

FACTORS INFLUENCING SCALING RELATIONSHIPS OF BODY MASS AND
ANTLER MASS IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

by

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TABLE OF CONTENTS

	Page
AKNOWLEDGEMENTS.....	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT.....	viii
CHAPTER	
I. FACTORS INFLUENCING SCALING RELATIONSHIPS BETWEEN BODY MASS AND ANTLER MASS IN WHITE-TAILED DEER (<i>Odocoileus virginianus</i>)	1
Introduction.....	1
Materials and Methods	5
Study Area	5
Data Collection	6
Diet	6
Statistical Analyses.....	7
Results	8
Discussion	11
APPENDIX SECTION.....	23
LITERATURE CITED	24

LIST OF TABLES

Table	Page
1. Sample sizes, means, and ranges of body mass and antler mass at each age, diet, and litter type (singleton, multiple) of male white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 2012–2021.....	17
2. Ontogenetic scaling relationship parameter estimates.....	18
3. Bayesian Information Criterion (BIC) model selection analysis.....	19
4. Static scaling relationships parameter estimates.....	20

LIST OF FIGURES

Figure	Page
1. Predicted regressions summarizing relationships between body mass and antler mass for male white-tailed deer fed either a low energy diet (L) or standard energy diet (S) at Kerr Wildlife Management Area, Texas, USA.....	21
2. Predicted regression lines summarizing the relationship between body mass and antler mass for male white-tailed deer aged 1.5 years fed either a low energy diet (L) or standard energy diet (S) and born to either a multiples or singleton litter at Kerr Wildlife Management Area, Texas, USA.....	22

ABSTRACT

Antlers are a costly trait that require skeletal reserves to grow to a large size. Thus, insight into variation in antler size requires understanding the connection between antler and body size, which can be summarized through ontogenetic and static scaling relationships. Both types of scaling relationships are needed to examine the influence of factors besides body mass on antler growth at different ages and whether the influence of these factors diminish with age. Size deficits influenced by diet variability and maternal effects might decline during ontogeny through compensatory growth. I sought insight into the influences of diet and maternal attributes of mother's age at birth of offspring and litter size on body-antler size relationships throughout ontogeny and at discrete ages. I also examined whether diet and maternal effects diminished with age of males. Data on age, maternal characteristics, body mass, and antler mass was gathered from captive, pen-raised white-tailed deer (*Odocoileus virginianus*, $n = 168$) that consumed either a low energy (1.77 kcal/gm) or standard energy diet (2.65 kcal/gm) from the time they were weaned until they died by age 5.5 years of age. Both types of scaling relationships were estimated with linear mixed effects models to account for repeated measurements of focal males and parents. Diet affected ontogenetic scaling relationships. Males consuming the low energy diet had a higher rate of increase in antler mass in relation to body mass when young and a lower rate of increase rate when old than males consuming the standard energy diet. A Bayesian Information Criterion model selection analysis indicated that diet and litter size (singleton or multiple births), but not mother's age at birth of offspring

influenced static scaling relationships. Static scalar coefficients up to 3.5 years of age were positively allometric, but isometric in 4.5- and 5.5-year-old-males. Furthermore, diet and litter type influenced both intercepts and slopes in only the youngest males (1.5-years) lending support to the idea that diet and maternal effects diminish with age. Body size – antler size relationships are complex. My findings indicate that diet and litter type had greater effect at younger ages during rapid growth than at older ages. Young males that are small because of maternal effects, for example, might still be able to possess larger body and antler sizes at older ages.

I. FACTORS INFLUENCING SCALING RELATIONSHIPS OF BODY AND ANTLER MASS IN WHITE-TAILED DEER

(ODOCOILEUS VIRGINIANUS)

Introduction

Secondary sexual characteristics like antlers provide an honest signal of phenotypic quality both to potential mates and rivals (Ditchkoff et al. 2001, Malo et al. 2005, Morina et al. 2018). As such, antlers are a handicap or costly to produce because much calcium and phosphorous is mobilized from skeletal tissue (Zahavi 1975, Ullrey 1982, Bubenik 1983, Gómez et al. 2012). Sufficient skeletal reserves are required to produce large antlers, which, in turn, requires a large body size (Ullrey 1982, Bubenik 1983, Landete-Castillejos et al. 2007, Gómez et al. 2012, Landete-Castillejos et al. 2019). Thus, insight into variation in antler size requires understanding the connection between antler and body size.

Scaling relationships can illuminate the degree to which organisms invest in sexually selected traits, such as antler size in relation to body size. Often scaling relationships are estimated when predictor (X) and response variable (Y) are naturally log transformed to linearize a possible nonlinear relationship. The log-transformed version of a scaling relationship is:

$$\ln(Y) = a + b * \ln(X), \quad 1$$

which can be back-transformed to the power function:

$$Y = aX^b \quad 2$$

The scalar, b , estimates change in response variable (Y) brought about by changes in the predictor (X). The scalar of body mass - antler mass relationships is usually > 1.0 or positive allometric (Gould 1974, Clutton-Brock et al. 1980, Plard et al. 2011, Lemaître et al. 2014, Tidière et al. 2017, Tidière et al. 2020). A positive allometric relationship between body size and antler size is expected when antler size is an honest signal of male quality.

There are numerous studies estimating interspecific body size - antler size scaling relationships, but relatively few intra-specific studies (Stewart et al. 2000, Ungerfeld et al. 2011, Melnycky et al. 2013, Jones et al. 2018). Intra-specific studies are needed to examine how an attribute develops from young to old age (Pélabon et al. 2013). Two types of intra-specific scaling relationships are ontogenetic and static (Gould 1966). Ontogenetic scaling relationships are estimated from data collected throughout an individual's life usually at discrete moments in time or age (e.g. age 1, 2, 3, so on). For antlers, ontogenetic scaling relationships are useful because they can reveal changes in growth rate in relation to body size and examine how antler growth might be affected by environmental factors like diet (Stewart et al. 2000, Lemaître et al. 2014, Tidière et al. 2017, Jones et al. 2018). The simple power function does not always fully characterize ontogenetic scaling relationships for long-lived species (Pélabon et al. 2013). For example, if growth rate changes as an individual ages, then a relationship with a quadratic term is needed to summarize the relationship:

$$\ln(Y) = a + b * \ln(X) + c * \ln(X)^2. \quad 3$$

Static scaling relationships estimate scaling relationships at particular ages or age classes (Huxley 1931, Ungerfeld et al. 2008, Plard et al. 2011, Ungerfeld et al. 2011,

Melnycky et al. 2013, Lemaître et al. 2014). Static scaling relationships are useful to determine if the scalar b in equation 2 changes with age. Static relationships can also be used to reveal whether environmental or maternal attributes are influential, and whether they change or diminish with age.

The impact of dietary nutrition on antler growth has been extensively studied in cervids. White-tailed deer that are fed a low energy diet have both reduced body and antler size compared with deer that are fed a higher energy diet (Jones et al. 2010, Spilinek et al. 2020). Males foraging on a high quality or digestible diet will increase antler allocation in 2.5 - 4.5 year-olds compared with deer on a low quality diet (Jones et al. 2018). Restricted intake of protein, energy, and calcium in 1.5 year-old white-tailed deer resulted in reduction of antler volume, beam diameter, main beam length, and number of tines (Ullrey 1982). McCullough and Smith (1991) showed that for male mule deer (*O. hemionus*) on the Kaibab Plateau the average number of points is strongly and positively correlated to the amount of winter rainfall and the cumulative rainfall from the previous two to three years.

Maternal effects are the influences of the mother's phenotype on the offspring phenotype (Wolf and Wade 2009). Female cervids in good nutritional condition likely are able to invest more in offspring during gestation than females in poor nutritional condition (Sams et al. 1996). Well-nourished mothers produce offspring that are heavier at birth (Smith 1987, Mech et al. 1991, Keech et al. 2000, Bårdsen et al. 2009, Monteith et al. 2009, Michel et al. 2019), have higher juvenile survival (Keech et al. 2000), and male offspring possess larger antlers (Monteith et al. 2009, Freeman et al. 2013). Also, offspring born to older mothers tend to be heavier and have increased survival rates than

younger mothers (Clutton-Brock 1984, Ozoga and Verme 1986, Verme 1989, Bårdsen et al. 2009, Wolcott et al. 2015). Litter size, another maternal effect, might also affect offspring. In Alaskan Moose (*Alces alces gigas*) litter size was inversely related to offspring survival to 1 year of age and offspring survival was positively related to birth mass (Keech et al. 2000). Wolcott et al. (2015) showed that variation in litter size and sexual composition, or litter type, influenced birth mass in white-tailed deer. White-tailed deer males born in singleton litters were heavier than males born to twin male or mixed-sex litters (Wolcott et al. 2015).

Maternal effects that result in body size variation in offspring are likely to decrease after birth (Verme 1962, Dale et al. 2008, Wolcott et al. 2014). Because antler size is coupled to body size, maternal effects on antler size might also diminish with age. There are, however, few studies that directly address whether effects from maternal attributes on antler growth diminish with age (Demarais and Strickland 2011) .

I estimated intra-specific scaling relationships between body mass and antler mass in captive, pen-raised white-tailed deer (*Odocoileus virginianus*) that were assigned to either a low energy (1.77 kcal/gm) or standard energy diet (2.65 kcal/gm) from the time they were weaned (Spilinek et al. 2020). I investigated the influence of diet and maternal effects on the scaling relationship between body mass and antler mass through both ontogenetic and static scaling relationships. I hypothesized that:

- 1) antler growth rate would decline with larger body size,
- 2) males on the low energy diet would have slower antler growth than males on the standard energy diet,

- 3) maternal attributes of mother's age at birth of offspring (MaB) and litter type influence antler growth,
- 4) and maternal effects from MaB and litter type will be apparent in younger-aged males and diminished in older-aged males.

To my knowledge this is the first study to examine how an environmental factor such as diet and maternal effects influence the relationship between body size and antler size.

Thus, providing a more realistic picture of how multiple factors might influence allometry of antler size.

Materials and Methods

Study Area

My study area was the Donnie E. Harmel White-tailed Deer Research Facility deer pens (hereafter Kerr pens) at Kerr Wildlife Management Area (Kerr WMA) in Kerr County, Texas, USA. Annual precipitation was 80 cm (Luna et al. 2012). Daytime temperatures in summer could reach 35 °C with moderate winter temperatures averaging 16 °C (Parra et al. 2014). The research facility consisted of five to seven rearing pens and three to eight breeding pens that were each 1.2, 3, or 4 ha in size and surrounded by a 2.7 m high game fence (Wolcott et al. 2015). The pens included bare ground, some ground vegetation, and live oak (*Quercus virginiana* Mill.) that provided 25%–50% canopy cover (Lockwood et al. 2007). Prevalent ground species were common horehound (*Marrubium vulgare* L.) and cowpen daisy (*Verbesina encelioides* (Cav.) Benth. & Hook. f. ex A. Gray). Notably, leaves of live oak trees have been browsed out of reach of white-tailed deer since 1974, and ground vegetation was unpalatable to deer (Wolcott et al.

2015). Consequently, vegetation in the pens was not a substantial part of the food available for deer.

Data Collection

The dataset consisted of four cohorts of male white-tailed deer from the Kerr WMA that were born in 2012, 2013, 2014, and 2016. Cohort sizes for 2012, 2013, 2014, and 2016 were 40, 58, 55, and 17 male white-tailed deer, respectively, for a total of 170 animals. The age of individuals was known because they were uniquely marked at birth. Also, the mother and father were known for every male as well MaB. For each cohort, the following morphological data were collected annually in October: left main beam length, right main beam length, Boone and Crockett score, left antler mass, right antler mass, and body mass. Lengths were recorded to the nearest mm and masses to the nearest tenth of a kg. I used antler mass as the measurement of antler size. I used antler mass as the response variable because antler mass was strongly correlated to Boone and Crockett score, total main beam length, left main beam length, and right main beam length (Supplementary Material, Table 2). Data collection began for all deer at age 1.5 years and ended at age 5.5 years, when deer were culled, or earlier if the male perished.

Diet

Males were fed ad libitum one of two kinds of pelleted feed from the time they were weaned until they perished. The diets differed in digestible energy (DE), low energy pellets had 1.77 kcal/g of DE and standard energy pellets had 2.65 kcal/g of DE (Spilinek et al. 2020). The standard energy diet was labeled as such to remain consistent with Spilinek et al. (2020). Each week pelleted diets were supplemented with a 1 kg mix of alfalfa and straw, per deer, to provide roughage to maintain rumen function (Spilinek et

al. 2020). Parents of the 2012, 2013, and 2014 cohort were not fed a specific diet. However, parents of the 2016 cohort were fed either a standard- or low-energy diet.

Statistical Analyses

The ontogenetic relationship was estimated with a linear-mixed effects model because males were repeatedly measured, and some males had the same mother or father. To estimate the ontogenetic relationship and assess if the relationship differed between diets the fixed effects model was: $\ln(\text{AM}) = \beta_0 + \beta_1 \ln(\text{BM}) + \beta_2 (\text{E}) + \beta_3 \ln(\text{BM})^2 + \beta_4 \ln(\text{BM}) * \text{E} + \beta_5 \ln(\text{BM})^2 * \text{E} + \varepsilon$, where AM is antler mass, BM is body mass, E is dietary energy, and ε is residual variation. The reference category was low energy, and coefficients β_2 , β_4 , and β_5 assessed if the intercept (β_0), linear slope (β_1), or quadratic term (β_3) differed between diets. There were three random factors, individual male, their mothers, and their fathers. Each random factor was modeled with a random intercept. For each fixed and random effects 95% confidence intervals were estimated from 1000 simulations of a parametric bootstrap.

Static scaling relationships were estimated using linear mixed effects models at one-year increments between 1.5 and 5.5 years of age. The random factor was mother, and it was modeled as an intercepts random effect. As the yearling age class (1.5 years) had the largest sample size I estimated eight models and conducted a Bayesian Information Criterion (BIC) model selection to assess whether diet, MaB, and litter type influenced static scaling relationships of yearlings (Schwarz 1978). Every model assessed if diet, MaB, and litter type influenced intercept and slope scaling relationships. I categorized litter type into three ways to assess whether categorization of litter type influenced static scaling relationships. The three litter types were Lit5, Litstwr, and

Litsm. The litter type Lit5 included five categories: singletons male, twins mixed sex, twins males, twins where the other sibling died before weaning, and triplets. The three categories for Litstwtr were: singleton, twins, and triplets. The two categories for Litsm lumped litter type into either singleton male or multiple births. All models for the BIC model selection analysis were estimated with maximum likelihood estimation but parameter estimates of mixed effects models were estimated using restricted maximum likelihood estimation (Wolcott et al. 2015). Because there were repeated observations for some mothers, sample sizes for calculating BIC values was the number of mothers (Jones 2011). My findings from the model selection analysis of yearlings were then used to model static relationships at 2.5, 3.5, 4.5, and 5.5 years of age as long as sample sizes permitted (≥ 5). The selected model was decomposed to estimate scalars and relationships for each combination of factors (e.g., diet and Litsm). For males aged 4.5 years the linear mixed effects model did not converge. Thus, two least-squares regressions were estimated, one with one predictor (ln-body mass) and the second with an interaction between ln-body mass and diet. A nested models analysis indicated that the simple linear regression with only log-body mass as a predictor was sufficient ($F_{2,67} = 0.90$, $P = 0.413$). For deer aged 5.5 years there were insufficient sample sizes for litter type and diet. All mixed effects models were estimated in the lme4 package of the R 3.6.0 platform (Team 2010).

Results

Sample sizes, means, and ranges of body mass and antler mass at each age, diet, and litter type are in Table 1. The dataset comprised 295 deer fed a low energy diet and 265 deer fed a standard energy diet. The span of ages that data was collected from focal males (and percentage of the data) were: 1.5 years – 13%, 1.5 to 2.5 years – 17%, 1.5 to

3.5 years – 17%, 1.5 to 4.5 years – 27%, and 1.5 to 5.5 years – 27%. Males on the low energy diet ranged in body mass from 28.58 to 92.08 kg and males on the standard energy diet ranged in body mass from 37.65 to 106.59 kg. Antler mass for males on the low energy diet ranged from 0.001 to 1.87 kg and from 0.04 to 2.24 kg for males on the standard energy. Mean age was similar between deer fed a low energy (mean = 2.99 years, SE = 0.07) and a standard energy diet (2.91, 0.08). The estimated ontogenetic model revealed that body mass and antler mass differed between diets because all three coefficients that assessed differences between diets (β_2 , β_4 , β_5) were influential (Table 2). The estimate for the quadratic term for deer fed a low energy diet (β_3) was negative but the quadratic term for deer fed a standard energy diet was not influential ($-3.37 + 2.73 = -0.64$, 95% CI: -2.01 to 0.73). The random effects indicated more heterogeneity in ontogenetic scaling relationships across focal males and mothers than fathers. Summarizing the scaling relationships, smaller males on both diets display positive allometric antler growth but males on the low energy diet had faster antler growth in relation to body mass between about 40 kg and 75 kg (Figure 1). Antler mass of low energy diet males, however, slowed noticeably at body masses between 80 and 92 kg. Males consuming the standard energy diet continued to display a linear relationship (in ln scale) between body and antler mass beyond 80 kg.

For 1.5-year-old deer, the static scaling relationships modeled by diet and for the singleton and multiple litter type was selected (Table 3). The Δ BIC (BIC of a model minus model with smallest BIC) of this model was at least 7 BIC units smaller than any of the remaining 7 models (Table 3). The selected model showed that diet and litter type had scaling relationships that differed in intercepts and slopes. Furthermore, for each

combination of diet and litter type, the scalars of the static scaling relationships were all greater than 1.0 because scalars ranged from 2.64 to 8.08 where the smallest of the low 95% confidence bounds was 1.15. The scalars for singleton litter types tended to have steeper scalars (low 8.08, standard 6.29) than multiple litter types (low 4.43, standard 2.64) regardless of diet. The intercepts for singleton litter type also tended to have smaller intercepts (low -33.59, standard -26.39) than multiple litter types (low -19.00, -11.80)

For 2.5-year-old males, the linear mixed effects model indicated no influence on intercepts or slopes from diet and litter type (Table 4). Again, the relationship between body mass and antler mass was positive allometric. The estimated scalar was 1.66 and the 95% confidence interval was greater than 1.0 (1.08 – 2.22). For 3.5-year-old males, the linear mixed effects model again revealed no influence from diet or litter type on intercept and slope coefficients (Table 4). Thus, regardless of diet and litter type, the scalar estimate was the same (1.77). Again, the scaling relationship was positive allometric (95% CI = 1.06 – 2.44). For both 4.5- and 5.5-year-old males, the static scaling models did not assess the influence of diet and litter type (Table 4). The estimated scalars for both ages indicated an isometric relationship as the 95% confidence intervals for both scalars overlapped 1.0. To summarize scalar estimates across all ages, younger males (1.5 – 3.5) had steep positive allometric relationships and males 4.5 and 5.5 years old had shallower isometric relationships. Diet and litter type influence scaling relationships of 1.5-year-old males but not older males. Heterogeneity in scaling relationships from the random effect of mother appear to be more substantial in 1.5-year-old males than in older males.

Discussion

This is the first controlled study to assess whether diet influenced ontogenetic scaling relationships and whether diet and maternal attributes influenced static scaling relationships of antler size in white-tailed deer or any cervid. My hypothesis that relative antler growth would decline with increasing body size was confirmed as correct.

However, the pattern of decline differed between males that consumed the low and standard energy diet. My hypothesis that males on the low energy diet would have slower relative antler growth than males on the standard energy diet was also confirmed as correct. Overall, low energy diet males had slower relative growth, yet they showed faster growth at a young age, and slower growth as they approached maturity than males fed a standard energy diet. My hypothesis that maternal attributes of MaB and litter type would influence antler growth was confirmed as correct for litter type, but not for MaB. Males from singleton litters showed steeper scalars of antler mass in relation to body mass than males from multiple litters in young age. My hypothesis that maternal effects would be apparent in younger-aged males and diminished in older-aged males was confirmed as correct.

Scaling relationships between body size and antler size have usually been estimated among species (Gould 1974, Clutton-Brock et al. 1980, Plard et al. 2011, Lemaître et al. 2014, Tidière et al. 2017, Tidière et al. 2020). The few studies that have estimated antler scaling relationships in a deer species have either estimated an ontogenetic scaling relationship or static scaling relationships, but none have estimated both and examined the connections (Stewart et al. 2000, Ungerfeld et al. 2011, Melnycky et al. 2013, Jones et al. 2018). The estimates from static scaling relationships between

body mass and antler mass reflected the findings from the ontogenetic scaling relationship with slight differences. The ontogenetic scaling relationship revealed that relative antler growth declined through ontogeny in low energy males exclusively. Static scaling relationships showed that both low energy and standard energy males exhibited accelerated relative antler growth as juveniles that declined as they approached maturity. This relationship was reflected by the static scalars: younger males (1.5 – 3.5 years) were positive allometric and older males (4.5 and 5.5 years) were isometric.

Older mothers tend to give birth to heavier offspring earlier than younger mothers (Verme 1989, Wolcott et al. 2015). Heavier males at birth tend to be heavier through ontogeny (Albon et al. 1987). Males born heavier should have lower mass-specific metabolic demands (Barboza 2009). Thus, males born heavier should be able to direct more energy into antler growth. Males with large bodies also have large skeletons and the majority of the minerals needed for antler growth comes from the skeleton (Muir et al. 1987). Thus, males with large bodies likely have more skeletal calcium and phosphorous at their disposal to allocate towards antler growth. Nonetheless, I detected no influence from MaB on static scaling relationships. MaB was also not significant in all models where it was included as a predictor. Perhaps MaB was not influential because it is an indirect not direct measure of birth mass, which has been shown to influence antler size. Schmidt et al. (2002), for example, showed that red deer that are born heavier tend to have longer antlers as yearlings.

Wolcott et al. (2015) investigated birth mass variability in captive white-tailed deer in relation to litter type. They found that males, on average, from singleton litters were born heavier than males from twin male litters. Verme (1989) also explored the

influence of litter type on birth mass of captive white-tailed deer and found that males from singleton litters were born heavier than males from twin male litters. Korsten et al. (2009) found that males from singleton litters were born heavier than males from mixed-sex litters and twin male litters in Soay sheep. No studies have analyzed the influence of litter type on antler size in cervids. I found that categorizing litter type as singleton and multiple influenced scaling relationships more strongly than litter types with more categorizations. The lactation energy required to produce twins is 1.6 times that of a singleton (Carl and Robbins 1988, Mauget et al. 1999). No studies have been published on the difference in energetic demand to produce twins and triplets in cervids. However, there is probably a difference in the energy required to produce twin male, twin mixed sex, and triplets, but not as large a difference as the one between singletons and multiple litter types. I found that singleton litters exhibited steeper positive allometric slopes of antler mass in relation to body mass than multiple litters. This is likely because singletons tend to be born heavier, on average, and have more energy available to invest in antler growth.

It is well established that an individual's diet influences body size and antler size in cervids (Ullrey 1982, McCulloch and Smith 1991, Jones et al. 2018, Spilinek et al. 2020). White-tailed deer that are fed a lower energy diet have both reduced body size and antler mass compared with deer that are fed a higher energy diet (Jones et al. 2010, Spilinek et al. 2020). Diet, in general, has also been shown to influence the relationship between body size and antler size. Jones et al. (2018) showed that well-nourished male white-tailed deer exhibited steeper positive allometric relationships as yearlings than poorly-nourished males. No other studies have investigated the influence of diet on

scaling relationships of antler size. In contrast to Jones (2018), I found that young males that were poorly-nourished exhibited steeper positive allometry than well-nourished males. Males that were well-nourished showed no accelerated investment in antler mass in relation to body mass in the ontogenetic relationship. This was especially surprising to see in young males, as the majority of nutritional energy is directed towards body development in the first year (Heffelfinger 2006). Perhaps there is a physiological deadline before which young males have to grow their antlers to a certain size. Lemaître et al. (2018) showed that yearlings with large antlers in relation to body size had disproportionately larger antlers as adults. They also showed yearlings with large antlers in relation to body mass showed decreased survival up to 6 years of age.

Maternal effects on body size and antler size have been shown to diminish over time (Verme 1962, Lukefahr and Jacobson 1998, Dale et al. 2008, Wolcott et al. 2014). I found that the influence from mother on static scaling relationships of antler size was strongest in 1.5-year-old males. The influence from mother diminished in males older than 1.5 years. Litter type's influence of static scaling relationships of antler size was also only present in 1.5-year-old males. I was not able to determine if litter type influenced males aged 5.5 years because sample sizes were too small (< 5). These findings reflect a diminishing influence of mother and litter type on relative antler size through ontogeny. One possible explanation for this result is that small-bodied males compensate for their initial small body mass through increased feeding frequency (Barboza 2009). Dale et al. (2008) showed that body size at birth was not predictive of body size later in ontogeny in caribou.

This study showed that young males that are poorly-nourished grow their antlers relative to body mass at a higher rate than young males that are well-nourished. This is contrary to the work done by Jones et al. (2018), which showed that young males that are well-nourished exhibit steeper positive allometry. My findings are also seemingly contrary to the fact that males dedicate most of their energy towards body development in the first year of life (Heffelfinger 2006). There must be reasons why I found that poorly-nourished males allocated relatively more energy towards antler mass. It is possible there is a biological need for young, developing males to grow their antlers to a certain size as juveniles. Lemaître et al. (2018) showed that yearlings with large antlers relative to body size tended to have large antlers relative to body size throughout ontogeny, yet had lower survivorship to maturity. Perhaps the extra cost of growing large antlers relative to body size as a yearling has fitness costs. My study also showed the importance of comparing the results of static scaling relationships and an ontogenetic scaling relationship. I found that static and ontogenetic scaling relationships mostly reflected one another, yet they differed in non-trivial ways. Static scaling relationships did not indicate differences in antler growth patterns by diet through ontogeny. The ontogenetic scaling relationship revealed that low energy males exhibited faster relative antler growth in young age and slower growth in old age compared to standard energy males. Also, the ontogenetic model showed that the rate of antler growth did not change with body size for males on the standard energy diet. Yet, the static scalars showed that males fed a low energy and standard energy diet exhibited steeper scalars in young age, which gradually diminished to maturity. An appeal of the ontogenetic scaling relationships is the large amount of data (total number of individual males and repeated measurements) and assessing influence of

heterogeneity across individual males, mothers, and fathers. In my study, there was more heterogeneity in scaling relationships attributed to mothers than fathers emphasizing maternal influences. Finally, my study showed that maternal effects from litter type on scaling relationships of antler size were present only in 1.5-year-old males. These results indicate that maternal effects are more apparent in younger-aged males and diminished in older-aged males, as has been shown in previous studies (Verme 1962, Lukefahr and Jacobson 1998, Dale et al. 2008, Demarais and Strickland 2011, Wolcott et al. 2014). The allometry of antler growth is more complex than previously thought.

Table 1: Sample sizes, means, and ranges of body mass and antler mass at each age, diet, and litter type (singleton, multiple) of male white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 2012–2021.

			Age				
			1.5	2.5	3.5	4.5	5.5
Sample Size	Low	Sing.	14	12	9	8	3
		Mult.	61	56	47	33	15
	Stand.	Sing.	9	7	5	5	2
		Mult.	62	49	36	25	14
Antler Mass Mean (kg)	Low	Sing.	0.11	0.47	0.69	0.86	1.36
		Mult.	0.14	0.47	0.74	1.02	1.17
	Stand.	Sing.	0.30	0.81	1.18	1.25	1.25
		Mult.	0.31	0.83	1.19	1.35	1.35
Antler Mass Range (kg)	Low	Sing.	0.00 – 0.36	0.12 – 0.73	0.46 – 1.09	0.50 – 1.20	0.79 – 1.78
		Mult.	0.01 – 0.45	0.14 – 1.06	0.14 – 1.06	0.42 – 1.87	0.48 – 1.68
	Stand.	Sing.	0.17 – 0.49	0.41 – 1.24	0.85 – 1.56	1.05 – 1.41	1.24 – 1.40
		Mult.	0.04 – 0.78	0.41 – 1.56	0.41 – 1.92	0.26 – 2.14	0.92 – 2.24
Body Mass Mean (kg)	Low	Sing.	44.43	53.41	61.61	66.90	77.64
		Mult.	44.30	55.47	55.47	71.06	78.91
	Stand.	Sing.	54.20	63.89	78.88	80.38	82.64
		Mult.	53.92	69.09	80.68	85.39	90.01
Body Mass Range (kg)	Low	Sing.	35.83 – 57.61	32.66 – 78.47	46.95 – 89.81	51.71 – 75.75	70.76 – 81.42
		Mult.	28.58 – 61.69	37.65 – 81.19	37.65 – 81.19	49.90 – 85.73	40.10 – 92.08
	Stand.	Sing.	49.90 – 59.19	46.72 – 75.30	73.48 – 84.37	64.41 – 88.45	75.30 – 89.99
		Mult.	37.65 – 68.49	48.53 – 94.80	46.72 – 101.60	64.86 – 103.87	67.59 – 106.59

Table 2. Ontogenetic scaling relationship parameter estimates. Summaries of parameter estimates and 95% confidence bounds of a linear mixed-effects model assessing the influence of diet on relationships between body mass (BM, BM2, kg) and antler mass (kg) through ontogeny in white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 2012–2021. The reference category is low-energy for diet.

Coefficient	LB	Estimate	UB
Intercept (β_0)	-87.11	-72.12	-58.66
BM (β_1)	24.61	31.31	38.73
Diet (β_2)	25.99	47.92	71.09
BM ² (β_3)	-4.29	-3.37	-2.54
BM * Diet (β_4)	-34.43	-22.96	-12.24
BM ² * Diet (β_5)	1.40	2.73	4.14
Random effect and residual	LB	SD	UB
Individual	0.19	0.29	0.37
Mother	0.01	0.23	0.33
Father	0.00	0.03	0.14
Residual	0.41	0.19	0.47

Table 3. Bayesian Information Criterion (BIC) model selection analysis. BIC model selection analysis of 8 mixed-effect models to predict influences on relationships between body mass (kg) and antler mass (kg) of 171, 1.5-year-old white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 2012–2016. Possible predictors were low and standard energy diet (Diet), mother’s age at birth of offspring, and 3 different categorizations of litter types (i.e., Litsm – singletons, multiples; Littwtr – singletons, twins, and triplets; Lit5 – singleton, twin mixed sex, twins males, twins where the other sibling died before weaning, and triplets). Number of parameters *nPar* and LL is log-likelihood.

Model	<i>nPar</i>	Δ BIC	LL
BM * Diet + BM * Litsm	7	0.00	-142.34
BM * Diet + BM * Litsm + BM * MaB	9	7.38	-141.52
BM * Diet + BM * Littwtr	7	7.39	-153.80
BM * Diet	5	15.22	-144.46
BM * Diet + BM * Littwtr + BM * MaB	9	15.76	-143.58
BM * Diet + BM * MaB	7	23.27	-156.03
BM * Diet + BM * Lit5	7	23.56	-141.57
BM * Diet + BM * Lit5 + BM * MaB	9	30.29	-143.37

Table 4. Static scaling relationships parameter estimates. Summaries of parameter estimates, and 95% confidence bounds, for linear mixed effects models (deer aged 1.5, 2.5, 3.5, and 5.5 years) and a simple linear regression model (4.5 years). All models assess the influence of diet and litter type (LT, singleton, multiple) on static scaling relationships between body mass (BM, kg) and antler mass (kg) of male white-tailed deer at Kerr Wildlife Management Area, Kerr County, TX from 2012–2021. For models that include both diet and litter type, the reference categories are low energy and multiple litter type. Also displayed is the standard deviations of the random effect for mother, residual standard deviation, and 95% confidence bounds. Findings from a least-squares model are reported for 4.5-year-old deer because linear mixed effect models failed to converge.

	1.5			2.5			3.5			4.5			5.5		
Coefficient	LB	Estimate	UB	LB	Estimate	UB	LB	Estimate	UB	LB	Estimate	UB	LB	Estimate	UB
Intercept	-22.60	-19.00	-15.24	-9.77	-7.52	-5.21	-10.51	-7.69	-4.79	-7.11	-4.88	-2.65	-7.11	-4.14	-1.27
BM	3.47	4.43	5.38	1.08	1.66	2.22	1.06	1.77	2.44	0.63	1.14	1.66	0.35	0.99	1.68
Diet	1.27	7.20	13.08	-1.62	1.98	5.72	-0.45	3.72	7.75	-	-	-	-	-	-
LT	-21.84	-14.59	-6.74	-2.42	0.76	4.33	-3.34	0.36	4.10	-	-	-	-	-	-
BM * Diet	-3.28	-1.79	-0.25	-1.30	-0.41	0.44	-1.76	-0.83	0.15	-	-	-	-	-	-
BM * LT	1.63	3.65	5.52	-1.05	-0.18	0.60	-0.97	-0.08	0.82	-	-	-	-	-	-
Random effect and residual	LB	SD	UB	LB	SD	UB	LB	SD	UB				LB	SD	UB
Mother	0.134	0.347	0.534	0.000	0.099	0.27	0.000	0.100	0.240				0.000	0.171	0.276
Residual	0.432	0.554	0.642	0.26	0.352	0.394	0.171	0.262	0.298				0.025	0.177	0.273

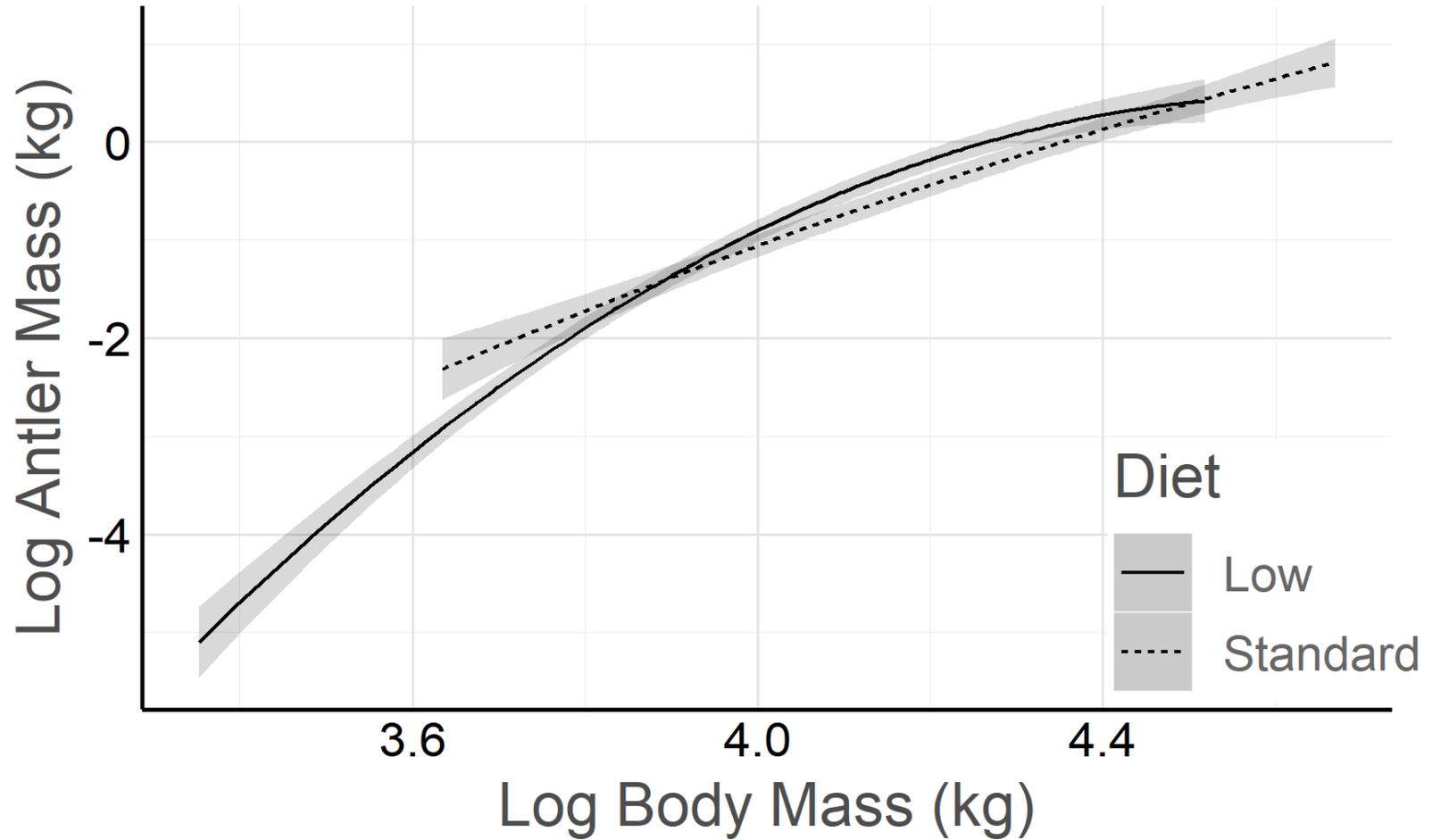


Figure 1. Predicted regression lines summarizing relationships between body mass and antler mass for male white-tailed deer fed either a low energy diet (L) or standard energy diet (S) at Kerr Wildlife Management Area, Texas, USA.

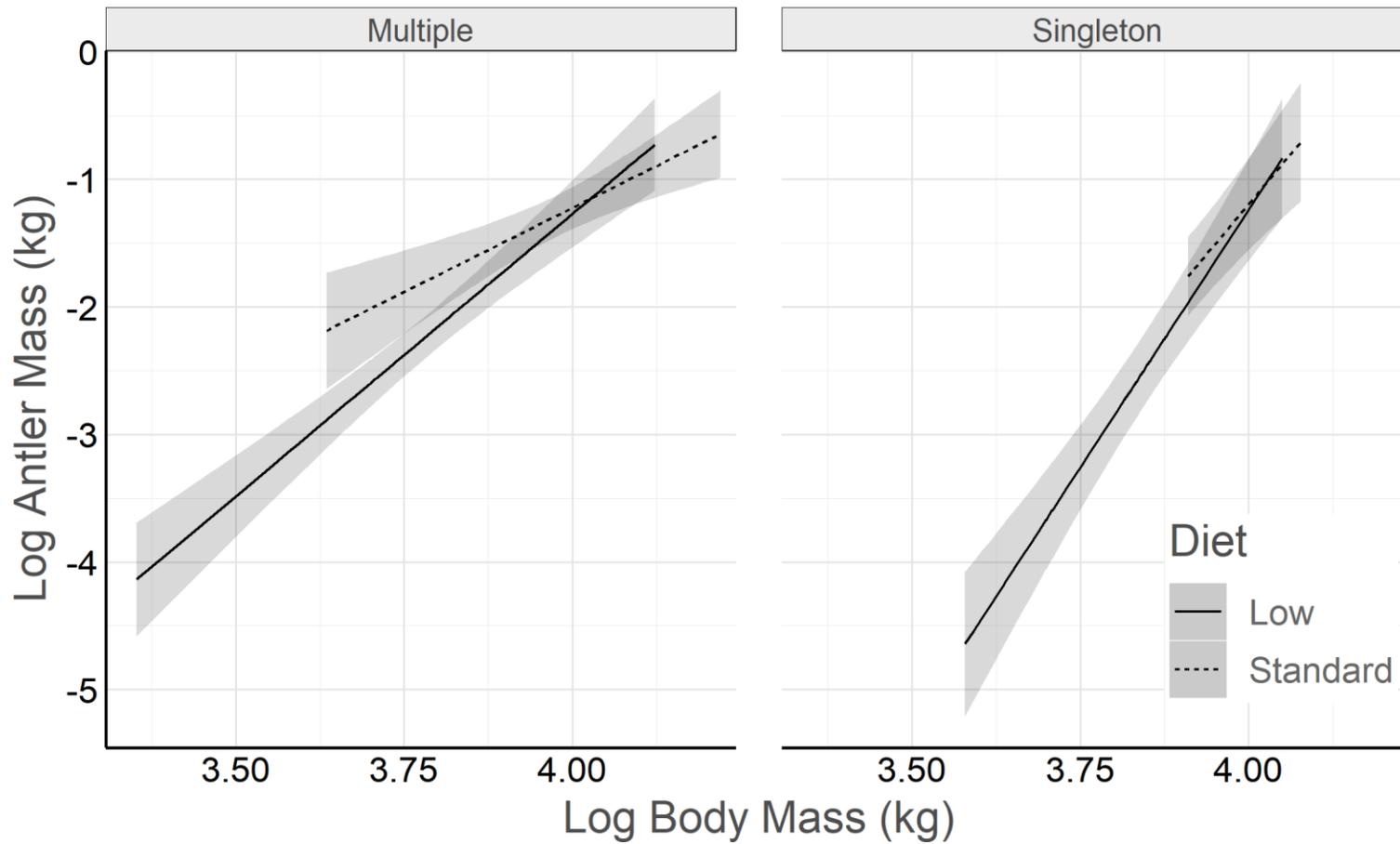


Figure 2. Predicted regression lines depicting the relationship between body mass and antler mass for male white-tailed deer aged 1.5 years fed either a low energy diet (L) or standard energy diet (S) and born to either a multiples or singleton litter at Kerr Wildlife Management Area, Texas, USA.

APPENDIX SECTION

Table A1. Correlation matrix of four different measurements of antler size: antler mass (AM), Boone and Crockett score (B&C), right main beam length (RMB), left main beam length (LMB), and total main beam length (TMB) for 171 male white-tailed deer at Kerr Wildlife Management Area, Texas, USA.

	B&C	RMB	TMB	LMB
AM	0.95	0.87	0.85	0.76

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