BIOLOGICAL AND ENVIRONMENTAL INFLUENCES ON DEVELOPMENTAL

VARIATION OF UNGULATES IN VARIABLE ENVIRONMENTS

by

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DEDICATION

This dissertation is dedicated to my wife Amy Elizabeth Wolcott and my two daughters Emma Rose Wolcott and Millie Kate Wolcott. Thank you for sharing in my passion for the outdoors. The joy that I see in your eyes is a constant inspiration and motivation to me. This dissertation would not have been possible without you.



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ABSTRACT

Fundamental to lifetime fitness is the amount of body development that occurs during the life of an individual. This is especially apparent in long-lived species in which age-structured populations and sexual dimorphism affect breeding success among individuals. A considerable amount of research has been conducted on ungulates in order to understand factors that affect developmental variation within populations. However, much of this work has been conducted in regions in which metabolism - and subsequently body development - is influenced by photoperiod and environmental seasonality. Recently, several studies have demonstrated that increasing environmental heterogeneity at high latitudes has negatively affected ungulate population dynamics. My dissertation focused on understanding factors that influence skeletal and somatic development of ungulates across variable environments. Specifically, I addressed developmental variation at critical life stages (natal to adulthood) and highlight new findings on body development in two species of new world cervids (Capreolinae). My dissertation demonstrated that seasonal limitations to body development, considered pervasive in ungulate populations, are less present in populations that experience benign winter conditions and higher degrees of environmental stochasticity. The new insights gleaned from this dissertation are beneficial in understanding how populations of these biologically and economically important species may adapt to changes in local climate.

CHAPTER I

GENERAL INTRODUCTION

Phenotypic traits are the result of selective processes created by biotic and abiotic factors. Localized heterogeneity in biotic and abiotic factors creates variation in phenotypic traits within populations. Variation of phenotypic traits within populations ultimately affects fitness components of individuals and, thus, drives adaptations to localized environments. Because selective processes occur on localized populations, there also can be considerable variation between populations in widely distributed species. Researchers and managers use long-term averages of particular phenotypic traits as proxies to understand factors that affect population dynamics and manage species accordingly.

Body mass and skeletal size, are commonly studied phenotypic traits because they are easily measured and are strongly influenced by variation in population abundance and the environment (Caughley 2004). Variation in growth of body mass and skeletal size (body development) can have dramatic fitness consequences for individuals. Lighter individuals are more prone to predation (Clutton-Brock et al. 1996, Keech et al. 2000, Tveraa et al. 2003), and often have lower rates of reproduction, recruitment, and survival (Sæther and Andersen 1996, Sand 1996). Body mass also has direct effects on fetal development, which can affect growth and reproduction (McCullough 1979, Monteith et al. 2009). Because of those relationships, managers often use variation in body mass as a proxy for the nutritional state of a population, and implement management actions to affect individual size (Caughley 2004).

For long-lived species, density-dependent processes have strong influences on demographic and life-history variation in a population. At low population size, recruitment rates are high as available resources provide ample nutrition for maintenance and production costs (McCullough 1979). As population level increases, the rate of recruitment decreases, in response to intraspecific competition, which reduces available resources as the population approaches ecological carrying capacity—*K*. Long-lived species in naturally occurring populations often stabilize around *K*, circumstances in which recruitment matches mortality. As populations approach *K*, density-independent processes also become important in affecting life-history variation (Owen-smith 1990, Sæther 1997). For example, environmental factors like precipitation affect primary productivity (Churkina and Running 1998), which provides a highly nutritional resource for ungulates. In years that experience low precipitation, nutritional resources of poor quality negatively affect body development of ungulates. Conversely, years of high precipitation affect body development positively.

Ungulates comprise a diverse set of species that are biologically and economically important. They have been well studied and much is known about the influence of biotic and abiotic factors on body development of these species. Much of the current theory in regards to ungulate body development has shown that seasonal metabolic and reproductive processes are largely dictated by responses to photoperiod. At high latitudes (roughly $\geq 40^{\circ}$), photoperiodism is correlated with seasonal variations in plant phenology. Because of this, ungulates at high latitudes have adapted developmental responses to photoperiod. In light of current climate trends, however, high-latitude climates are becoming more heterogeneous and correlations between photoperiod and plant

phenology are decreasing. There is now considerable concern with how cervids will adapt to changing environmental conditions and more research is needed on populations that already have adapted to heterogeneous environmental conditions.

Ungulates at high latitudes experience high seasonality in nutritional resources with short and predictable growing seasons creating a small time frame for individuals to assimilate enough resources for maintenance and production in preparation for the upcoming harsh conditions during winter (Rachlow and Bowyer 1991, Bowyer et al. 1998). In response to this seasonality in primary productivity, high-latitude ungulates voluntarily reduce digestible energy requirements during winter (Ullrey et al. 1969, 1970). Ungulates at low latitudes experience longer growing seasons that vary inter-annually, depending upon precipitation. The increased variation in precipitation and relatively mild winters, allow digestible energy requirements to remain relatively stable throughout the year (Strickland 2005). Differences in metabolic response between high- and low-latitude ungulates indicate that life-history tactics may vary between these latitudes.

Although much research has been conducted on ungulate life history at high latitudes, far fewer investigations have looked at development in low-latitude ungulates. Thus, the purpose of this dissertation is to assess influences on body development of ungulates at multiple life stages in variable environments. Chapter II will assess biological and environmental influences that impact the natal life stage. This study was conducted at a latitude in which photoperiod is less correlated with plant phenology. The findings from this study will aid in our understanding of how ungulates may adjust birth mass and timing of parturition in response to increasing environmental heterogeneity at high latitudes. Chapter III will assess biological and environmental influences on post-

natal life stages (juvenile to adult, 0.5–2.5 years of age). This study will address the short- and long-term influences of biological and environmental factors on body mass of southern mule deer (*Odocoileus hemionus fuliginatus*). This research will demonstrate that low-latitude ungulates are able to compensate for periods of missed growth to overcome cohort effects – an effect considered pervasive in ungulate populations that reduce fitness components of entire cohorts. Chapter IV will assess probable mechanisms for the compensation demonstrated in Chapter III. It will use two study sites, with differences in winter severity to determine the duration of environmental influence on skeletal and somatic development. It will demonstrate that low-latitude ungulates are able to continue skeletal development in the presence of benign winter conditions, whereas high-latitude ungulates are limited by harsher winter conditions.

Together, these studies provide valuable information concerning body development of ungulates in variable environments. The findings from this dissertation highlight several important items that must be considered to continue proper management of these species. Management decisions must be made with the consideration that developmental responses within a target population may not follow trajectories currently presented in the literature. More emphasis must be placed on understanding these seemingly basic concepts across entire distributional ranges. While much is known about body development of ungulates at high latitudes, more work is necessary at low latitudes. Understanding these basic concepts will allow us to better predict how these populations will respond to current climatic trends.

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CHAPTER II

BIOLOGICAL AND ENVIRONMENTAL INFLUENCES ON PARTURITION DATE AND BIRTH MASS OF A SEASONAL BREEDER¹

Abstract

Natal features (e.g. Julian birth date and birth mass) often have fitness consequences and can be influenced by endogenous responses by the mother to seasonal fluctuations in nutritional quality and photoperiodic cues. We sought to further understand the biological and environmental factors that influence the natal features of a polytocous species in an environment with constant nutritional resources and limited seasonal variation. During a 36-year study we assessed the influence of biological factors (maternal age and litter type [i.e., litter size and sexual composition]) and environmental factors (total precipitation and mean maximum temperature during months encompassing conception, the last trimester of gestation, and the entire length of gestation) on Julian birth date and birth mass using linear-mixed effects models. Linear and quadratic functions of maternal age influenced both natal features with earliest Julian birth dates and heaviest birth masses occurring at prime-age and older individuals, which ranged from 5–9 years of age. Litter type influenced Julian birth date and birth mass. Interestingly, environmental factors affected Julian birth date and birth mass even though mothers were continuously allowed access to a high-quality diet. Random effects revealed considerable variation among mothers and years. This study demonstrates that, in long-lived polytocous species, environmental factors may have a greater influence on

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natal features than previously supposed and the influence from biological factors is also complex. The documented responses to environmental influences provide unique insights into how mammalian seasonal reproductive dynamics may respond to current changes in climate.

Key Words birth mass, conception, gestation, Julian birth date, maternal age, *Odocoileus*, parturition date, photoperiod, precipitation, temperature, white-tailed deer.

Introduction

The amount of body development that an individual achieves in the first year of life is fundamental to survival in long-lived species [1–4]. The amount of body development that is possible during that period is a function of mass at birth and quality of nutritional resources available to the mother [5–7]. For many populations of mammals, seasonality in food supplies leads to birth synchrony, which is often necessary to time parturition to annual pulses of high-quality nutritional resources [8–10]. If an individual is born too early, body development necessary for survival may not be complete and survival probabilities during the first few weeks after parturition become greatly reduced [11,12]. If an individual is born too late in spring, growth rates and low-quality nutrition limit the ability for that individual to reach a body mass necessary for overwinter survival [13,14]. Thus, timing of parturition to conditions that are most amenable for survival and growth of young is often a function of conception date or adjustment of gestation length [15–17].

Much of the current theory about seasonal breeding is contingent on maternal condition and photoperiod [6,18–20]. Maternal condition is controlled by a number of factors including social rank [21], age [22], previous breeding experience [23], individual variation [24–26], and nutrition [27–29]. Litter type (i.e., litter size and sexual composition) also has been shown to affect length of gestation and timing of parturition. In sexually dimorphic, monotocous species, gestation length is often longer, parturition dates later, and birth mass heavier for males [1]. In polytocous species, however, complications from both sex and size of litter on parturition date have led to inconclusive findings [30–31]. Much of maternal condition is dependent on the ability of an individual to obtain nutritional resources as efficiently as possible, with prime-age individuals often having the most success [32]. Because of this, litter size and birth mass is often influenced by maternal age in a quadratic manner, with prime-age individuals producing the largest litter sizes and heaviest offspring [18,19,33].

Timing of reproduction in mammals has evolved as a response to seasonal availability of resources at high latitudes, where there is a strong correlation between photoperiod and plant growth. Because of this correlation, it is possible to use photoperiod as a predictive cue to time late gestation and parturition for when nutritional resources are most available. The mammalian neuro-endocrine pathways use photoperiodic and metabolic information from the individual to stimulate the reproductive processes in preparation for breeding [34]. However, as the latitude decreases toward the equator, environmental stochasticity increases and photoperiod is less correlated with environmental conditions conducive for reproduction [34]. Thus, Bronson [34] has suggested that endogenous responses to photoperiod should not be as

strong in long-lived mammalian species at latitudes < 30° and that other environmental factors must be used in low latitudes as cues in order to maintain seasonal breeding in populations.

While a substantial amount of research has focused on understanding factors that affect parturition and survival of neonates in regard to environmental settings and maternal condition [5–7], most of these studies are confounded by variation in available nutritional resources and strong endogenous responses to photoperiodic cues [3,20]. Current findings suggest that long-lived populations of mammals at high latitudes are becoming increasingly affected by changes in global climate through trophic mismatch [35]. Thus, it is important to understand how these populations can adjust to changes in seasonality through cues other than photoperiodism as environmental conditions at high latitudes become increasingly similar to conditions at low latitudes. Thus, holding nutritional resources constant in an environment where photoperiod is less influential would be useful to more fully understand the biological and environmental factors that influence natal features of a long-lived species. By providing a constant high-quality diet, factors that may generally be swamped by high variation in nutrition and strong endogenous responses to photoperiodic cues may be more accurately assessed.

Our study provides a unique opportunity to understand the factors that influence natal features of long-lived species. For 36 years, a known-age population of captive white-tailed deer was fed a high-quality diet at a latitude with benign winter conditions. Within this population of captive white-tailed deer, measurements of parturition date (Julian birth date) and birth mass were recorded for all live births. Further, the study site was located, latitudinally, at the transitional zone suggested by Bronson [34] in which

environmental stochasticity reduces correlations between nutrition and photoperiod. Given the conditions of nutritional quality in this study, we predicted that environmental cues would not be influential to these well-conditioned mothers and that only biological factors would be used by mothers to adjust Julian birth date and birth mass. Our study had two main objectives. First, we sought to understand the biological influences of litter type and maternal age on Julian birth date and birth mass. Because maternal experience is often a large component of reproduction, we postulated that maternal age would influence both Julian birth date and birth mass, whereas litter type only would be influential in affecting birth mass. The second objective was to assess the role of both biological and environmental influences (precipitation and temperature during the period of conception, the period encompassing the last trimester of gestation, and the entire length of gestation) on Julian birth date and birth mass. By controlling for biological factors known to influence natal features and maternal nutrition, we predicted that Julian birth date and birth mass would not be affected by environmental conditions. Further, any environmental conditions found to significantly influence Julian birth date or birth mass could yield important information on how high-latitude species may adapt seasonal reproductive cues in the presence of changes in high-latitude climates.

Materials and Methods

Ethics Statement

Prior to the initiation of the study, all animal research was reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) of the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS).

Statutes of the Animal Welfare Act were followed by Kerr Wildlife Management Area personnel and registered with the USDA APHIS Animal Care permit# 74-R-0146.

Study Area

The study was conducted at the Donnie E. Harmel White-tailed Deer Research Facility (hereafter pens) located on the Kerr Wildlife Management Area in Kerr County, Texas, USA (30° 5.2' N, 99° 30.4' W). During the study, the facility was comprised of five to seven mating pens and three to eight rearing pens. The pens were enclosed by 2.7m high-game fencing with an area of 0.3 ha for each mating pen and 0.5-1.6 ha for each rearing pen. Vegetation in the pens was limited to non-palatable herbaceous plants such as common horehound (Marrubium vulgare) and cowpen daisy (Verbesina encelioides), as well as scattered live oak (Ouercus virginiana) trees, which had been browsed out of reach of white-tailed deer since 1974 [36]. Nutrition for all deer ≥ 1.5 years of age was comprised of ad libitum access to water and food pellets (16% minimum crude protein and 18.5% acid detergent fiber) as well as a source of roughage (peanut hay or alfalfa hay) provided weekly (<1 kg per animal per week, [37]). The nutritional quality of the diet was sufficiently high to account for both body maintenance and lactation costs for all individuals, because there was no difference in post-lactation body condition between individuals that reared zero, one, or two young [37]. Each pen contained one or more feeding troughs and one watering trough.

From 1974–2012, several types of breeding programs occurred at the pens; however, much of the study program was the same throughout this time span. At ≥ 1.5 years of age, female deer were separated into one of five to seven mating pens. Each October, one male (average age = 3.5, range = 1.5–10.5) was placed into each mating pen

and allowed to mate with all available females until the end of December, when the male was removed. Within one day of parturition, neonates were captured, individually marked, and weighed to the nearest 0.1 kg. After weaning, fawns were placed into rearing pens where they spent the next year of development, until the female portion was reintroduced into the mating pens at 1.5 years of age. Deer were initially collected from several ecological regions in Texas, establishing the original stock in 1974. Five sires collected from the Edwards Plateau ecological region were added to the closed research herd in 2007. Because all individuals were uniquely marked, ages were known for all females. To reduce the number of categorical variables describing the heterogeneity of breeding programs, all programs were fitted into three main program types. In the first program (study program 1), no animals experienced any nutritive stress and were fed a continuous 16% crude protein diet throughout their lifetime. The second program (study program 2) was a selective breeding program in which sires were selected as breeders if their first set of antlers possessed spike antler characteristics. The last program (study program 3) consisted of sires that encountered nutritive stress (8% crude protein) from 0.5–1.5 years of age and were given the ad libitum high-quality diet thereafter.

Environmental factors were collated from a weather station in Kerrville, TX, USA (30° 4.0' N, 99° 7.0' W), which was located approximately 38 km from the pens. Precipitation variables consisted of monthly total precipitation during periods deemed important to conception and parturition of neonates (October–December and April–June). We included two additional predictor variables by summing the monthly total precipitation from October–June (prior to conception and throughout gestation) and April–June (encompassing the months surrounding the last trimester of gestation).

Months encompassing the last trimester of gestation were deemed important because most fetal growth occurs during this period [38]. Predictor variables for mean maximum temperature were calculated similarly to those of total precipitation. Mean maximum temperature was recorded for the individual months of October–December and April– June, and was also averaged between the months of October–June and April–June. Mean maximum temperature was used because it can affect activity patterns and rumination time in ungulates [39,40]. Average annual precipitation at the pens, during the study, was 802.9 mm (min = 333.1 mm, max = 1298.7 mm, *SE* = 38.5 mm, *CV* = 0.30) with most precipitation occurring from May–June (average = 195.0 mm) and September–October (average = 180.8 mm, Fig. 2.1). Winters were mild, with mean minimum temperatures in January of 0.6 °C, and summers were hot with mean maximum temperatures in August of 34.2 °C.



Figure 2.1 Walter climate diagram derived from a weather station in Kerrville, TX, USA from 1977–2012. The solid line represents the average total precipitation (mm) and the dashed line represents the average mean temperature for each month.

Statistical Analyses

During this study, females had the opportunity to breed several times throughout their lifetime. Because of this, mixed-effects models were used in all analyses with unique identifiers for both maternal identity and birth year included as random effects. Since <5% of births during this study consisted of triplets, only births of singletons and twins were included in analyses. Also, since there were only two births by females 14 years or older, these births were removed from all analyses. A Kolmogorov-Smirnov test was first conducted to test for normality in Julian birth dates [41]. Linear mixed-effects models were used for both response variables (Julian birth date and birth mass) to initially determine which biological factors significantly influenced each response variable. Subsequently, model selection analyses and also incorporated different possible timeframes of environmental influences on the two response variables.

Biological factors included in the analyses for both response variables were maternal age, the quadratic term for maternal age, and litter type as well as the nuisance variable for study program. The quadratic term for maternal age was included to assess the possibility of a reproductive threshold or senescence in older deer [42–44]. To determine which form of the quadratic term was present, a subset of the data containing all individuals at the apex of the quadratic term and older were used to determine whether reproductive senescence was present for each response variable [45]. If neither the linear nor quadratic term for age was significant in elderly individuals, reproductive senescence was absent and a reproductive threshold was present. This post-hoc analysis was included in all analyses in which the 95% CI for the quadratic term on age did not overlap 0. Litter type was partitioned differently depending on the response variable. In the Julian birth

date analysis, one individual from each twin litter was removed to avoid doubling a Julian birth date. Litter types in the Julian birth date analysis were categorized as F =singleton female, M = singleton male, FF = twin females, MM = twin males, and FM =twin mixed litter. For the birth mass analysis, all individuals were included in the analysis and, thus, litter type was further categorized as F1 = singleton female, M1 = singleton male, F2 = females from twin female litters, M2 = males from twin male litters, FMix =females from mix litters, and MMix = males from mix litters.

We then evaluated linear mixed-effects models for both response variables that assessed the added influence of environmental factors. In each model, we included the biological variables with statistically significant *F*-ratios (P < 0.05) in the previous analysis (maternal age, litter type, and study program) with environmental variables (total precipitation or average maximum temperature) that were present during the period when dams could conceive, and encompassing the last trimester of gestation. A total of 19 regressions were built that assessed environmental influences from October–December (influence on conception), April–June (influence encompassing the last trimester of gestation), and October–June (influence throughout gestation). The first regression included only the biological factors that significantly influenced the two response variables in the previous analyses. All further models considered these biological influences with additional environmental influences added as covariates. The next set of six regressions assessed the influence of precipitation on the two response variables by incorporating individual months into each regression (i.e., October, November, December, April, May, and June). We then considered three more regressions by summing total precipitation during the possible length of conception (October-December), the period

encompassing the last trimester of gestation (April–June), and the entire length of gestation (October–June). The next set of nine regressions followed the same design as noted previously, but included mean maximum temperatures instead of total precipitation as a predictor variable.

All statistical analyses were conducted in R version 3.0.2 [46]. We analyzed linear mixed-effects models with the lme4 package [47]. For both the Julian birth date and birth mass analyses, the model that best explained variation in Julian birth date or birth mass was selected with the Akaike Information Criterion (AIC_c, [48]). Model averaging was conducted in the AICcmodavg package [49], and was used when competing models were $<2 \Delta AIC_c$ units different. Maximum likelihood estimation was used to calculate parameters during the model-selection process. Parameter estimates and 95% CI for the selected model were then reported with restricted maximum likelihood estimation [50]. Coefficients of determination were calculated for each linear mixed-effects model by calculating the variance explained by the fixed factors (marginal R^2) and by fixed and random factors (conditional R^2 , [51]). In analyses where model averaging was conducted, marginal and conditional R^2 values were calculated using the standard deviations for the fixed and random effects derived from the model with the smallest AIC_c.

Results

During the 36-year study of white-tailed deer, 2,290 neonates were born to 510 individual mothers for a total of 520 singletons (222 females and 298 males) and 885 twin litters (193 female twin litters, 243 male twin litters, and 449 mixed twin litters). Number of births per individual female varied during the study, with an average of 4.5

young born during the lifetime of an individual mother (min = 1, max = 17, SE = 0.2). Average maternal age was 4 years (SE = 0.05), with a range of 2–13 years. The mean date of parturition during our study was 13 June (Julian date = 164, SE = 0.5), with the earliest birth occurring on 13 April (Julian date = 103) and the latest on 10 September (Julian date = 253). A Kolmogorov-Smirnov 1-sample test revealed that dates of Julian birth were normally distributed during this study (D = 0.527, P = 0.944, Fig. 2.2). Average neonate body mass was 2.6 kg (min = 0.7, max = 6.1, and SE = 0.01).



Figure 2.2 Percent frequency of Julian birth dates for litters (n = 1,403) of captive white-tailed deer at Kerr Wildlife Management Area, Kerr County, Texas, USA from 1977–2012. The vertical, solid line represents the mean Julian birth date (164, 13 June) and the vertical, dashed lines represent the standard deviation (144 and 185, 24 May and 4 July, respectively).

All biological factors tested (maternal age and litter type) influenced Julian birth date, as well as the nuisance variable (study program, Table 2.1). Inclusion of environmental factors, in the model-selection analysis, indicated that several models fit the data equally well. Five models were within two ΔAIC_c of each other (Table 2.2). Model averaged estimates of the five models indicated that maternal age had a negative relationship on Julian birth date, with every 1 year increase in maternal age decreasing Julian birth date by 4.1 days (CI = -5.7 to -2.5, Table 2.3). The quadratic term for maternal age increased Julian birth date as maternal age increased, with the earliest predicted birth dates occurring at 9 years of age (Fig. 2.3). The post-hoc analysis assessing the possibility of a threshold or senescent effect after prime age demonstrated that linear and quadratic terms were not significant ($F_{1,59} = 0.434$, P = 0.513 and $F_{1,59} =$ 0.398, P = 0.531, respectively), thus, there was a threshold effect. On average, mothers in the youngest age class (2 years of age) gave birth on the latest dates (171, 20 June) and the oldest mothers (13 years of age) gave birth to individuals around the same time as a 6-year old mother (160, 9 June). Predicted values of Julian birth date for each litter type indicate that mixed-sex litters were born earlier than all other litter types (Julian birth date = 161.9, SE = 1.5). Julian birth dates for all other litter types (F = 165.5, SE = 1.7; FF = 166.1, SE = 1.7; M = 165.6, SE = 1.6; and MM = 164.8, SE = 1.6) were not significantly different from each other (Fig. 2.3). While the summary from the model-averaged regression included parameter estimates of environmental influences for November temperature, June precipitation, and October-June precipitation, the only 95% CI that did not overlap 0 was April–June precipitation. Julian birth date was influenced by April– June precipitation with every 1 mm increase in precipitation decreasing Julian birth date

by 0.02 days. April–June precipitation was highly variable during the study (min = 85.2 mm, max = 543.6 mm, average = 253.9 mm, CV = 0.51). Variance components for the random effects in the Julian birth date analysis could not be derived from the model-averaged analysis, thus, we reported values derived from the model with the lowest AIC_c (M10, biological factors and April–June precipitation as main effects). Variance components for this model were dam id (SD = 11.26), birth year (SD = 4.85), and residual error (SD = 15.22). The marginal R^2 for this model was 0.09 and the conditional R^2 was 0.45. Inclusion of the random effects (dam id and birth year) and fixed effects explained more variation in birth mass than fixed effects alone.

Table 2.1 Sources of variation utilizing restricted maximum likelihood estimation for a linear mixed-effects model assessing the influence of reproductive components on parturition date (Julian date) of singleton and twin white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 1977–2012. Headers denote the source of variation (SOV), mean squares (MS), degrees of freedom for the numerator and denominator (df_N, df_D), F-test (*F*), and p-value (*P*). Sources of variation included LitType (litter types comprised of singleton female and male, twin females and males, and twin mixed litters), MaternalAge (known maternal age) and its quadratic term, and StudyProgram (grouped study programs consisted of StudyProgram1 = 16% protein diet throughout life, StudyProgram2 = sires possessed spike antler characteristics when they were 1.5 years of age, and StudyProgram3 = sires consumed 8% protein diet from 0.5– 1.5 years of age and then placed on 16% protein diet for the rest of life). Random effects consisted of dam identification and year of birth.

SOV	MS	df_N	$df_{\rm D}$	F	Р
LitType	1093.8	4	1235	3.397	0.009
MaternalAge	9892.9	1	1241	24.560	< 0.001
MaternalAge ²	2093.3	1	1243	10.487	0.001
StudyProgram	3150.5	2	571	13.692	< 0.001

Table 2.2 Models analyzed and summaries of model selection for the influence of biological variables (litter type, maternal age, study program), and environmental variables on parturition date (Julian date) of penned white-tailed deer from the Kerr Wildlife Management Area, Kerr County, TX from 1977–2012. Each model contained predictor variables for litter type (LitType), age of the mother and its quadratic term (MaternalAge), study program (StudyProgram) and environmental predictors for each model. Precipitation and temperature values for each month as well as summed (precipitation) and average (temperature) total from Aug–Jun and Apr–Jun. Precipitation was calculated as the total precipitation in a month (mm). Temperature was calculated as the mean maximum temperature per month (°C). The number of parameters in each model is K, AIC_c is the Akaike value for each model, ΔAIC_c is the change in value compared to the most highly selected model and Weight is the Akaike weight for each model. Models are arranged from highest to lowest Akaike weight.

Model	Predictors	К	AIC_c	$\Delta {\rm AIC}_c$	weight
M10	() + Apr-JunPrecip	13	12110.1	0	0.17
M12	() + NovTemp	13	12110.4	0.3	0.14
M7	() + JunPrecip	13	12110.6	0.5	0.13
9M	() + Oct-JunPrecip	13	12111.8	1.7	0.07
M1	(LitType + MaternalAge + MaternalAge ² + StudyProgram)	12	12112.0	1.9	0.07
M5	() + AprPrecip	13	12112.4	2.3	0.05
M4	() + DecPrecip	13	12113.3	3.2	0.03
M17	() + Oct-DecTemp	13	12113.4	3.3	0.03
M6	() + MayPrecip	13	12113.4	3.3	0.03
M16	() + JunTemp	13	12113.6	3.5	0.03
M2	() + OctPrecip	13	12113.7	3.6	0.03
M13	() + DecTemp	13	12113.8	3.7	0.03
M3	() + NovPrecip	13	12113.8	3.7	0.03
M14	() + AprTemp	13	12113.8	3.7	0.03
M15	() + MayTemp	13	12113.9	3.8	0.03
M19	() + Apr-JunTemp	13	12114	3.9	0.03
M8	() + Oct-DecPrecip	13	12113.9	3.8	0.03
M11	() + OctTemp	13	12114	3.9	0.02
M18	() + Oct-JunTemp	13	12114	3.9	0.02

Table 2.2 Models analyzed and summaries of model selection for the influence of biological variables (litter type, maternal age,

d-effects model assessing s on parturition date nty, TX from 1977–2012. MM), and Mix (twin mixed couped study programs teristics when they were 1.5 aced on 16% protein diet for recipitation over the defined Random effects consisted of	Upper 95% CI	203.058	3.860	3.016	-0.857	2.390	-2.475	0.376	11.907	-1.094	-0.0005	0.006	0.0008	0.002
estimation for a linear mixe) and environmental factors anagement Area, Kerr Cou twin females and males (FF, StudyProgram consisted of gi possessed spike antler charac 5-1.5 years of age and then pl of months by summing total p rature for the defined month. ance (<i>SD</i> = 15.22).	Lower 95% CI	167.007	-2.722	-2.940	-6.386	-3.903	-5.731	0.092	3.720	-7.544	-0.029	-1.880	-0.045	-0.015
aximum likelihood and study program at Kerr Wildlife M ale and male (F, M), n age of the mother. idyProgram2 = sires protein diet from 0.5 ach month or range (ach month or range (ige maximum tempe is), and residual vari	SE	9.194	1.678	1.518	1.409	1.604	0.830	0.072	2.087	1.644	0.007	0.481	0.012	0.004
tilizing restricted m type, maternal age, in white-tailed deer ised of singleton fem ised of singleton fem c term was the know et throughout life, Stu = sires consumed 8%) was calculated for e alculated as the avera ear of birth ($SD = 4.8$	Estimate	185.032	0.569	0.038	-3.622	-0.757	-4.103	0.234	7.814	-4.319	-0.015	-0.937	-0.022	-0.007
Table 2.3 Parameter estimates u the influence of biological (litter (Julian date) of singleton and tw Litter types (LitType) were compr sex). MaternalAge and its quadrati (StudyProgram1 = 16% protein did years of age, and StudyProgram3 = the rest of life). Precipitation (mm) time span. Temperature (°C) was c dam identification ($SD = 11.26$), y	Coefficient	(Intercept)	LitTypeFF	LitTypeM	LitTypeMix	LitTypeMM	MaternalAge	MaternalAge ²	StudyProgram2	StudyProgram3	Apr–JunPrecip	NovTemp	JunPrecip	Oct-JunPrecip


obtained from model-averaged parameter estimates of competing models. Predicted Julian birth date was estimated across the range of female singleton, Study program = study program 1, April–June precipitation = 25.62 cm, October–Jun precipitation = 61.17 cm, June Figure 2.3 Predicted values from a linear mixed effect model estimating the parturition date (in Julian days) of captive whiteeach variable deemed important while controlling for all other variables (variable constants included: Maternal age = 4, Litter type = precipitation = 10.26 cm, and November temperature = 20.4 °C). The solid lines represent the predicted estimate for Julian birth date and the dashed lines are the standard error envelopes for the estimates. Random effects were treated as categorical variables and tailed deer at Kerr Wildlife Management Area, Kerr County, Texas, USA from 1977–2012. Regression coefficients were included a unique identifier for each mother and the year of birth for each fawn.

Results for the birth mass analysis demonstrated that all biological factors influenced birth mass (Table 2.4). Inclusion of environmental factors, in the model selection analysis, suggested that December temperature explained the most variation in birth mass (Table 2.5). A summary of the selected model (Table 2.6) demonstrated that maternal age and precipitation each had a positive relationship on birth mass, with every 1 unit increase in maternal age and temperature (year, °C) increasing birth mass by 0.14 and 0.05 kg, respectively (Fig. 2.4). The quadratic term for maternal age decreased birth mass as maternal age increased with the heaviest predicted birth masses (2.9 kg) occurring at 5 years of age (Fig. 2.4). The post-hoc analysis assessing the possibility of a threshold or senescent effect after prime age revealed that linear and quadratic terms were not significant ($F_{1,756} = 0.058$, P = 0.810 and $F_{1,756} = 0.058$, P = 0.810, respectively), thus, there was a threshold effect. The lightest birth masses occurred at 2 years of age and heaviest at 5 years of age and older. Predicted values of birth mass for each litter type demonstrated that birth mass varied significantly among litter types. Females from mixed litter types had the lowest birth mass (FMix, 2.54 kg, SE = 0.04) followed by females of twin litters (F2, 2.61 kg, SE = 0.04), males of mixed litters (MMix, 2.68 kg, SE = 0.04), males of twin litters (M2, 2.70 kg, SE = 0.04), females of singleton litters (F1, 2.82 kg, SE = 0.04), and the heaviest birth masses were males of singleton litters (M1, 2.99 kg, SE = 0.04). Total birth mass for singleton and twin litters varied with total birth mass of singleton litters weighing less than twin litters (F1 = 2.82 kg, M1 = 2.99 kg, F2 = 5.22 kg, Mix = 5.22 kg, and M2 = 5.40 kg). Variance components for the random effects in the birth mass analysis were dam id (SD = 0.28), birth year (SD = 0.14), and residual error (SD = 0.41). The marginal R^2 was 0.12 and the conditional R^2 was 0.44. Inclusion of the

random effects (dam id and birth year) along with the fixed effects explained more

variation in birth mass than fixed effects alone.

Table 2.4 Sources of variation utilizing restricted maximum likelihood estimation for a linear mixed-effects model assessing the influence of reproductive components on birth mass (kg) of singleton and twin white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 1977–2012. Headers denote the source of variation (SOV), mean squares (MS), degrees of freedom for the numerator and denominator (df_N, df_D), F-test (*F*), and p-value (*P*). Sources of variation included LitType (litter types comprised of singleton female and male, twin females and males, and twin mixed litters), MaternalAge and its quadratic term (known age of the mother), and StudyProgram (grouped study programs consisted of StudyProgram1 = 16% protein diet throughout life, StudyProgram2 = sires possessed spike antler characteristics when they were 1.5 years of age, and StudyProgram3 = sires consumed 8% protein diet from 0.5– 1.5 years of age and then placed on 16% protein diet for the rest of life). Random effects consisted of dam identification and year of birth.

SOV	MS	df_{N}	df_D	F	Р
LitType	6.2	5	2160	40.994	< 0.001
MaternalAge	8.2	1	2258	59.280	< 0.001
MaternalAge ²	5.7	1	2256	36.442	< 0.001
StudyProgram	1.0	2	965	5.933	0.003

Table 2.5 Models analyzed and summaries of model selection for the influence of biological variables (litter type, maternal age, study program), and environmental variables on birth mass (kg) of captive white-tailed deer from the Kerr Wildlife Management Area, Kerr County, TX from 1977–2012. Each model contained predictor variables for litter type, age of the mother, and study program and added predictors for each model are shown below. Precipitation was calculated as the total precipitation (mm) in a month or range of months. Temperature was calculated as the mean maximum temperature (°C) per month or range of months. Number of parameters in each model is K, AIC_c is the Akaike value for each model, ΔAIC_c is the change in value compared to the most highly selected model and Weight is the Akaike weight for each model. Models are arranged from highest to lowest Akaike weight.

Model	Predictors	K	AIC_c	$\Delta \mathrm{AIC}_c$	weight
M13	() + DecTemp	13	3026.8	0.0	0.82
M2	() + OctPrecip	13	3032.6	5.8	0.05
M6	() + MayPrecip	13	3033.9	7.1	0.02
M17	() + Oct–DecTemp	13	3034.7	7.9	0.02
M11	() + OctTemp	13	3034.8	8.0	0.02
M1	(LitType + MaternalAge + MaternalAge ² + StudyProgram)	12	3035.3	8.5	0.01
M5	() + AprPrecip	13	3036.1	9.3	0.01
M18	() + Oct–JunTemp	13	3036.6	9.8	0.01
M8	() + Oct–DecPrecip	13	3036.7	9.9	0.01
M12	() + NovTemp	13	3037.0	10.2	0.01
M14	() + AprTemp	13	3037.2	10.4	0.01
M16	() + JunTemp	13	3037.2	10.4	0.01
M4	() + DecPrecip	13	3037.1	10.3	0.01
M7	() + JunPrecip	13	3036.9	10.1	0.01
9M	() + Oct–JunPrecip	13	3037.3	10.5	0.00
M10	() + Apr-JunPrecip	13	3037.3	10.5	0.00
M15	() + MayTemp	13	3037.3	10.5	0.00
M19	() + Apr-JunTemp	13	3037.3	10.5	0.00
M3	() + NovPrecip	13	3037.3	10.5	0.00

Table 2.5 Models analyzed and summaries of model selection for the influence of biological variables (litter type, maternal age,

M), twin females a was its quadratic to udyProgram2 = sin ned 8% protein die e average maximu r of birth (SD = 0.	ind males (FF, N erm. StudyProgr es possessed sp t from 0.5–1.5 y m temperature (14), and residua	AM), and Mix (t am consisted of ike antler charac ears of age and °C) in the month l variance (SD =	then placed on 16% prote of December. Random e 0.41).	1.5 years of age, and ein diet for the rest of life). effects consisted of dam
Estimate	УE	đI	Lower 93% CI	Upper 93% CI
1.591	0.250	29	1.102	2.077
-0.213	0.039	2196	-0.290	-0.137
-0.288	0.037	2154	-0.361	-0.216
0.170	0.040	2181	0.092	0.249
-0.128	0.038	2210	-0.202	-0.054
-0.142	0.037	2154	-0.215	-0.070
0.140	0.018	2237	0.105	0.176
-0.010	0.002	2238	-0.013	-0.007
-0.102	0.049	190	-0.196	-0.007
-0.118	0.038	622	-0.191	-0.041
0.052	0.015	27	0.022	0.082
	why, twin remarks a was its quadratic to udyProgram2 = sin ned 8% protein die e average maximu r of birth (SD = 0. -0.213 -0.2128 -0.1102 -0.213 -0.223 -0.223 -0.223 -0.223 -0.223 -0.223 -0.223 -0.223 -0.233 -	why, twin retinates and mates (Fr., h was its quadratic term. StudyProgr udyProgram2 = sires possessed sp ned 8% protein diet from 0.5–1.5 y e average maximum temperature (r of birth (SD = 0.14), and residua Estimate SE 1.591 0.250 -0.213 0.039 -0.213 0.039 -0.213 0.037 0.170 0.040 -0.203 0.170 0.037 -0.128 0.037 -0.142 0.040 -0.128 0.037 -0.112 0.040 -0.010 0.002 -0.118 0.038 -0.118 0.038 -0.118 0.038 -0.118 0.038 -0.118 0.038 -0.015 0.015	udyProgram2 = sires possessed spike antler characted 8% protein diet from $0.5-1.5$ years of age andr of birth (SD = 0.14), and residual variance (SD =EstimateSEdf 1.591 0.250 29 -0.213 0.039 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.213 0.037 2196 -0.170 0.037 2181 -0.128 0.037 2181 -0.128 0.037 2181 -0.128 0.037 2181 -0.128 0.037 2181 -0.142 0.037 2154 0.140 0.037 2154 -0.112 0.037 2238 -0.112 0.037 2238 -0.118 0.038 622 -0.118 0.038 0.052 0.015 2738 0.052 0.015 2738	udyProgram2 = sires possessed spike antler characteristics when they were and 8% protein diet from $0.5-1.5$ years of age and then placed on 16% prote a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage maximum temperature (°C) in the month of December. Random 6 a varrage

Table 2.6 Parameter estimates utilizing restricted maximum likelihood estimation for a linear mixed-effects model assessing
the influence of biological (litter type, maternal age, and study program) and environmental factors on birth mass of white-
tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 1977-2012. Litter types (LitType) were comprised of
singleton female and male (F, M), twin females and males (FF, MM), and Mix (twin mixed sex). MaternalAge was the known age o
the mother and MaternalAge ² was its quadratic term. StudyProgram consisted of grouped study programs (StudyProgram1 = 16%
protein diet throughout life, StudyProgram2 = sires possessed spike antler characteristics when they were 1.5 years of age, and
StudyProgram3 = sires consumed 8% protein diet from 0.5–1.5 years of age and then placed on 16% protein diet for the rest of life).
DecTemp was calculated as the average maximum temperature (°C) in the month of December. Random effects consisted of dam
identification (SD = 0.28), year of birth (SD = 0.14), and residual variance (SD = 0.41).



Kerr Wildlife Management Area, Kerr County, Texas, USA from 1977-2012. Predicted birth mass was estimated across the range of each variable deemed important while controlling for all other variables (variable constants included: Maternal age = 4, Litter type = female singleton, Study program = study program 1, and December temperature = 16.0 °C). The solid lines represent the predicted Figure 2.4 Predicted values from a linear mixed effect model estimating the birth mass (kg) of captive white-tailed deer at estimate for birth mass and the dashed lines are the standard error envelopes for the estimates. Random effects were treated as categorical variables and included a unique identifier for each mother and the year of birth for each fawn.

Discussion

This study assessed the influences of biological and environmental factors on natal features (Julian birth date and birth mass) of a long-lived, polytocous species. The first objective was to understand the biological influences of litter type and maternal age on Julian birth date and birth mass. As expected, the biological factors of maternal age and litter type affected both of these natal features. The second objective was to assess the influence of environmental factors on Julian birth date and birth mass. Interestingly, we found that environmental conditions influenced these natal features even while holding nutritional resources constant and accounting for maternal traits. Total precipitation during the months that encompassed the last trimester of gestation (April– June) influenced Julian birth date, and December temperatures influenced birth mass.

Natal features are commonly dependent on biological factors related to age, social rank, nutritional condition, and previous breeding experience of mothers. We found that maternal age influenced both natal features until 5–9 years of age, which is considered prime to late-prime age for this species [52]. There was no evidence of senescence after prime age was exceeded, which was most likely a function of the high quality and easily digested forage that was available ad libitum. In polytocous species, we expected Julian birth date would be later for litter sizes larger than one offspring to accommodate for the reduced allocation of resources to a particular offspring. Our findings suggest that mothers with a mixed litter type tended to give birth earlier with no statistical differences among any other litter type. When considering the influence of litter type on birth mass, results from this study are similar to other studies on free-ranging polytocous species, with males and females from singleton litters weighing more than individuals of either

sex from twin litters [31,53,54]. Recent studies have suggested that prenatal hormonal interactions between fetuses in twin litters influence birth mass [53,55,56]. Disparity in birth mass between females and males in mixed and same-sex twin litters (2.5 kg and 2.7 kg, respectively) in our study further confirms that maternal and fetal influences have a role in allocating resources amongst twin fetuses [57]. Hormonal interactions that affect birth mass may also be an underlying cause for the unexpected earlier birth dates of mixed litters, but more work is needed to fully understand causation.

Based on the differences in study program during the 36 years, study program was considered a confounding variable that could influence natal features. We had no *a priori* expectation for study program and found an influence among study programs on Julian birth date and birth mass. Factors within study programs that could influence natal features might include genetic characteristics and age of the sire (study program 2) or reduction of nutritional quality to sires at 0.5–1.5 years of age (study program 3). Because of study-design constraints in the current study, it was not feasible to utilize sire traits as informative variables. The inclusion of sire as a random effect could have been beneficial to explain some of the variation in natal features. However, each sire was, generally, only bred during a single year and, thus, it was more appropriate to allow the variation among sires to be accounted for within the study program nuisance variable.

In many environments, precipitation and temperature are drivers of primary productivity [58] that directly affect the nutritional quality of forage for herbivores. While environmental conditions have been shown to positively influence neonatal postparturition survival in ungulates, evidence of environmental influences on parturition date or birth mass has been limited to old world cervids (Cervinae, [59]). Lack of evidence for

environmental influences on seasonal reproduction in new world ungulates has been largely attributed to endogenous responses to photoperiod as a predictor for seasonal dynamics in vegetation. Bronson [34] suggested that environmental influences should be more influential at latitudes <30° because of reduced correlations between photoperiod and seasonal dynamics in vegetation. Indeed, at a similar latitude, reduced seasonality and benign winter conditions were recently shown to influence body development among cohorts in a long-lived species differently than in studies at higher latitudes [60].

Because of the constant high level of nutritional quality in this study, we anticipated that environmental influences would not be important predictors of Julian birth date or birth mass. However, mothers still used precipitation during the period encompassing the last trimester of gestation as a cue for favorable environmental conditions in which to birth their young, and birth mass was influenced by temperature during the period closer to conception. Interestingly, these two natal features are influenced at different periods of gestation rather than being connected to each other (i.e., parturition occurring only after favorable birth mass is achieved). These findings suggest that the presumably well-conditioned mothers were exhibiting risk-sensitive reproductive allocation in both Julian birth date and birth mass [61–63]. Mothers used precipitation cues during the latter stages of gestation to determine favorable environmental conditions for rearing young. Neonates are more vulnerable than adults to inclement weather, and climatic settings indirectly influence mothers through availability of nutritional resources to provision young during the energetically demanding time of lactation [10,64]. Further, mothers can use temperature during the winter months to determine how to best allocate resources for overwinter survival and birth mass [65]. Since all mothers were presumed

to be well-conditioned, there should be no concern over food availability throughout their lifetime. However, these findings suggest an endogenous or innate response to environmental cues was still present. This innate response from well-conditioned mothers may also explain differences in variation explained by the fixed and random effects in our analyses.

In a large-scale study on reproductive seasonality in captive ruminants in zoological parks, Zerbe et al. [20] reported no evidence for environmental influences on parturition date when controlling for nutrition. This outcome may be due to resolution issues caused by their calculations of breeding peaks (greatest number of births within 5 days of each other), because small interannual variation in precipitation or temperature may be swamped out by a breeding peak analysis. In our analysis, April–June precipitation decreased the Julian birth date by 0.02 days for every 1 mm increase in precipitation. While this regression coefficient seems small, the high interannual stochasticity at our study area led to a 7-day adjustment in Julian birth date across the range of possible precipitation values. Given a daily natal growth rate of 0.24 kg [66], early born individuals could increase their body mass by 1.7 kg over the 7-day period and be approximately 50–70% heavier than late-born individuals.

Although environmental and biological factors were influential predictors of Julian birth date and birth mass, only 9% of the variation in Julian birth date and 12% of the variation in birth mass was explained by those factors. With the inclusion of the random effects for dam id and birth year, the explanation of variation increased to 45% and 44%, respectively. This result indicates that it is necessary to account for subjectspecific effects, because of individual variation in longitudinal studies. Recently, much

emphasis has been placed on the role of individual variation in maternal care [19,25]. Those studies suggested that some mothers were naturally better at producing healthy fawns, even in poor environmental conditions. This appears to be true in the current study as well. Further, it is often assumed that supplemental feeding of ungulates will reduce interanimal variability by increasing the overall condition of the herd [67]. Our study demonstrates that with a high nutritional plane, individual variation of the mothers still greatly influences these natal features and actually accounts for more of the variation than any biological or environmental influence. The random effect for birth year was also necessary in explaining variation in Julian birth date and birth mass. This random effect aided in accounting for interannual variation because of unidentified latent variables that affect maternal condition (e.g., density of deer in pens or disease).

Understanding factors that influence natal features in long-lived species is often difficult because nutritional state of mothers is affected by recruitment of young from previous reproductive events and climatic heterogeneity [17,28,63]. By controlling for nutrition, in an environment with limited photoperiodic influence, our study demonstrates that both biological and environmental factors influenced natal features of a long-lived polytocous species. These natal features, in turn, affect future survival and reproductive performance. How these factors influence natal features is quite complicated and is dependent on maternal and paternal experience as well as environmental influences at both conception and late-term gestation. This study highlights the ability of a long-lived seasonal breeder to use environmental conditions as a cue for reproductive timing and development. As high-latitude climates become increasingly similar to low-latitude

climates, this information is necessary to more fully understand how long-lived mammals may adapt to changing conditions.

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CHAPTER III

OVERCOMING COHORT EFFECTS IN A MEDITERRANEAN ECOSYSTEM: THE ROLE OF DENSITY AND PRECIPITATION ON SOUTHERN MULE DEER BODY MASS²

Abstract

Cohort effects on body mass of deer species are caused by both density-dependent and -independent factors. Cohort effects occur in the year of birth and affect body size throughout life. We hypothesized that deer in low latitudes should be able to overcome cohort effects through compensatory or catch-up growth because mild and wet winter conditions are more amenable for animal growth. We analyzed 27 years of mule deer harvest data from Camp Pendleton, California. Using generalized least-squares regression with restricted maximum likelihood estimation to estimate parameters, we determined that eviscerated body mass of southern mule deer (Odocoileus hemionus fuliginatus) was affected by precipitation and relative abundance. We also found that deer were able to recover from periods of poor nutrition and overcome cohort effects by 2.5 years of age, which has not been demonstrated in other ungulate populations. This study demonstrates that body mass can be used as a tool to assess the nutritional state of a population in an environment with high interannual variation in biotic and abiotic factors. Further, managers in environments where mild and wet winters extend growing seasons should consider the possibility that deer may be able to recover from periods of missed growth when making harvest recommendations.

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Key Words California, Camp Pendleton, catch-up growth, compensatory growth, density, low latitude, *Odocoileus*, precipitation, southern mule deer.

Introduction

Individual phenotypic traits can vary markedly within a population from year to year depending on the biotic and abiotic factors that the population experiences (Post et al. 1997, Monteith et al. 2013). Disparity in phenotypic traits, such as body mass, often has dramatic consequences for individuals. Within a species, lighter individuals are more prone to predation (Clutton-Brock et al. 1996, Keech et al. 2000, Tveraa et al. 2003) and often have lower reproduction, recruitment, and survival (Sæther and Andersen 1996, Sand 1996). Maternal body mass also has direct effects on fetal development, which can affect growth and reproduction (McCullough 1979, Kjellander et al. 2006). Because of these relationships, managers often use variation in body mass as a proxy for the nutritional state of a population (Caughley 2004). This knowledge is then used to implement management strategies (i.e., increase or decrease hunting pressure) to affect population abundance and growth (Demarais et al. 2000, Keyser et al. 2005).

In long-lived species, population density often has a large influence on variation in body mass (McCullough 1979; Gaillard et al. 2000, 2003). Density-dependent factors affect long-lived species particularly when population abundance is close to carrying capacity (*K*; McCullough 1999). As a population nears *K*, competition for resources among individuals intensifies and body mass decreases accordingly (McCullough 1999). When managers observe an overall decrease in body mass, within a population, hunting

pressure is often increased in anticipation that the population is nearing K (Demarais et al. 2000).

Density-independent factors also have been shown to affect ungulate populations (Coulson et al. 2000, Bårdsen and Tveraa 2012). Environmental factors, like snow cover or precipitation can directly affect ungulate food supplies by limiting foraging ability or by reducing nutritive qualities of plant species through drought. In many regions, precipitation is a driving factor of primary productivity (Churkina and Running 1998). When precipitation is seasonal and has little inter-annual variation, density-dependent factors often play a large role in variation of body mass (McCullough 1979, Bonenfant et al. 2002). In environments with high inter-annual variation in precipitation, the role of density-independent factors on body mass may become more apparent (Teer et al. 1965, McCullough 1999), particularly at high densities where greater foraging pressure from the herbivore population can bring about interactions between density-dependent and - independent factors (McCullough 2001, Stewart et al. 2005).

Although many studies have evaluated effects of density-dependent and independent factors on body mass, most of these were conducted in temperate or continental climates at high latitudes (Coulson et al. 2000, Bårdsen and Tveraa 2012). High latitudes often include harsh winter conditions, which limit the ability of ungulates to recover from periods of poor nutrition (Keech et al. 2000, Monteith et al. 2009, Cook et al. 2013). Because of this, cohort effects are common among ungulate populations. Cohort effects can result from density-dependent, -independent, or both factors (Albon et al. 1987, Mech et al. 1991, Bonenfant et al. 2002). Manifestations of cohort effects occur during gestation as well as in the year of birth and, ultimately, affect body size

throughout life (Mech et al. 1991, Bonenfant et al. 2002). Cohort effects may be overcome through compensatory or catch-up growth, but there is little evidence of this occurring in wild ungulate populations (Suttie et al. 1983, Solberg et al. 2008). Compensatory growth occurs when the growth rate of an individual exceeds the level of an individual who did not experience a period of nutritional restriction (Broekhuizen et al. 1994). Catch-up growth occurs when an individual continues to grow over a longer period of time (Hector and Nakagawa 2012). At high latitudes, catch-up growth is more restricted because the growing season, when high quality forage is abundant, occurs during a narrow, seasonal time frame. At lower latitudes, given sufficient precipitation and a longer growing season, the ability to overcome cohort effects might be possible (Albon et al. 1987, Stenseth et al. 1998, Bonenfant et al. 2002). When environmental conditions are amenable to primary productivity, the increased duration of the growing season should allow individuals to extend the growth period and recover from reduced growth after inclement conditions. At low latitudes, cohort effects might be overcome, at a later life stage, even when density-dependent and -independent factors affect individual growth rate at an earlier life stage.

Because cohort effects play such a large role in many ungulate populations, the primary objective for this study was to assess if southern mule deer (*Odocoileus hemionus fuliginatus*), were able to overcome cohort effects that may occur because of poor biotic and abiotic conditions during the fawn life stage. To achieve this objective, we first assessed the intra-annual processes by which density-dependent and -independent factors affect the body mass of southern mule deer in our study system. Because of increased vegetation growth during wet winters in Mediterranean environments, we

hypothesize that animals in this environment have the opportunity to recover for missed growth and are able to overcome cohort effects. Specifically, we tested the prediction that density-dependent and -independent processes have short-term effects on body mass of young animals. Further, we predicted that by asymptotic body size (size at which skeletal growth is negligible, 2.5 years of age in mule deer), cohort effects could be overcome in the mild climate of this environment. We analyzed a 27-year dataset that was collected from annual mule deer harvests in a Mediterranean ecosystem of California. This long-term dataset enabled us to assess the consequences of climatic stochasticity and deer abundance on body mass of southern mule deer between 0.5 and 2.5 years of age.

Study Area

We conducted research at the Marine Corps Base Camp Pendleton (hereafter Pendleton). Pendleton was comprised of 506 km² and was located in north-coastal San Diego County, California, USA (latitude 33°22'N, longitude 117°24'W). The base was topographically diverse, including coastline, bluffs, mesas, canyons, and mountains. The Pacific Ocean formed the western boundary, which transitioned into coastal terraces and then into coastal mountains approximately 800 m above sea level on the northeastern edge of the study area (Asmus and Weckerly 2011). Many vegetation communities were available for use by mule deer including sage scrub, chaparral, oak woodlands (*Quercus* spp.), riparian scrub, and riparian forest. Plants in those communities commonly eaten by mule deer included white sage (*Salvia apiana*), California sagebrush (*Artemisia californica*), laurel sumac (*Malosma laurina*), lemonade berry (*Rhus integrifolia*), chamise (*Adenostoma fasciculatum*), black sage (*S. mellifera*), grape (*Vitis* spp.),

cottonwood (*Populus* spp.), coast live oak (*Q. agrifolia*), Engelmann oak (*Q. engelmannii*), coyote brush (*Baccharis pilularis*), mule fat (*B. salicifolia*), poison oak (*Toxicodendron diversilobum*), arroyo willow (*Salix lasiolepis*), and Goodding's black willow (*S. gooddingii*; Pious 1989). Predators of mule deer at Pendleton consisted mainly of coyote (*Canis latrans*) and puma (*Puma concolor*).

Pendleton experiences a Mediterranean climate in which most of the precipitation occurs during the cooler months of December through March and is nearly rainless during the summer months of May through September. Mean monthly temperatures typically ranged from 14° C in January to 22° C in August (Asmus and Weckerly 2011), with approximately 335 frost-free days. Although interannual variation in temperature is limited (CV = 0.03), precipitation is highly variable across years. Annual precipitation during the 27-year study (1985–2011; average = 25.35 cm, min. = 7.73 cm, max. = 53.09 cm, CV = 0.45) was similar to reported historical averages from 1944–1984 (26.02 cm, 6.63 cm, 64.11 cm, 0.46). Minimum and maximum precipitation values, during the study, were comparable to the long-term values and the range over the 27-year period accounts for the potential range of nutritional resources in the area. Across the 27-year study, annual precipitation from 1 year to the next was unpredictable (lagged 1-, 2-, and 3-year autocorrelation coefficients were < |0.19| and statistically not significant, P > 0.05).

Methods

Mule deer were harvested, during the years of 1985–2011, from late August until early December at Pendleton as part of its annual deer hunt. From 1985–1989, harvest management consisted of 200 antlerless permits and 200 buck-only permits issued per

year. From 1990–2011, harvest management consisted of 300 either-sex permits issued per year. Harvest size during the duration of the study was not affected by the change in harvest management (F. W. Weckerly, Humboldt State University, unpublished report).

Biological staff at Pendleton determined sex and age of deer as they were brought into the processing station. Age was determined by tooth eruption and replacement for deer 1.5 years of age or younger (Severinghaus 1949). Lower, central incisor pairs (I1) were collected from deer that were \geq 2.5 years of age and sent to Matson's Lab in Milltown, Montana, USA, for age estimation via cementum-annuli analysis (Asmus and Weckerly 2011). Ages were categorized as fawn (0.5 years of age), yearling (1.5 years of age), and adult (2.5 years of age). We considered only individuals that were 0.5 to 2.5 years of age in statistical analyses because these ages include the life stages where growth rates are highest (Anderson et al. 1974). By 2.5 years of age, the mule deer at Pendleton had achieved 80% (male) and 96% (female) of their asymptotic eviscerated body mass.

Eviscerated body mass was recorded to the nearest kilogram after the entrails and organs were removed. We used eviscerated body mass because the mass of gut contents varies across diel periods, and between sexes because of diet, reproductive state, and tooth wear (Holand 1994, Jenks et al. 1994, Veiberg 2009, Weckerly 2010). Further, eviscerated body mass is highly correlated with total body fat content, which is a strong predictor of fitness in ungulates (Holand 1992, Stephenson et al. 1998). For all statistical analyses, we transformed eviscerated body mass with the natural log to meet the assumption of homoscedasticity (Sokal and Rohlf 2012). We also included the date that the animal was harvested in statistical analyses and calculated it for each year based on the earliest hunt date for the entire study. We included date of harvest because

eviscerated body mass is affected by changes in social behavior as the breeding season progresses (Yoccoz et al. 2002, Mysterud et al. 2003).

We collated data on precipitation from Oceanside Municipal Airport (latitude 33°13'N, longitude 117°21'W), located on the southern border of Pendleton. We used annual precipitation (precipitation) as a proxy of annual primary productivity (Lane et al. 1998). We summed precipitation from 1 September of the previous year to 31 August of the year of harvest, for each year, to accommodate for the time when mule deer were harvested. We used an annual summation of precipitation in this study because annual precipitation has been shown to be a stronger predictor of total plant biomass in Mediterranean grasslands than any single month (Duncan and Woodmansee 1975, Figueroa and Davy 1991).

We developed an estimate of relative abundance to assess the possibility of intraspecific competition by using a ratio between the total numbers of deer harvested in a particular year by the hunter effort. Studies of ungulates have used indices of hunter harvest (HHI) as a proxy for abundance and have shown them to be strongly correlated with absolute abundances (Fryxell et al. 1991, Bowyer et al. 1999, Skalski et al. 2007). Hunter harvests typically show year-to-year associations (Fryxell et al. 2010). Consequently, we included a 1-year lagged autocorrelation coefficient in models that had HHI (Pinheiro and Bates 2000). Lags of 2 and 3 years did not have statistically significant autocorrelation coefficients (P > 0.05).

Statistical analyses

We evaluated 7 generalized least-squares regressions to assess possible influences of precipitation and HHI, during the year animals were harvested, on eviscerated body

mass of mule deer. We used generalized least-squares regression because autocorrelation is often inherent in time-series predictor variables and was present in the hunter-harvest index. We selected the regression that best explained differences in eviscerated body mass using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). We used generalized least-squares regressions with maximum likelihood estimation in the selection process and obtained parameter estimates of the selected regression from restricted maximum-likelihood estimators (Pinheiro and Bates 2000).

We evaluated 7 regressions that could possibly explain the effects of densitydependent and -independent factors on eviscerated body mass. Regression 1 assessed the influence of sex, age, and date of harvest on eviscerated body mass without the influence of any density-dependent or -independent factors. We considered this regression in the analysis because growth trajectories differ between males and females in sexually dimorphic species (Weckerly 1998). Because regression 1 considered variables that were known to affect eviscerated body mass, we included these variables in all other regressions. Regression 2 and 3 assessed the influence of the main effects from either precipitation or HHI on eviscerated body mass. Regression 4 included both precipitation and HHI as main effects. Regression 5 and 6 assessed the influence of main and interactive effects from either precipitation or HHI on eviscerated body mass. Lastly, regression 7 assessed main and interaction effects for both precipitation and HHI on eviscerated body mass. To assess whether precipitation or HHI had a stronger influence on eviscerated body mass, we estimated the relative importance of the 2 variables following Burnham and Anderson (2002). Relative variable importance quantifies the

importance of a predictor variable by summing the Akaike weights of all regressions that contain that variable.

We assessed the ability for individuals to overcome cohort effects using the predictor variables of the selected regression from the first analysis. We evaluated 2 more regressions (yearling and adult) to assess the possibility of overcoming cohort effects at the fawn life stage by growth recovery during the yearling and adult life stages. We did not include fawns in the second analysis because the influence of precipitation and HHI during the year of their birth had already been assessed in the first analysis. The response variable for the yearling regression was the natural log transformed eviscerated body mass of yearling individuals and the response variable for the adult regression was the natural log transformed eviscerated body mass of adult individuals. We used precipitation and HHI values that were present during the fawn life stage for each cohort in this analysis. This allowed for the assessment of growth recovery by estimating the long-term impacts of precipitation and HHI on eviscerated body mass. If precipitation and HHI values that occurred during the fawn life stage of a cohort were no longer significant predictors of eviscerated body mass at the yearling or adult life stage, then we concluded that individuals must be able to recover for periods of missed growth (Keech et al. 1999).

Results

Over 27 years, measurements were collected from 1,730 hunter-harvested mule deer that were aged from fawn to adult. Eviscerated body mass varied by both age and sex (Table 3.1). Regression 4 was the most supported regression, because it possessed the highest Akaike weight, the lowest AIC value, and the other regressions lacked substantial

support (Table 3.2). A summary of regression 4 (Table 3.3) revealed that date of harvest had a marginal influence on eviscerated body mass and that both sex and age affected eviscerated body mass, with females weighing less than males and younger age class deer weighing less than successively older age class deer. Precipitation demonstrated a positive influence on eviscerated body mass with every 1 cm increase in annual precipitation increasing eviscerated body mass by 0.07 kg. HHI had a negative influence on eviscerated body mass with every 0.1 increase in HHI decreasing eviscerated body mass by 0.1 kg. The 1-year lagged autocorrelation coefficient for this model was 0.20 (95% CI = 0.15-0.25). An assessment of the relative importance of precipitation and HHI on eviscerated body mass indicated that both predictors had similar importance. Summing together the Akaike weights for models that contained precipitation or HHI as a predictor yielded a total weight of 1.0 for each variable.

Cohort effects on eviscerated body mass were present up to the yearling life stage (Tables 3.3 and 3.4). Fawn eviscerated body mass was influenced by HHI (t = -2.78, P = 0.006) and precipitation in the year they were born (t = 4.75, P < 0.001). Eviscerated body mass of yearlings was influenced by HHI (t = 3.48, P < 0.001) in the year they were born but not by precipitation (t = 0.61, P = 0.54). Adults (2.5 years of age) showed no cohort effects in eviscerated body mass. Neither precipitation (t = 0.0006, P = 0.222) nor HHI (t = 0.1722, P = 0.875) in the year adults were born influenced eviscerated body mass.

Table 3.1 Summary of eviscerated body mass measurements (mass, kg), relative abundance (HHI, hunter-harvest index) of
southern mule deer (<i>Odocoileus hemionus fuliginatus</i>), and precipitation (cm) from Camp Pendleton, California, USA, from
1985–2011. Eviscerated body mass measurements were calculated from 1,730 mule deer, which were sampled during Pendleton's
annual deer harvest. Males and females were subdivided into 3 age categories with fawns being aged at 0.5 years of age, yearlings at
1.5 years of age, and adults at 2.5 years of age. We developed HHI for each year by calculating a ratio between number of deer
harvested and total hunter effort. We summed precipitation from 1 September of the previous year to 31 August of the year of harvest,
for each year, to accommodate for the time when mule deer were harvested.

		Male mass			Female mass		11111	Duration
	Fawn	Yearling	Adult	Fawn	Yearling	Adult	ШП	rrecipitation
Ν	203	307	279	225	333	383	27	27
Aean	21.3	36.7	44.4	19.3	32	35.2	0.135	25.35
ange	11.3–29.5	25.4-49.9	29.5-68.5	10.0-28.1	21.8-40.8	25.4-43.5	0.044–0.196	6.13-51.95
SD	3.7	4.8	6.4	3.4	3.9	3.6	0.041	11.09
CV	0.2	0.1	0.1	0.2	0.1	0.1	0.303	0.43

Table 3.2 Models analyzed and summaries of model selection for eviscerated body mass of mule deer sampled from Camp Pendleton, California, USA, 1985–2011, with maximum-likelihood estimation. Predictors include D = date the animal was harvested, S = sex, A = age, P = precipitation, and HHI = relative abundance proxy, with an added parameter to account for a lag of 1-year autocorrelation; (+) denotes regression which included the main effects of selected predictors, (×) denotes main and interaction effects between the 2 predictors in the model. We present the number of parameters in each model (*K*), Akaike values for each model (AIC), change in AIC values among models (Δ AIC), and Akaike weights for each model (Weight).

Model	Predictors	K	AIC	ΔΑΙϹ	Weight
4	D+S×A+P+HHI	11	-1886.10	0.00	0.88
7	D+S×A×P×HHI	27	-1882.17	3.93	0.12
3	D+S×A+HHI	10	-1865.76	20.33	0.00
6	D+S×A×HHI	15	-1859.40	26.69	0.00
5	D+S×A×P	14	-1818.46	67.63	0.00
2	D+S×A+P	9	-1812.94	73.15	0.00
1	D+S×A	8	-1787.60	98.50	0.00

Table 3.3 Estimates of coefficients for the selected regression, which included variables for sex, age, date animal was harvested, precipitation, and hunter-harvest index (HHI) as well as all second-order interactions between sex and age. Estimates are for the eviscerated body mass of mule deer sampled from Camp Pendleton, California, USA, 1985–2011 and are natural log transformed. Female was the reference category for sex and we present males as a parameter (SexM). Adult was the reference category and we present fawn (AgeF) and yearling (AgeY) as parameters for age. We treated precipitation as an integer. Column headers consist of coefficients in the model study, estimate of the coefficient, standard error for the estimate, and *t*-tests to ascertain whether the coefficient differed significantly from 0. Coefficients with a colon denote an interaction between 2 coefficients.

Coefficient	Estimate	SE	t	Р
(Intercept)	3.581	0.023	158.06	< 0.001
Date	-0.0003	0.0001	-1.76	0.079
SexM	0.215	0.012	18.56	< 0.001
AgeF	-0.631	0.014	-45.95	< 0.001
AgeY	-0.104	0.012	-8.42	< 0.001
Precip	0.002	0.0001	4.75	< 0.001
HHI	-0.294	0.106	-2.78	0.006
SexM:AgeF	-0.102	0.018	-5.62	< 0.001
SexM:AgeY	-0.084	0.017	-5.05	< 0.001

Table 3.4 Estimates of coefficients for 2 regressions examining the influence of precipitation and hunter harvest index (HHI) in the year deer were born on the eviscerated body mass of yearling and adult animals. Estimates are for the eviscerated body mass were harvested during the hunt season between late August and early December. Female was the reference category for sex. The lag of 1-year autocorrelation coefficient for the yearling and adult animal regressions was 0.20 (95% CI: 0.15–0.25). Sample size of of mule deer sampled from Camp Pendleton, California, USA, 1985–2011 and are natural log transformed. Date was when animals yearlings was 640 and 662 for adults.

Cofficient		Yearli	ŋg			Adu	lt	
COEFFICIENT	Estimate	SE	t	Р	Estimate	SE	t	Р
(Intercept)	3.554	0.0272	130.8	<0.001	3.6149	0.0274	131.75	<0.001
Date	-0.0036	0.0002	-1.74	0.083	-0.0005	0.0002	0.0002	0.027
SexM	0.1259	0.0103	12.18	<0.001	0.2038	0.0104	0.0104	<0.001
Precipitation	-0.0004	0.006	0.61	0.54	-0.0008	0.0006	0.0006	0.222
IHH	-0.502	0.1443	3.48	<0.001	0.0271	0.1722	0.1722	0.875
Discussion

Our study demonstrated that eviscerated body mass of southern mule deer was influenced by both density-dependent and -independent factors in a Mediterranean ecosystem, yet cohort effects did not manifest. We hypothesized that animals in our study system should have the opportunity to recover from periods of missed growth and that any apparent cohort effects on eviscerated body mass could be overcome at later life stages. We found that annual precipitation and HHI were significant predictors of intraannual eviscerated body mass. These short-term influences included a positive relationship between precipitation and eviscerated body mass and a negative relationship between HHI and eviscerated body mass. Long-term effects, assessed through a cohort analysis, concluded that precipitation and HHI, during the year of birth, influenced eviscerated body mass at the fawn life stage. At the yearling life stage, HHI during the year of birth, was the only variable that influenced eviscerated body mass, however, this influence had dissipated by the time animals reached 2.5 years of age, the adult life stage.

Precipitation and abundance are both factors that affect ungulate body mass (Weladji and Holand 2003, Toïgo et al. 2005). The relative importance of variables suggests that precipitation and HHI both play equally important short-term roles in affecting eviscerated body mass of individuals intra-annually at Pendleton. Ultimately, these 2 factors are intertwined with each other. As a population approaches *K*, the physical condition of individuals declines. Consequently, they are poorly buffered against environmental extremes, which can increase correlations with environmental variables.

In the presence of spatial heterogeneity, ungulates will selectively feed within their habitat to reduce density-dependent effects (Wang et al. 2006). We surmise that

vegetation diversity, frequent wildfire, and subsequent plant phenology are sufficient at Pendleton to allow mule deer to effectively overcome the disadvantage of temporal effects. Many plant species within coastal sage scrub communities on Pendleton are adapted to survive summer drought conditions by desiccating and becoming dormant (Pase and Brown 1994). Many of these species, such as California sagebrush, white sage, and black sage, are also important food plants for southern mule deer. Additionally, evergreen shrubs such as lemonade berry and laurel sumac provide food for deer all year with new growth occurring in winter. Precipitation events, typically starting in October, prompt plant species within the coastal sage scrub community, along with forbs and grasses, to grow vigorously. These events produce succulent new growth for deer well into December. In contrast, plants within riparian communities including cottonwoods, willow, poison oak, and grape are deciduous during the winter; yet provide food alternatives in the driest months of summer. Riparian areas also provide surface water for mule deer where females with fawns are present significantly more often during the driest months than either females without fawns or males (Bowyer 1984).

The short-term effect on eviscerated body mass from precipitation is probably created by the high interannual environmental stochasticity present at Pendleton. This outcome is caused by precipitation influencing the amount of forage and the nutritional quality available throughout the year. Density-dependent factors (HHI) also affect eviscerated body mass in a short-term manner. HHI probably does this by limiting resources in the population through intraspecific competition with individuals competing for scarcer, less nutritious forage as the population increases. Although precipitation is highly variable across years at Pendleton, HHI is less variable. The assessment of short-

term influences on eviscerated body mass suggest that both variables affect individual mass equally. Consequently, we suggest that the deer population at Pendleton is probably close to *K* and, thus, limited nutritional resources affect eviscerated body mass readily through density-dependent and -independent mechanisms.

Cohort effects are prevalent in ungulate populations, and those effects occur throughout the life of an individual (Mech et al. 1991, Bonenfant et al. 2002, Monteith et al. 2009). Our analysis of long-term effects indicate that precipitation during the year of birth only explains variation in fawn eviscerated body mass, whereas HHI is a significant predictor of fawn and yearling eviscerated body mass. By the adult life stage, however, neither precipitation nor HHI, during the year of birth, are significant predictors of adult eviscerated body mass. Although ungulates often demonstrate cohort effects throughout their lifespan, our analysis indicates that cohort effects for southern mule deer at Pendleton only occur into the yearling life stage and are overcome by the adult life stage. Consequently, deer at Pendleton are able to recover for reduced body mass after the yearling life stage. This allows these individuals to achieve comparable eviscerated body mass at the adult life stage (2.5 years of age) to that of another adult individual that did not experience a period of nutritional restriction at an earlier life stage.

The ability to recover for missed growth after a nutritionally poor year is still poorly understood in ungulate species. In controlled experimental studies with ungulates, full recovery of missed growth, or catch-up growth has been observed (Wairimu et al. 1992), but there is little evidence of full compensatory growth in free-range ungulates (Keech et al. 2000, Dale et al. 2008). Results from studies of ungulates generally show partial or no recovery (Suttie et al. 1983, Solberg et al. 2008). Most of these studies occur

at high latitudes where environmental conditions are much more seasonal and animals experience harsh winter conditions. Ullrey et al. (1969, 1970) found that daily digestible energy requirements for white-tailed deer (Odocoileus virginianus) at high latitudes decrease in response to photoperiod and prolonged periods of food restriction. In contrast, ungulates in semiarid environments, with variable rainfall patterns and high temperatures that limit net primary productivity, often have lower maintenance requirements as an adaptive response to a low productivity environment (Strickland et al. 2005). This is thought to be because greater metabolic rates are needed for tissue synthesis during the presence of seasonally abundant food sources at higher latitudes (Hudson and Christopherson 1985). By reducing maintenance requirements, ungulates in lower latitudes may be able to partition resources more readily toward compensating for missed growth, whereas ungulates in higher latitudes will still need to account for strong seasonal fluctuations in metabolic requirements. If resources are available, lower maintenance costs and the ability to forage for more nutritional resources may allow deer in lower latitudes to fully recover for missed growth by increasing growth rates or extending the duration of optimal growth. Our study indicates environmental conditions at Pendleton may be conducive to full recovery of eviscerated body mass by 2.5 years of age and that the short-term effects from precipitation and HHI must play a role in overcoming any cohort effects. Although our study does not directly assess growth recovery by accelerated growth rates or increases in growth duration, it does demonstrate that one of these processes has to occur to overcome cohort effects.

Management Implications

Deer managers use harvest data to assess population dynamics and make management decisions. These analyses generally include yearling male body mass to assess population density, animal nutritional state, or range conditions (Shea et al. 1992, Keyser et al. 2005). This study demonstrates that body mass can be used as a tool to assess the nutritional state of a population for several age classes in a system with high interannual environmental variation. Our study also demonstrates that deer are able to recover from periods of poor nutrition and overcome cohort effects that are prevalent in ungulate populations. Managers in environments with spatial heterogeneity, extended growing seasons, and mild winters should consider the possibility that deer may be able to recover from periods of missed growth when making harvest recommendations.

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CHAPTER IV

TEMPORAL VARIATION IN ENVIRONMENTAL INFLUENCES ON BODY DEVELOPMENT IN A NEW WORLD CERVID: POTENTIAL MECHANISMS FOR GROWTH COMPENSATION³

Abstract

Body development is influenced by density-dependent and -independent factors, which affect fitness components in ungulate populations. Those factors, paired with harsh conditions during winter, can limit body development and lead to variation among cohorts (cohort effects), which are considered pervasive in ungulate populations. Recent studies indicated that cohort effects can be mediated in some environments; however, the mechanism for this compensation is still poorly understood. We used two long-term datasets to assess differences in duration of environmental influences on body development at two different latitudes with similar primary productivity and different winter conditions. We used Akaike's Information Criterion to determine which duration of environmental influence most strongly affected two measures of body development at both sites. We documented differences in duration of environmental influence on skeletal development between sites but not for somatic development. Skeletal development at the high-latitude site was limited to precipitation in the warm-weather months (March-August), whereas annual precipitation explained the most variation in skeletal development at the low-latitude site. Somatic development was most strongly influenced by annual precipitation at both sites. Effects of abundance and precipitation on both

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measures of development were dependent on sex and age of the individual at both sites. Presumably, deer at the low-latitude site are able to extend the period of growth, through catch-up growth, when winter conditions are amenable rather than exceeding optimal growth rates through compensatory growth to overcome cohort effects.

Key Words abundance, annual precipitation, catch-up growth, compensatory growth, latitude, *Odocoileus*, seasonal precipitation, temporal variation.

Introduction

Skeletal size and body mass are phenotypic traits that affect fitness components (e.g., survival and reproduction) of large herbivores (Clutton-Brock 1991). Phenotypic traits are influenced by density-dependent and -independent factors, which affect individuals *in utero* and throughout life (Post et al. 1997, Monteith et al. 2013, 2014). Density-dependent and -independent factors (e.g., population abundance and environmental variables) affect body development by influencing the quality and quantity of food resources available to individuals (Sæther 1997, Stewart et al. 2005). If body development is not sufficient, survival is reduced (Festa-Bianchet et al. 1997, Loison et al. 1999) and future reproductive and fitness components are altered (Albon et al. 1987).

Skeletal size is a developmental feature that determines the ultimate size and mass that an individual can achieve. Although many phenotypic traits fluctuate throughout the year (e.g., kidney fat, rump fat, and body mass), intra-annual fluctuation in skeletal size does not occur once adult size is reached. This outcome occurs because the skeletal framework is not readily remobilized into energy to meet maintenance costs

(Brockhuizen et al. 1994). Instead, during nutritional restriction, energy is created from the remobilization of somatic tissue (e.g., kidney fat, rump fat, or muscle mass). Skeletal size (e.g., hind foot length), however, is still influenced by density-dependent and independent factors (Klein 1964, Zannèse et al. 2006). When nutritional quality is limited, skeletal growth is reduced or ceases completely. As nutritional resources become more available, skeletal growth resumes (if the epiphyseal plate is present) once metabolizable energy and nutrient intake exceeds maintenance requirements Brockhuizen et al. 1994).

Intra-annual variation in body mass differs between age classes and sexes. In females, variation in body mass occurs throughout the year to meet energy demands from gestation, lactation, and overwinter survival (Parker et al. 1993). In early winter, body reserves begin to deplete when food resources become limited (Ditchkoff and Servello 1998). Depletion of body mass continues (and is further intensified during late gestation in pregnant females) into early spring, when new vegetative growth becomes available. As temperatures warm and forage becomes readily available, body reserves recover and development continues. Nonetheless, from late spring through late summer, females that produced young have added lactation expenses, which slow recovery of body mass. Once young are weaned, females must accumulate reserves necessary for overwinter survival and future reproduction before nutritional resources are again limited in early winter. In males, body reserves are depleted as the rutting period begins in late autumn (Hewitt 2011). This depletion continues through overwinter resource limitation and ends in early spring. Antler growth begins, generally, in late winter to spring and ends in late summer (Hewitt 2011). Differences in energetic demands between sexes and between gravid and non-gravid females are readily apparent when comparing spatial segregation and

digestive tracts of individuals. Gravid females will spend nearly as much time foraging as larger males, but will select for forage that is higher in nutrition and lower in fiber content (Barboza and Bowyer 2000).

Seasonal restriction of nutrients, which limit skeletal size and body mass in certain months, can be compounded by environmental stochasticity within months in which body development is more common. Thus, if environmental conditions are poor or abundance levels are high during months in which body development occurs, individuals may not be able to compensate for periods of missed growth. These situations create variations in body size among cohorts (cohort effects), which are considered pervasive in ungulate populations (Albon et al. 1987, Gaillard et al. 1997, Post et al. 1997, Rose et al. 1998, Forchammer et al. 2001, Bonenfant et al. 2002). Cohort effects influence body size throughout the lifetime of an individual, which affects social rank (Clutton-Brock et al. 1982), survival (Keech et al. 2000), and reproduction (Clutton-Brock 1991, Sand 1996).

Recently, several studies have indicated that density-dependent and -independent factors can mediate cohort effects in some environments (Webb et al. 2014, Wolcott et al. 2014). Specifically, cohort effects might be lacking in environments with high interannual variability in environmental conditions and mild winter conditions. Those necessary climatic conditions become more prevalent as latitude decreases toward the equator. Although Webb et al. (2014) and Wolcott et al. (2014) bring new insight into body development of ungulates at low latitudes; those authors were not able to determine mechanisms for this compensation. Possible mechanisms for compensation can include an increase above optimal growth rate (compensatory growth) or an extension of the growth period (catch-up growth; Hector and Nakagawa 2012).

A comparison of the time duration in which factors influence body development between latitudes could yield important findings to support which mechanism of growth is most likely to occur in overcoming cohort effects at low latitudes. For example, if body development at high and low latitudes were influenced during the same time duration, compensatory growth would be the most probable mechanism because low-latitude ungulates would need to increase growth rates above optimal levels to overcome cohort effects. Conversely, if body development were influenced at different time durations between latitudes, catch-up growth would be the most probable mechanism for compensation at low latitudes by extending the period of growth rather than increasing the rate of growth. Because body development is generally limited to warm-weather months, catch-up growth would be the most probable mechanism for compensation if low-latitude ungulates were influenced over a longer duration of time or high-latitude ungulates were negatively influenced by cold-weather months.

Therefore, the purpose of this study is to more fully understand the variation in body development of ungulates at different latitudes. White-tailed deer (*Odocoileus virginianus*) provide a unique opportunity to assess variation in influences of densitydependent and -independent factors on body development, because they are the most abundant and latitudinally widespread species within the family Cervidae (Hewitt 2011). The distributional range of white-tailed deer extends from the Yukon Territory (<100 km from the Arctic Circle, Veitch 2001), to the equator, and into the South American countries of Peru and Bolivia (Hewitt 2011). The high variability in environmental conditions across those latitudes allows for a considerable amount of phenotypic plasticity, because local populations adapt to specific environmental conditions

(Strickland and Demarais 2000). Because of phenotypic plasticity and adaptability to local environments, we hypothesized that body development of white-tailed deer would respond to the same environmental factor at different durations of time depending on the latitude of the population. Thus, we assessed the influence of density-dependent and independent factors on two measures of body development at two sites, which were different in latitude. We predicted three outcomes for body development at these two sites. First, we predicted that an annual measure of abundance would negatively influence skeletal and somatic development (measured as hind foot length and body mass, respectively) at both sites. Second, we predicted that the time duration for environmental influences on body development would be different between the sites. Specifically, the influence of environmental variables on body development should be seasonal at high latitudes and annual at low latitudes. Finally, because there are differences in developmental processes between skeletal and somatic frameworks, we predicted that the duration of environmental influences could differ between measures of body development within a site. We assessed the influence of abundance and annual or seasonal environmental conditions on skeletal size and body mass using two datasets from white-tailed deer collected in temperate environments with differences in winter weather conditions.

Study Area

The study was conducted at two locations in the contiguous United States of America: Hatchie National Wildlife Refuge (Hatchie NWR) and the Edwin S. George Reserve (George Reserve). Hatchie NWR (latitude 35°29'N, longitude 89°15'W) was

located in Haywood County, Tennessee, and consisted of 4,677 ha of primarily bottomland hardwood habitat, which was maintained as a refuge for migrating and wintering waterfowl. Bottomland hardwood habitat at Hatchie NWR consisted primarily of oaks (*Quercus* spp.) and hickories (*Carya* spp.), and upland habitat was primarily agricultural row-crop fields sown with soybean (*Glycine max*), milo (*Sorghum* spp.), and corn (*Zea mays*). George Reserve (latitude 42°27'N, longitude 84°0'W) was located in Livingston County, Michigan, and consisted of 464 ha of eight major types of vegetation: hardwood forest; pine forest; grassland; tamarack swamp; bog; marsh; swamp margin; forest ecotone (McCullough 1979). Colonel Edwin S. George deeded the reserve to the University of Michigan in 1930 as a property to be maintained by natural processes, but it was necessary to humanely address overpopulation of reintroduced deer within the highfenced area.

Both sites are located within temperate climates, with a historical average annual precipitation at Hatchie NWR (1906–2012) of 130.79 cm (min = 79.94 cm, max = 192.01 cm) and at George Reserve (1900–2012) of 84.27 cm (min = 42.78 cm, max = 190.02 cm). Monthly maximum snowfall depth, summed annually, was limited at Hatchie NWR with average depths of 8.2 cm (min = 0.0 cm, max = 43.2 cm). At George Reserve, snowfall depth was much greater; with an annual average of 62.1 cm (min = 5.1 cm, max = 208.2 cm) with, on average, 76.9 days with snow cover (range = 0 to 116). Average temperatures at Hatchie NWR were lowest in the month of January (average = 4.2°C, min = -4.9° C, max = 9.5°C), with the coldest months including December–February (average range = 4.2 to 6.1°C). Average temperatures at George Reserve also were lowest in the month of January (average = -4.3° C, min = -11.4° C, max = 1.7° C) with the coldest

months also including December–February (average range = -4.3 to -2.0°C). Winter conditions at Hatchie NWR were much milder than at George Reserve, with the average minimum temperature below freezing only in January (average = -1.5°C), whereas average minimum temperature at George Reserve consisted of continuous months below freezing from December to March (average range = -3.1 to -8.2°C). Average temperatures at Hatchie NWR were highest in July (average = 26.9°C, min = 24.1°C, max = 29.5°C), with the warmest months including June–August (average range = 25.2 to 26.9°C). Average temperatures at George Reserve also were highest in July (average = 22.6°C, min = 19.9°C, max = 26.0°C) with the warmest months also including June– August (average range = 20.1 to 22.6°C).

Annual net primary productivity of plant species was similar at both locations, with onset of maximum net primary productivity occurring approximately in July at Hatchie NWR and approximately June at George Reserve (Hicke et al. 2002). The main difference in plant phenology between the two sites was the onset and length of the growing period. At Hatchie NWR, onset of plant growth began earlier and dormancy occurred later than at George Reserve, with estimated mean frost-free days at Hatchie NWR of approximately 205, and at George Reserve of approximately 160 (Flint 1972, Collins and Wilbur 1979).

Methods

Data collection

Deer were collected annually at each location. At Hatchie NWR, from 1984–2005 and 2008–2013, 300–600 gun-hunt permits were issued annually to hunters. At George Reserve, from 1967–1968, deer were culled using a drive method with approximately 8– 20 personnel moving deer past other personnel with rifles. In all successive years at George Reserve (1969–1974 and 1981–1982), personnel in trucks with rifles and spotlights culled deer at dusk and dawn (McCullough 1979). At both locations, collected deer were brought to a processing station where personnel with biological training collected data (sex, age, eviscerated body mass, and skeletal morphometrics). At Hatchie NWR, age was estimated by tooth eruption, replacement, and wear (Severinghaus 1949). At George Reserve, age was estimated by counting cementum layers on the first molar by reflected light (Ransom 1966, McCullough 1979). Age was then partitioned into three categories as young (0.5 years of age), yearling (1.5 years of age), and adult (2.5 years of age). Only individual deer thatwere estimated to be 2.5 years- of- age were considered in the adult age class, because accuracy of aging methods decreases with successively older individuals (Gee et al. 2002) and most total body development occurred by this age (Roseberry and Klimstra 1975).

At both locations, skeletal and somatic development was derived from measures of hind foot length (to the nearest 1.0 cm) and eviscerated body mass (to the nearest 1.0 kg). A hind foot was measured from the end of the phalanges to the tip of the calcaneus (Zannèse et al. 2006). Hind foot length has been shown to be an accurate measure of total skeletal development in studies of early to mid-life (between the ages of 0.5 and 2.5 years). The hind foot develops more rapidly than other skeletal structures (Suttie and Hamilton 1983) and responds readily to density-dependent and -independent factors (Zannèse et al. 2006). Eviscerated body mass was measured as the total mass of the animal after removal of the entrails and organs. Eviscerated body mass was used as a

measure of somatic development because whole-body mass can vary due to variation in mass of gut contents by age, sex, and diel period (Holand 1994, Jenks et al. 1994, Weckerly 2010).

Environmental data were collated during periods of deer collection from the nearest weather station to each of the locations. For Hatchie NWR, the nearest weather station was located approximately 7 km away in Brownsville, Tennessee (latitude 35°34'N, longitude 89°15'W), and, for George Reserve, the nearest weather station was located approximately 29 km away in Ann Arbor, Michigan (latitude 42°17'N, longitude 83°42'W). Summed total precipitation was then subdivided into three categories, which were deemed important to body development of white-tailed deer at both latitudes. The first precipitation variable included total precipitation summed from October, the year prior to collection of deer, to September, the year of collection of deer (annual precipitation). The second variable included total precipitation summed from December–February prior to collection of deer (cold precipitation), and the final variable included total precipitation).

Density-dependent influences from abundance also were estimated for both sites. At Hatchie NWR, a hunter-harvest index was calculated using a ratio of the number of permits issued to hunters and the number of harvested deer for each year. Hunter-harvest indices are strongly correlated with actual abundance and are commonly used in studies of ungulates (Fryxell et al. 1991, Bowyer et al. 1999, Skalski et al. 2007). Hunter-harvest indices often are prone to statistical issues of temporal autocorrelation, because of changes in management strategies in response to population levels. Nevertheless, within

the 28-year study at Hatchie NWR, tests for autocorrelation within the hunter-harvest index demonstrated no statistically significant autocorrelation coefficients (P > 0.05). At George Reserve, total abundance was calculated by reconstructing the population using estimated ages from every known mortality event to assess the year of birth for each individual (McCullough 1979).

Statistical analyses

Because the purpose of this study was to test for differences in the duration of environmental influences on skeletal and somatic development of white-tailed deer between sites, a total of four separate model-selection analyses were conducted. Those analyses were necessary to individually test the influence of precipitation and abundance on two separate response variables (hind foot length and eviscerated body mass) at Hatchie NWR and George Reserve. For each model-selection analysis, the same 21 regressions were evaluated to assess the influence of precipitation and abundance on body development (see Supplemental 4.8. for predictor variables present in each regression for each model selection analysis). Because growth trajectories for skeletal and somatic development differ between sex and age in sexually dimorphic species (Weckerly 1998), all regressions that were developed included predictor variables that assessed the additive influence for sex and age as well as the multiplicative influence between sex and age, including the most reduced regression. The next four regressions that were developed assessed the additive influence of one added predictor variable (abundance and warm, cold, or annual precipitation). The next four regressions allowed the added predictors, listed previously, to have an additive influence as well as a multiplicative influence between the added predictor and sex, the added predictor and age,

and sex and age. Because density-dependent influences often are present in long-lived species, the remaining 12 regressions included abundance as a predictor variable while including one of the precipitation variables. In six of those models, the additive influence of abundance remained consistent while one of the precipitation variables was allowed to have an additive influence (three models) or an additive influence and multiplicative influence between the precipitation variable, sex, and age (three models). The final six regressions assessed both the additive influence of abundance and the multiplicative influence between abundance, sex, and age, as well as allowing one of the precipitation variables to have an additive influence (three models) or an additive influence and multiplicative influence between the precipitation variable, sex, and age, as well as allowing one of the precipitation variables to have an additive influence (three models) or an additive influence and multiplicative influence between the precipitation variable, sex, and age, as well as allowing one of the precipitation variables to have an additive influence (three models) or an additive influence and multiplicative influence between the precipitation variable, sex, and age (three models).

For each model selection analysis, the regression that best explained differences in the response variable was then selected with Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). Model averaging was conducted in the MuMIn package (version 1.10.5; Bartoń 2014) if competing models were <2 Δ AIC_c units different (Burnham and Anderson 2002). The initial model selection analysis for George Reserve indicated that precipitation for cold, warm, and annual time frames were influential in predicting eviscerated body mass. A summary of the averaged modeled demonstrated that 95% confidence intervals (CI) for all coefficient estimates during warm and cold precipitation periods encompassed zero. Because of this outcome, a reduced model-selection analysis was conducted, which removed models that included warm and cold precipitation as predictors, because those values were included within the annual precipitation factor. Inspection of residual plots for the most highly selected regression in each of the four model analyses demonstrated that the assumption of

homoscedasticity was met and that no data transformation was necessary. All statistical analyses were conducted in R version 3.0.2 (R Core Team 2013).

Results

During the study, 2,760 and 292 white-tailed deer were measured at Hatchie NWR and George Reserve over a 28- and 11-year period, respectively. At both locations, variation of hind foot length and eviscerated body mass was dependent on age and sex (Table 4.1). In each age and sex category, hind foot length was shorter and eviscerated body mass lighter at Hatchie NWR than at George Reserve. At both locations, environmental conditions were similar to historical averages. Total precipitation values were larger at Hatchie NWR seasonally and annually (Table 4.2). Abundance levels at Hatchie NWR were more stable throughout the study than at George Reserve (CV = 29%and CV = 40%, respectively).

Hind foot length

The model selection analysis for hind foot length at Hatchie NWR demonstrated that two regressions were competing for explaining variation in hind foot length (Table 4.3). A summary of the model-averaged coefficients indicated interdependencies between the factors for sex, age, and annual precipitation influenced length of the hind foot at Hatchie NWR (Table 4.4). On average, males were larger than females (Coefficient estimate = 41.3 ± 8.7 standard error, SE) and yearling and adults were larger than young (-42.0 ± 6.7). Nonetheless, yearlings and adults were similar in size to each other (6.0 ± 6.5), and the disparity in body size between young and adult age classes was more pronounced in males (-51.9 ± 11.4) than females. Annual precipitation had an overall positive influence on hind foot length (0.1 ± 0.03) , but this influence was minimally apparent in young (0.1 ± 0.05) and even less apparent in young males (0.2 ± 0.08) . Abundance of deer did not influence length of the hind foot at Hatchie NWR (-7.3 ± 6.3).

At George Reserve, a single regression was selected as the model that best explained variation in hind foot length, with warm precipitation and abundance influencing skeletal development additively (Table 4.5). On average, males were larger than females (34.3 ± 4.0) and adult deer were larger than young and yearlings (Young = – 55.3 ± 3.3 , Yearling = -9.3 ± 3.5). The disparity of hind foot length between the young and adult age class was greater in males than females (-23.0 ± 5.0) but not in yearlings (-7.7 ± 5.3). Warm precipitation had a positive influence and abundance a negative influence on hind foot length for all ages and sexes equally (0.2 ± 0.1 and -0.1 ± 0.03 , respectively).

Eviscerated body mass

Model selection analysis demonstrated that a single regression best explained variation in body mass at Hatchie NWR (Table 4.3). In this regression, the influence of annual precipitation and abundance on body mass was dependent on sex and age (Table 4.6). Similar to results for hind foot length, on average, males were heavier than females (32.9 ± 2.8) and yearlings and adults were larger than young (-17.3 ± 2.2) but not different from each other (-3.6 ± 2.2) . The disparity in body mass between young and adults as well as yearlings and adults was greater in males than in females (-35.6 ± 3.7) and -22.2 ± 3.5 , respectively). The influence of annual precipitation was dependent on sex and age. On average, males were more negatively influenced by precipitation than females (-0.07 ± 0.02) . This negative influence, however, was only present in adult

individuals with slope adjustments for young and yearlings of 0.1 ± 0.02 and 0.06 ± 0.02 , respectively. The influence of abundance on body mass also was dependent on sex and age at Hatchie NWR. Again, males were more strongly negatively influenced by abundance than were females (-18.5 ± 6.8), however, this negative influence was not present in young males (22.7 ± 9.7).

At George Reserve, the reduced model selection analysis demonstrated that two regressions were competing for explaining variation in body mass. A summary of the model-averaged coefficients indicated the interdependencies between the factors for sex, age, and abundance as well as the additive properties of annual precipitation influenced body mass (Table 4.7). On average, males were heavier than females (18.2 ± 6.2) and adults were heavier than young (18.4 ± 3.7) but not yearlings (-4.6 ± 2.9) . The disparity between young and adult body mass was greatest in males (-13.8 ± 6.1) . Annual precipitation negatively influenced each sex and age class equally (-0.04 ± 0.02) , and abundance negatively influenced males more than females (-0.1 ± 0.04) .

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Phenotypic trait			Male			Т	remale				Male				Femal	e
	и	X	sd	range	и	X	sd	range	и	X	sd	range	и	X	sd	range
Fawn hfl	368	370	21	263-449	363	360	18	315-421	70	437	19	387-475	59	426	17	368-465
Yearling hfl	882	440	18	371-490	340	416	17	337-470	51	499	15	469–533	44	473	18	407–506
Adult hfl	280	449	16	404-492	527	421	17	372–463	27	515	14	490–539	41	481	16	448–525
Fawn mass	368	20	4	9-44	363	17	4	7–33	70	29	9	16-54	59	26	4	18–37
Yearling mass	882	41	9	25–63	340	32	4	20–49	51	48	5	34–57	44	42	4	32-48
Adult mass	280	55	6	32-85	527	36	4	25–49	27	58	8	42–76	41	47	5	38–63

Table 4.1 Phenotypic traits of hind foot length (hfl, mm) and eviscerated body mass (mass, kg) from white-tailed deer collected

when the relate, brownsvin summed total precipitation (c) was indexed as a ratio betwee George Reserve is a count of	m) for cc m the nu the total	id une Edwold (Dec-Fe mber of hur population	m >. George eb), warm (N nter-issued p within the hi	e Reserve , Functurey , M far–Aug), and annual (O ermits and the number of igh-fenced reserve.	t, USA. ct–Sep) f harvest	riecipita time dur ed indiv	ations. Ab ations. Ab iduals per	expressed as ure undance at Hatchie year. Abundance at
Tootoe			Hatchie			Ð	eorge Res	erve
r actol	и	X	ps	range	и	X	bs	range
Cold precipitation	28	37.4	12.4	14.0-68.3	11	15.1	5.7	2.5-22.0
Warm precipitation	28	69.3	16.4	36.2-100.6	11	44.5	11.4	20.7-62.2
Annual precipitation	28	139.4	25.5	91.7–192.8	11	78.8	14.8	53.7-108.1
Abundance	28	0.228	0.061	0.064-0.318	11	102	41	13–167

Table 4.2 Summaries of density-dependent and -independent variables present during the study period at Hatchie National Wildlife Refuge. Brownsville. TN and the Edwin S. George Reserve. Pinckney, MI, USA, Precipitation was expressed as the

and abundance on hind foot length an Brownsville, TN (Hatchie) and the Ec the parentheses were sex, age, and the i included in all models and environment variable or allowed an additive and mul	nd body mass of white-tailed deer collected dwin S. George Reserve, Pinckney, MI (Geo nteraction between sex and age. The additive cal and abundance variables were allowed to h ltiplicative influence (*) with sex and age on t	d at Ha eorge R e and m have ad the resj	tchie Natio (eserve). Pr ultiplicativo lditive influ ponse varia	edictor var edictor var e effects of ences (+) c ble.	ife Refuge, iables denc sex and ag on the respo	ted within e were onse
Model selection response variable	Predictors	K	AIC _e	ΔAIC_c	weight	R^{2}
	() * Annual precip	13	23715.2	0	0.31	0.76
Hatchie hind toot length	() * Annual precip + Abundance	14	23715.9	0.7	0.22	0.76
George Reserve hind foot length	() + Warm precip + Abundance	6	2469.9	0	0.69	0.79
Hatchie body mass	() * Annual precip + () * Abundance	19	16879.9	0	0.83	0.83
	() * Abundance + Annual precip	14	1771.3	0	0.38	0.84
Ucuige reserve boury lilass	() + Annual precip + Abundance	6	1772.3	1	0.23	0.83

Table 4.3 Model selection table for the regression or regressions within AAIC_c <2.0 used to assess the influence of precipitation

Table 4.4 Model-averaged coefficient estimates for hind foot length of white-tailed deer at Hatchie National Wildlife Refuge, Brownsville, TN, USA collected across 28 years. Headers denote coefficients used in the regression (Coefficient), as well as the estimate (Estimate), standard error (SE), and confidence interval (CI) for each coefficient. Predictor variables within the selected regression included sex, age, precipitation, and abundance. Female was the reference category for sex and males are presented as a parameter (SexM). Adult was the reference category fawn (AgeF) and yearling (AgeY) were parameters for age. Precipitation (AnnualPrecip) was treated as an integer and consisted of summed monthly total precipitation values from October prior to deer collection to September during the year of deer collection. Abundance was treated as an integer and was derived from a ratio between the number of permits issued within a year and the number of deer harvested. Coefficients with a colon denote an interaction between coefficients.

Coefficient	Estimate	SE	Lower 95% CI	Upper 95% CI
(Intercept)	411.354	4.471	402.587	420.122
SexM	41.27	8.673	24.263	58.276
AgeF	-42.026	6.673	-55.111	-28.941
AgeY	5.954	6.532	-6.854	18.762
AnnualPrecip	0.072	0.03	0.014	0.131
AgeF:SexM	-51.888	11.397	-74.236	-29.540
AgeY:SexM	-15.544	10.515	-36.161	5.074
SexM:AnnualPrecip	-0.091	0.06	-0.208	0.027
AgeF:AnnualPrecip	-0.133	0.047	-0.224	-0.042
AgeY:AnnualPrecip	-0.078	0.045	-0.167	0.011
AgeF:SexM:AnnualPrecip	0.235	0.079	0.08	0.391
AgeY:SexM:AnnualPrecip	0.079	0.073	-0.064	0.222
Abundance	-7.261	6.28	-19.575	5.052

Table 4.5 Coefficient estimates for hind foot length of white-tailed deer at the Edwin S. George Reserve, Pinckney, MI, USA collected across 11 years. Headers denote coefficients used in the regression (Coefficient), as well as the estimate (Estimate), standard error (SE), and confidence interval (CI) for each coefficient. Predictor variables within the selected regression included sex, age, precipitation, and abundance. Female was the reference category for sex and males are presented as a parameter (SexM). Adult was the reference category fawn (AgeF) and yearling (AgeY) were parameters for age. Precipitation (WarmPrecip) was treated as an integer and consisted of summed monthly total precipitation values from March–August prior to deer collection. Abundance was treated as an integer and was derived from a ratio between the number of permits issued within a year and the number of deer harvested. Coefficients with a colon denote an interaction between coefficients.

Coefficient	Estimate	SE	Lower 95% CI	Upper 95% CI
(Intercept)	485.97	5.681	474.788	497.153
SexM	34.295	4.049	26.325	42.266
AgeF	-55.292	3.32	-61.828	-48.757
AgeY	-9.291	3.547	-16.272	-2.309
WarmPrecip	0.201	0.083	0.039	0.364
Abundance	-0.127	0.033	-0.193	-0.062
AgeF:SexM	-23.001	4.981	-32.805	-13.198
AgeY:SexM	-7.688	5.257	-18.035	2.658

Table 4.6 Coefficient estimates for body mass of white-tailed deer at Hatchie National Wildlife Refuge, Brownsville, TN, USA, collected across 28 years. Headers denote coefficients used in the regression (Coefficient), as well as the estimate (Estimate), standard error (SE), and confidence interval (CI) for each coefficient. Predictor variables within the selected regression included sex, age, precipitation, and abundance. Female was the reference category for sex and males are presented as a parameter (SexM). Adult was the reference category fawn (AgeF) and yearling (AgeY) were parameters for age. Precipitation (AnnualPrecip) was treated as an integer and consisted of summed monthly total precipitation values from October prior to deer collection to September during the year of deer collection. Abundance was treated as an integer and was derived from a ratio between the number of permits issued within a year and the number of deer harvested. Coefficients with a colon denote an interaction between coefficients.

Coefficient	Estimate	SE	Lower 95% CI	Upper 95% CI
(Intercept)	38.506	1.464	35.637	41.376
SexM	32.944	2.845	27.365	38.523
AgeF	-17.299	2.191	-21.596	-13.002
AgeY	-3.552	2.176	-7.819	0.714
AnnualPrecip	-0.004	0.009	-0.021	0.013
Abundance	-6.265	4.242	-14.581	2.052
AgeF:SexM	-35.592	3.734	-42.914	-28.271
AgeY:SexM	-22.210	3.458	-28.989	-15.430
SexM:AnnualPrecip	-0.071	0.017	-0.105	-0.037
AgeF:AnnualPrecip	-0.014	0.014	-0.042	0.013
AgeY:AnnualPrecip	-0.012	0.014	-0.038	0.015
SexM:Abundance	-18.508	6.767	-31.777	-5.239
AgeF:Abundance	0.823	6.697	-12.308	13.954
AgeY:Abundance	1.328	6.794	-11.994	14.649
AgeF:SexM:AnnualPrecip	0.098	0.023	0.052	0.144
AgeY:SexM:AnnualPrecip	0.063	0.021	0.021	0.105
AgeF:SexM:Abundance	22.726	9.721	3.665	41.787
AgeY:SexM:Abundance	17.363	9.208	-0.692	35.418

Table 4.7 Model-averaged coefficient estimates for body mass of white-tailed deer at the Edwin S. George Reserve, Pinckney, MI, USA collected across 11 years. Headers denote coefficients used in the regression (Coefficient), as well as the estimate (Estimate), standard error (SE), and confidence interval (CI) for each coefficient. Predictor variables within the selected regression included sex, age, precipitation, and abundance. Female was the reference category for sex and males are presented as a parameter (SexM). Adult was the reference category fawn (AgeF) and yearling (AgeY) were parameters for age. Precipitation (AnnualPrecip) was treated as an integer and consisted of summed monthly total precipitation values from October prior to deer collection to September during the year of deer collection. Abundance was treated as an integer and was derived from a ratio between the number of permits issued within a year and the number of deer harvested. Coefficients with a colon denote an interaction between coefficients.

Coefficient	Estimate	SE	Lower 95% CI	Upper 95% CI
(Intercept)	52.749	3.295	46.275	59.222
SexM	18.213	6.162	6.114	30.312
AgeF	-18.400	3.717	-25.708	-11.092
AgeY	-4.591	2.946	-10.389	1.206
Abundance	-0.021	0.027	-0.074	0.032
AnnualPrecip	-0.044	0.019	-0.082	-0.006
AgeF:SexM	-13.804	6.112	-25.822	-1.786
AgeY:SexM	-7.087	4.952	-16.831	2.657
SexM:Abundance	-0.088	0.041	-0.168	-0.008
AgeF:Abundance	-0.036	0.036	-0.106	0.034
AgeY:Abundance	-0.009	0.032	-0.072	0.053
AgeF:SexM:Abundance	0.056	0.058	-0.058	0.17
AgeY:SexM:Abundance	0.023	0.051	-0.077	0.124

Discussion

Skeletal and somatic development in ungulates is influenced by densitydependent and -independent factors, which limit nutritional quality and quantity available to individuals within a population. Because of phenotypic plasticity and adaptability to local environments, we hypothesized that body development of white-tailed deer would respond to the same environmental factor at different durations of time depending on the latitude of the population. Specifically, we predicted that annual measures of abundance would negatively influence skeletal and somatic development at both sites. Our results support this prediction, and we note that the strength of the influence can be dependent on age and sex of the individual. We also predicted that body development of ungulates should be influenced by the same environmental influences at different durations of time depending on the latitude. Our results provide evidence that supports this prediction regarding skeletal development, which ceases rather than decreases when nutritional resources are limited. We demonstrated that skeletal development at George Reserve was most strongly influenced by total precipitation during the warm period of March-August, while Hatchie NWR was most strongly influenced by total annual precipitation. Our final prediction was that measures of skeletal and somatic development could be influenced by the same density-independent factor at different time durations. Our results indicated that skeletal development at George Reserve was most strongly influenced by total precipitation in warm months, and somatic development most strongly influenced by total precipitation throughout the year.

Seasonal cycles in body development are created by endogenous responses to photoperiod and changes in environmental conditions during cold weather, which reduce
metabolic activity and limit available nutritional resources (Ullrey et al. 1970). If nutritional restriction occurs during body development, seasonal cycles in growth can impact individuals throughout their lifetime. To compensate for missed growth, growth rates may be increased above optimal levels through compensatory growth, or the growth period may be extended through catch-up growth. At high latitudes, harsh winter conditions enforce a seasonal cycle of body development; thus, compensatory growth is the most probable mechanism for high-latitude ungulates. Nonetheless, this mechanism of compensation is energetically costly and creates many fitness consequences of its own (Metcalfe and Monaghan 2003, Mangel and Munch 2005). Because of this, full compensation has rarely been reported and cohort effects are considered pervasive in ungulate populations. At low latitudes, however, maintenance costs are reduced in ungulates as an adaptive response to intra-annual environmental stochasticity (Strickland et al. 2005). Lower maintenance costs, paired with winter conditions that are often suitable to sustain nutritional resources necessary for body development, allows for the possibility of extending the period of growth through catch-up growth at low latitudes. Indeed, our findings demonstrated that catch-up growth is the most reasonable mechanism for compensation in low-latitude ungulates. The divergence in duration of environmental influences on skeletal development between study sites demonstrates that, given winter conditions amenable to body development, the growth period can be extended at Hatchie NWR.

Hind foot length is a skeletal feature that is not readily remobilized when maintenance costs exceed energy intake. During nutritional restriction, skeletal growth ceases until intake of metabolizable energy and other nutrients exceeds maintenance

requirements. Because of this, hind foot length should be influenced most strongly when nutritional resources are available. At Hatchie NWR, annual precipitation affected hind foot length with influence varying by sex and age. This result indicates that skeletal development probably occurs throughout the year at Hatchie NWR but is limited in some years when winter months are harsh and available nutrition is restricted. At George Reserve, the warm-weather months of March-August positively influenced hind foot length. In those months, the interaction between warming temperature and precipitation stimulate plant productivity and increase quantity and quality of nutritional resources available to individuals. The harsh winter conditions at George Reserve likely create an environment in which growth of hind foot length ceased in nearly every year of our study. Hind foot length was dependent on the environmental conditions during the warmweather months because growth ceased in the cold-weather months. Thus, if environmental conditions are poor during the warm-weather months, development of hind foot length will be reduced, with no possible compensation during the cold-weather months.

Body mass is influenced by density-dependent and -independent factors that limit nutritional quantity and quality throughout the year. There has been a considerable amount of discussion related to whether summer or winter range is the most limiting season in lifetime development of body mass (Ryg and Langvatn 1982, Suttie and Hamilton 1983, Regelin et al. 1985, Sæther et al. 1996). Our findings indicated that positive and negative influences from environmental variation throughout the year combined to affect body mass of white-tailed deer. This outcome occurred because somatic tissues (e.g., muscle or fat mass) can be readily synthesized or remobilized to

meet the necessary energy requirements throughout the year. Annual precipitation negatively influenced most age and sex classes at both sites, whereas Wolcott et al. (2014) reported a positive relationship between annual precipitation and body mass in southern mule deer (*Odocoileus hemionus fuliginatus*). This result is probably because differences in the mesic conditions at the two current study sites and the more xeric condition in the previous study. The negative influence on body mass is most likely because of precipitation events increasing thermoregulatory and locomotor expenses of deer during cold-weather months (Post et al. 1997). Indeed, annual precipitation was correlated with the 3 months of cold-weather precipitation at both sites (Hatchie NWR R^2 = 0.70, George Reserve R^2 = 0.69). This result demonstrates that increased precipitation during the cold months limits physiological processes in these deer which, ultimately, effects body mass throughout the year. Abundance at both locations negatively influenced body mass through intraspecific competition. Abundance at George Reserve influenced body mass more strongly than at Hatchie NWR. This outcome probably occurred because of the wide range in abundances at George Reserve during the study.

Although it may seem counterintuitive that hind foot length and body mass at George Reserve were influenced by precipitation across different durations of time, the relationship between body mass and skeletal growth reveals that this seeming discrepancy is possible. Body mass is influenced by environmental variables throughout the year because deposition and depletion of somatic and adipose tissue is labile. While body mass can vary intra-annually, asymptotic body mass is, ultimately, dependent on skeletal size. Because skeletal development was limited to the warm months at George Reserve, stochastic environmental events during the period of growth can lead to cohort

effects in skeletal development. Hence, somatic development can still fluctuate intraannually, but asymptotic mass will, ultimately, depend on asymptotic skeletal size.

Ideally, a large number of sites would be beneficial when assessing differences in body development across latitudes. Nonetheless, long-term datasets measuring the influence of the environment on skeletal and somatic development across several age classes are exceedingly rare. Further, as the disparity between latitudes increases, differences in ecological factors like ecosystem responses to precipitation (e.g., differences in mesic and xeric environments) and net primary productivity also increase. Hatchie NWR and George Reserve provide a good representation of a latitudinal difference while still maintaining ecosystem processes common in mesic and temperate environments. We anticipate that further increases in latitudinal differences would yield similar results; however, seasonal restrictions in plant phenology would most likely further reduce duration of body development at higher latitudes. Thus, shorter time intervals for assessing the influence of environmental variables on body development would be necessary, with probability of cohort effects becoming more likely.

Ungulates comprise a highly diverse set of species that are longitudinally and latitudinally widespread. When studying these species, it is common to make broad generalization into their ecology. Although generalizations often are necessary to test patterns of body development on a global scale, wildlife managers often use these generalizations to make management decisions on local populations. Our study demonstrates that there are considerable intraspecific differences in development depending on localized conditions. Because of this result, more research is needed to assess the influences of environmental variables on body development across a wide

range of latitudes to properly address the developmental characteristics of those economically important species. In light of how current trends in the global climate influence high-latitude ungulates (e.g., trophic mismatch), there is a pressing need to assess how trends will affect low-latitude ungulates as well.

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Supplemental Table 4.8 Summary of 21 regressions considered in four separate model selection analyses assessing the influence of density-dependent and - independent factors on two response variables (hind foot length and eviscerated body mass) of white-tailed deer at two locations (Hatchie National Wildlife Refuge, Brownsville, TN and the Edwin S. George Reserve, Pinckney, MI). Header denotes predictors within the regressions selected for the 4 model selection analyses (Predictors) and number of parameters within each regression (K). Predictor variables within the parentheses include sex, age, and the interaction between sex and age. Additive influences of predictor variables are denoted by (+) and both additive and multiplicative influences are denoted by (*). Precipitation was treated as an integer and consisted of summed monthly total precipitation values for three separate time durations: October prior to deer collection to September during the year of deer collection (Annual precipitation), March–August prior to deer collection (Warm precipitation), or December–February (Cold precipitation).

Predictors	K
(Sex * Age)	7
() * Abundance	8
() + Abundance	13
() + Annual precipitation	8
() + Annual precipitation + Abundance	9
() * Annual precipitation	13
() * Abundance + Annual precipitation	14
() * Annual precipitation + Abundance	14
() * Annual precipitation + () * Abundance	19
() + Cold precipitation	8
() + Cold precipitation + Abundance	9
() * Cold precipitation	13
() * Abundance + Cold precipitation	14
() * Cold precipitation + Abundance	14
() * Cold precipitation + () * Abundance	19
() + Warm precipitation	8
() + Warm precipitation + Abundance	9
() * Warm precipitation	13
() * Abundance + Warm precipitation	14
() * Warm precipitation + Abundance	14
() * Warm precipitation + () * Abundance	19

CHAPTER V

CONCLUSIONS

This dissertation provided new insights into variation of life-history and phenotypic traits in two species of ungulates. This work extended current theory related to biological and environmental influences on body development of long-lived ungulates and increased our knowledge of ungulate development from birth and into adulthood in variable environments. Much of the current theory in regards to ungulate body development has shown that seasonal metabolic and reproductive processes are largely dictated by responses to photoperiod. At high latitudes, photoperiodism is correlated with seasonal variations in plant phenology. Because of this relationship, ungulates at high latitudes have adapted developmental responses to photoperiod. In light of current climate trends, however, high latitude climates are becoming more heterogeneous and correlations between photoperiod and plant phenology are decreasing. There is now considerable concern with how ungulates will adapt to changing environmental conditions and more research is needed on ungulate populations that have already adapted to heterogeneous environmental conditions.

The purpose of this dissertation was to assess influences on body development of ungulates at multiple life stages in variable environments. The focus of Chapter II was on the natal life stage. Timing of parturition and birth mass is crucial for early-life survival of ungulates. Chapter II provided unique insights into environmental influences that affect timing of parturition and birth mass while controlling for known biological influences. Linear and quadratic functions of maternal age influenced both natal features

with earliest Julian birth dates and heaviest birth masses occurring at prime-age and older individuals, which ranged from 5–9 years of age. Litter type influenced Julian birth date and birth mass. Interestingly, environmental factors affected Julian birth date and birth mass even though mothers were continuously allowed access to a high-quality diet. Random effects revealed considerable variation among mothers and years. This chapter demonstrated that environmental factors might have a greater influence on natal features than previously supposed. The documented responses to environmental influences in this chapter provided unique insights into how mammalian seasonal reproductive dynamics may respond to current changes in climate.

In ungulates, probability of recruitment into the population increases after the first 6 months -of- life. After recruitment, body size is still an important factor in determining lifetime fitness. Current theory indicates that cohort variation in body size is common in ungulates. Cohort effects are because of biotic and abiotic influences affecting body development of fawns, population wide, by limiting availability of nutrition. Moreover, cohort effects are thought to become pervasive at high latitudes because harsh winter conditions limit body development to particular periods within a year, thereby reducing the ability to compensate for periods of missed growth. Chapter III assessed short- and long-term influences of biotic and abiotic factors on body mass of southern mule deer (*Odocoileus hemionus fuliginatus*) in an environment with mild winter conditions. This chapter determined that eviscerated body mass of southern mule deer was affected by precipitation and relative abundance within the period of a year. This research also demonstrated that mule deer were able to compensate for periods of missed growth

2.5 years of age. These findings demonstrate that our current knowledge of body development in ungulates is limited and that more work is necessary to fully understand developmental dynamics of localized populations in these widely distributed species.

Although Chapter III demonstrated that ungulate populations are able to overcome cohort effects, given the proper environmental conditions, the mechanism for this compensation was unknown. Possible mechanisms for compensation can include an increase above optimal growth rate (compensatory growth) or an extension of the growth period (catch-up growth). Chapter IV used two long-term datasets to assess differences in duration of environmental influences on body development (skeletal size and body mass) at two different latitudes with similar primary productivity and different winter conditions. This study demonstrated differences in duration of environmental influence on skeletal development between sites but not for somatic development. Skeletal development at the high-latitude site was limited to precipitation in the warm-weather months (March-August) while annual precipitation explained the most variation in skeletal development at the low-latitude site. Somatic development was most strongly influenced by annual precipitation at both sites. These findings indicate that, deer at the low-latitude site are able to extend the period of growth, through catch-up growth, when winter conditions are amenable rather than exceeding optimal growth rates through compensatory growth to overcome cohort effects.

Ungulate species comprise a set of widely distributed species that are both biologically and economically important. Because of this, a considerable amount of research has been conducted in order to properly manage them. The findings from this dissertation highlight several important items that must be considered to continue proper

conservation and management of these species. These species are adapted to local conditions and, therefore, decisions regarding the conservation and management of these species are context dependent. Management decisions must be made with the consideration that developmental responses within a target population may not follow trajectories currently presented in the literature. More emphasis must be placed on establishing, maintaining, and analyzing the collection of data from these often-harvested species across entire distributional ranges. In light of current trends in global climate, this dissertation has added new insights into how ungulate populations may adapt to increasing interannual heterogeneity in environmental conditions and provides valuable information for the continued conservation and management of these species.