of cattle but only when precipitation was low and neonates born in sandier areas had increased mortality risk. We found low and variable juvenile survival to 1-year (14-32%), variable adult survival (77-100%), and coyotes (*Canis latrans*) accounted for most mortalities of neonate and juvenile deer. Our results illuminate the drivers of population performance for deer in a dynamic rangeland system. Furthermore, understanding how predators respond to pulsed resources can provide insight into the relative importance of interactions with prey. We tested the predator swamping hypothesis in neonatal deer ($n = 92$), which suggests prey

synchronize births as a defense strategy to minimize predation of offspring. We found no support for the predator swamping hypothesis. We fit coyotes with GPS collars ($n = 137$) during 2018-2022 to investigate the effects of the spatiotemporal availability of neonatal deer on coyote habitat selection between two social statuses (resident and non-resident). We found as the relative abundance of deer neonates increased, resident coyotes increased selection for deer neonate habitat. Our work suggests by exhibiting shifts in selection, coyote behavior may negate the benefit of predator swamping.

PREVIEW

DEDICATION

I dedicate this thesis to my grandfather, Robert Spatafore, and my great-uncle Joseph Podolinsky. Their love and support instilled in me a passion for the outdoors and curiosity about the natural world from a young age. That passion began in my grandfather's yard, where I earned a penny for every "gumball" I picked up. It continued through family traditions, as my great-uncle passed down a love of hunting and fishing to my father, which was then shared with my brother and me through annual trout fishing trips on opening day in Pennsylvania and later expanded to include opening day of deer season. These core memories have shaped my life in unimaginable ways, and I strive to make them proud in everything I do.

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I thank my friends and colleagues for their encouragement and motivation during my time in the program. I am grateful for my friends back home for their understanding as I devoted time and distance to pursuing my career. I also thank those within my program for their guidance and analytical support, and my lab mates for their help during extensive capture efforts and for fostering a positive and enjoyable work environment. Deer captures would not have been the wonderful learning experience I remember without Kendall Bancroft, Calvin Ellis, Miranda Hopper, Bryan Spencer, Calvin Ellis, and all my other lab mates that dedicated time out of their weekends to help on such an extensive effort. I extend my appreciation to the Patton Center for Deer Research and the many volunteers and technicians who assisted in deer captures, coyote captures, and data collection. I also thank Forrest Fay and Cole Anderson for their friendship and guidance in a newfound passion for duck hunting during my time in Texas.

I thank the East Foundation for providing funding and support for the project. I am especially grateful to Landon Schofield and Dr. Ashley Reeves for their support, kindness, and commitment to the project. Their mentorship and advice have contributed greatly to my personal and professional growth. I also thank Dr. Andrea Montalvo and Andy Lopez for contributing to my professional and personal growth while living on the San Antonio Viejo Ranch. I also thank

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CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Michael J. Cherry and Randall W. DeYoung of the Department of Rangeland and Wildlife Sciences at Texas A&M University—Kingsville as well as John. M. Tomeček of Texas A&M University's Department of Rangeland, Wildlife, and Fisheries Management (College Station).

The white-tailed deer data analyzed for Chapter 1 was collected, in part, by Seth Rankins, Miranda Hopper, Kendall Bancroft, Garrett Peachey, Drs. Jacob L. Dykes, Randall W. DeYoung, J. Alfonso Ortega-Santos, David G. Hewitt, and Michael J. Cherry. Cattle stocking data from East Foundation properties analyzed in Chapter 1 was provided by Garret Stribling, Eddie Reyna, and Landon Schofield. The coyote data analyzed for Chapter 2 was provided by Professor John. M. Tomeček.

All other work conducted for the thesis was completed by the student independently.

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NOMENCLATURE

CGRDA	Coloraditas Grazing Research and Demonstration Area
GPS	Global Position System
IDD	Ideal Despotism Distribution
iSSF	Integrated Step-Selection Function
LOF	List of Figures
LOT	List of Tables
SAVR	San Antonio Viejo Ranch
TOC	Table of Contents
VIT	Vaginal Implant Transmitter
VHF	Very High Frequency

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PREVIEW

CHAPTER 1

DRIVERS OF POPULATION PERFORMANCE OF WHITE-TAILED DEER IN SOUTH TEXAS¹

Abstract

Understanding drivers of population performance is critical for effective wildlife management. For ungulates, variation in adult female survival can have the greatest proportional effect on population growth rate, yet adult survival is typically high and stable. Conversely, juvenile survival is an important determinant of population growth because it is highly variable and influenced by environmental stochasticity, landscape characteristics, and land management. We assessed population performance of white-tailed deer (*Odocoileus virginianus*) not exposed to predator control, supplemental feed, or harvest on working rangelands in South Texas, USA. Our study identified causes of mortality, estimated survival, and evaluated the influence of various factors driving white-tailed deer recruitment. We identified evidence of lactation of white-tailed deer (≥ 3.5 years old) captured during autumn from 2011-2025 to understand influences on recruitment ($n = 338$). We found lactation rates decreased with the presence of cattle but only when precipitation was low. During 2020-2024, we collared white-tailed deer at birth, 4-months-old, 8-months-old ($n = 251$), and as adults ($n = 63$) to monitor age-specific survival and assessed the ultimate and proximate causes of mortality. We found coyotes (*Canis latrans*) accounted for most mortalities of neonate and juvenile white-tailed deer. Across years, probability of survival through the first 12-weeks of life ranged from 30-38%, and through the first year of life ranged from 14-32%, while adult female survival was 85% (95% CI = 0.79-0.92). We found neonates

¹ This Chapter is written in the style of the Journal of Wildlife Monographs

born in sandier areas, which support vegetation communities that are considered lower quality habitat for white-tailed deer, had increased mortality risk. Our results illuminate the drivers of population performance for white-tailed deer in a dynamic rangeland system and demonstrate the importance of the interactive effects of environmental conditions and land management on recruitment, a key determinant of population growth. Our approach of linking broad-scale reproductive patterns with fine-scale survival processes provides a more complete understanding of the mechanisms driving population performance of long-lived species.

INTRODUCTION

Linking spatial variation in population dynamics to environmental conditions lies at the heart of population ecology and wildlife management. Population growth is influenced by vital rates, such as survival, in vivo fecundity, and recruitment (Sibly and Hone 2002, Hervieux et al. 2013). These vital rates have variable influences on population performance (Johnson et al. 2010). Numerous factors influence vital rates including predation and environmental extremes (Bakker et al. 2009, Bishop et al. 2009). Large mammals exhibit a hierarchical demographic response to environmental stochasticity, wherein recruitment and juvenile survival respond first to unfavorable conditions, followed by fecundity, and survival of reproductively active females (Gaillard et al. 1998, 2000). Therefore, patterns of high variability in vital rates can occur, with particular importance in populations exposed to stochastic environments (Rodriguez-Caro et al. 2021). Thus, understanding the relative influence of factors that drive population performance, such as environmental conditions, is fundamental for effective wildlife management.

Population performance reflects how survival and reproduction combine to influence population growth and persistence, therefore is crucial to understand and untangle the mechanisms behind population trends (White and Bartmann 1998, DeCesare et al. 2012). In

large mammals, variation in adult female survival can have the highest proportional effect on population growth rate, yet high and stable adult female survival typically buffers population growth against stochasticity (Gaillard et al. 2000). However, juvenile survival is often the most critical component of large mammal population dynamics because it is typically the most dynamic parameter influencing variation in recruitment and population growth rates (Unsworth et al. 1999, Gaillard 2000). Therefore, juvenile survival is a widely studied determinant of recruitment and often is correlated with population performance (Paterson et al. 2019).

Ungulates, such as white-tailed deer (*Odocoileus virginianus*), are ecologically and economically important (Hewitt 2015). Monitoring vital rates (e.g. survival and recruitment) can provide valuable insight into factors influencing population performance and inform management decisions. Although adult survival is generally stable, habitat quality, population structure, disease, resource availability, management practices, and harvest (Grovenburg et al. 2011a, Moratz et al. 2018) can influence survival rates. Typically, hunter harvest is the most common cause of mortality in regions where large carnivores have been extirpated (Brinkman et al. 2004, Bowman et al. 2007). Furthermore, natural causes (e.g. disease, starvation, predation) can be a more prominent source of mortality (DePerno et al. 2000) in the absence of harvest and large carnivores. Vehicle collisions are another anthropogenic source of mortality when extensive road networks are present (Grovenburg et al. 2011a). Furthermore, severe winter weather influences mortality rates in more northern regions (DelGiudice et al. 2002), however it is not thought to be a major source of mortality in subtropical or tropical systems. Although multiple factors contribute to adult mortality, this vital rate is resilient to many constraints and populations are often governed by fluctuations in juvenile recruitment (Gaillard et al. 1998, 2000).

Juvenile survival rates vary across species ranges and are a dynamic parameter influencing variation in recruitment (Gingery et al. 2018). Reliable estimates of juvenile survival rates are crucial, as this is the life stage most susceptible to mortality and sensitive to environmental conditions (Shuman et al. 2017, Gaillard et al. 1998, DelGiudice et al. 2006, Chitwood et al. 2015a). Survival estimates of juveniles in the southeastern U. S. range from 14-50% (Aubin et al. 2022, Chitwood et al. 2015b, Kilgo et al. 2012, Nelson et al. 2015, Watine and Giuliano 2016), whereas estimates from northern systems range from 45-90% (Burroughs et al. 2006, Vreeland et al. 2004, Kennedy 2015, Grovenburg et al. 2011b, Grovenburg et al. 2012, Warbington et al. 2017). Spatial variation in predation rates mandate site-specific research to determine cause-specific mortality and thus allow researchers to understand factors limiting recruitment (Linnell et al. 1995, Shuman et al. 2017).

Juvenile survival, a key driver of recruitment, is often influenced by intrinsic traits such as sex, birth mass, and date of birth (Saalfeld and Ditchkoff 2007, Bishop et al. 2009, McCoy et al. 2013). It is suggested that males are more active than females (Jackson et al. 1972), which could lead to more encounters with predators and lower survival of males. One study found males to be more than twice as likely to die when compared to females (McCoy et al. 2013). Heavier juveniles can have greater survival when compared to lighter individuals (Saalfeld and Ditchkoff 2007, Dion et al. 2020). Greater mass at birth can be beneficial to overcome adverse conditions early in life and may be correlated with maternal investment (Dion et al. 2020). Timing of parturition has also been reported to influence neonate survival, where multiple studies have found survival probability decreased for later-born neonates (Kilgo et al. 2012, Michel et al. 2017). Across regions, these patterns highlight intrinsic traits influencing survival.

However, regional landscape composition and configuration can also play a role in shaping juvenile mortality risk (Gingery et al. 2018).

Resource availability varies across regions and plays an important role in determining the nutritional condition of deer (Therrien et al. 2008), which could influence juvenile mortality risk. Regional differences in soil productivity affects the availability of forage resources for white-tailed deer across the species range, thereby shaping body condition and reproductive performance (Strickland and Damarais 2008, Simard et al. 2008). Consequently, spatial variation in soil fertility can translate into differences in neonate production and recruitment across landscapes (Garner et al. 2011). Landscape composition also influences the bed site characteristics available for neonates to select (Chitwood et al. 2015b). Cover at the bed site allows for predator avoidance and can provide thermoregulatory benefits (Kjellander et al. 2012). Furthermore, habitat management practices such as agriculture (Hefley et al. 2013), timber harvest (Masters et al. 1993), prescribed fire (Lashley et al. 2015) and urbanization (Harveson et al. 2007) alter deer habitat and potentially population dynamics. Grazing management decisions also exhibit impacts to rangeland resources and wildlife habitat (Sawyer et al. 2020).

Grazing introduces competition with cattle and may have direct negative consequences for deer (Thill and Martin 1986, Chaikina and Ruckstuhl 2006, Hines et al. 2021, Fulbright et al. 2021, Spencer et al. 2024). Cattle and white-tailed deer operate on opposite sides of the browser-grazer dietary strategy continuum (Fulbright and Ortega-Santos 2013, Esmaeili et al. 2021). However, during periods of low resource availability, dietary overlap between species can increase by constraining dietary choices for both species (Ortega et al. 1997, Chaikina and Ruckstuhl 2006, Hines et al. 2021). Intensive grazing practices may lead to negative consequences for deer by increasing search times needed to meet nutritional requirements

(Cohen et al. 1989, Kie et al. 1991). Additionally, water can be a limiting factor for both wildlife and livestock (Leeuw et al. 2001, Webb et al. 2007). Although commonly constructed for livestock use, some wildlife species, including deer, may depend on anthropogenic water sources when surface water is sparse. Cattle can monopolize water sources thus directly limiting access to water for deer (Prasad and Guthery 1989, Cooper et al. 2008). Cattle monopolizing water sources can add to the degradation of vegetation through trampling and grazing of areas closer to water sources (Leeuw et al. 2001) and result in deer avoiding these areas. Understanding the interplay between multiple management objectives on working rangelands is crucial for managers trying to optimize multiple objectives on working lands.

South Texas rangelands are semi-arid where surface water is uncommon and often managed to integrate multiple objectives including agricultural production and wildlife management. In South Texas, white-tailed deer are among the most economically important wildlife species (Foley et al. 2016), thus land use objectives for wildlife commonly incorporate white-tailed deer management. However, cattle grazing is common and can improve or degrade habitat for wildlife species (Vavra 2005). The timing and intensity of grazing can impact wildlife habitat, rangeland resources, and the long-term sustainability of multiuse enterprises (Sawyer et al. 2020). Thus, South Texas provides a well-suited model system to explore relationships of land management practices and environmental conditions on white-tailed deer population performance.

Our objective was to investigate recruitment, survival, and causes of mortality for white-tailed deer on working rangelands in South Texas. We sought to gain understanding of population performance in semi-arid rangelands where variation in recruitment is commonly thought to be influenced by environmental conditions. We hypothesized recruitment would be

influenced by effects of biological attributes, landscape characteristics, environmental conditions, and land management. To test our hypothesis, we conducted a 15-year study to assess broad scale patterns of recruitment using lactation status as an index of recruitment. We predicted that the effects of land management practices (e.g. cattle grazing) would be amplified under poorer environmental conditions (e.g. rainfall). We then conducted a known-fate survival study to test our hypothesis and understand the mechanistic processes driving recruitment. We identified causes of mortality, estimated survival, and analyzed effects of biological attributes, landscape characteristics, environmental conditions, and land management on survival. In accordance with our hypothesis, we evaluated survival of multiple age classes, including neonatal (12-weeks), juvenile (1-year), yearling (1.5-years), and adult female (≥ 2 years). We predicted predation would be the leading source of mortality for all age classes. Furthermore, given the dynamic nature of our system, we predicted considerable variation in neonatal and juvenile survival between years. However, we predicted adult female survival would remain high and exhibit limited temporal variability. Finally, we used our understanding of broad scale patterns to predict the mechanisms driving mortality risk of neonates. We predicted mortality risk would be higher for neonates in areas with cattle present because competition can reduce vegetation quantity and structure, thereby limiting hiding cover and maternal resource acquisition in our semi-arid system (Cooper et al. 2008, Fulbright 2023).

STUDY AREA

Our study occurred on the East Foundation's San Antonio Viejo Ranch in South Texas, USA. Our study area was managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The study area consisted primarily of shrub savannas, composed of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia*

spp.), and cat-claw acacia (*Acacia greggii*), interspersed with early to mid-successional grasses including three awns (*Aristida* spp.), little bluestem (*Schizachyrium scoparium*) and windmill grasses (*Chloris* spp.; French et. al. 2019, Montalvo et al. 2020).

The climate was characterized by its propensity to reoccurring drought cycles (Cleaveland et al. 2011). The 30-year average was 56.4 cm of precipitation per year and the average rainfall experienced during the study (2011-2025) was 53.8 cm (Figure 1). The maximum daily temperatures averaged 36.8 degrees C in the summer (June, July, August; PRISM Climate Group 2025). Monthly minimum daily temperatures averaged 8.4 degrees C in the winter (PRISM Climate Group 2025). Water troughs and livestock ponds were dispersed across the study site to offer year-round permanent water, as natural water sources were uncommon.

We focused efforts in the Coloraditas Grazing Research and Demonstration Area (CGRDA, Figure 1). The CGRDA encompassed 7502 hectares (ha) of native rangeland and spanned two distinct ecoregions: The Coastal Sand Sheet, characterized by sandier soils, open grasslands, and scattered mesquite brush mottes, and the South Texas Brush Country, dominated by clay-loam soils and forests composed of dense thorny brush (TPWD 2014, Natural Resources Conservation Service 2019). The southeast portion of the CGRDA was characteristic of the Coastal Sand Sheet where sandier soils, open grassland, and scattered mesquite brush mottes were common. The northwest portion of the CGRDA was more indicative of the South Texas Brush Country where tighter soil formations and dense thorn scrub were present.

The CGRDA encompassed 10 pastures, delineated by 1.3 m net wire fences, subject to experimentally stocked cattle across multiple grazing regimes throughout the duration of the study (Montalvo et al. 2020). From January 2011 through March 2014, the entire CGRDA was