ECOLOGICAL SIGNIFICANCE AND UNDERLYING MECHANISMS OF BODY SIZE

DIFFERENTIATION IN WHITE-TAILED DEER

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Body size varies according to nutritional availability, which is of ecological and evolutionary relevance. The purpose of this study is to test the hypothesis that differences in adult body size are realized by increasing juvenile growth rate for white-tailed deer (*Odocoileus virginianus*). Harvest records are used to construct growth rate estimates by empirical nonlinear curve fitting. Results are compared to those of previous models that include additional parameters. The rate of growth increases during the study period. Models that estimate multiple parameters may not work with harvest data in which estimates of these parameters are prone to error, which renders estimates from complex models too variable to detect inter-annual changes in growth rate that this simpler model captures

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

Page

Tables

Figures

CHAPTER I

THESIS OVERVIEW: BODY SIZE, GROWTH PATTERNS, AND GROWTH

RATE

Body size variability, it geographic distribution, and its underlying

mechanisms are subjects of ecological interest. Several ecogeographic trends

have been observed that describe the distributions of body sizes both within and

between species, including Bergmann's rule, Cope's rule, and Rensch's rule.

The underlying mechanisms behind body size differentiation are the subjects of

much study and yet little agreement (Meiri and Thomas 2007; McNab 2010;

Huston and Wolverton 2011). Whatever the mechanism underlying

differentiation, the link between latitudinal patterns in body size with the global

distributions of soil fertility, net primary productivity, and growing season (Geist

1987; 1998; Meiri et al. 2007; McNab 2010; Huston and Wolverton 2011) is

compelling evidence that resource availability drives body size differentiation.

Body size variability is ecologically relevant both within and between species.

Interspecific studies of body size are useful in linking natural selection to species

distributions (Lindstedt and Boyce 1985; Brown 1993; Jones and Purvis 1997;

Albert and Johnson 2011). Body size differentiation within species is ecologically

informative because it reflects an organism's adaptation to local conditions; large

size within a species is generally advantageous (Barbraud et al. 1999; Gaillard et

al. 2000; Zedrosser et al. 2006; Monteith et al. 2009; Huston and Wolverton

1

2011), although small sizes may be maintained because small size is advantageous when resources are limiting or disturbances are frequent over long time durations (Geist 1998; Wolverton et al. 2009). In addition, intraspecific competition can drive small individuals into marginal habitats (Owensmith 1993; Wileski and Wredge 2010).

For studies of intraspecific body size differentiation, complications have arisen because there has not been consistency between what measurement constitutes body size (Blackburn et al. 1999). An animal's mass may be visualized as composed of two parameters: Reversible mass and irreversible mass. Reversible mass includes fat and muscle tissue, and may be tapped as energy reserves in times of starvation. Irreversible mass composes bones, organs, and any other structure that cannot be tapped for energy (Roos et al. 2002). Here, body size refers to irreversible mass in addition to reversible mass. Body growth refers to irreversible mass alone, which for vertebrates is often indicated by some skeletal measurement. Body condition is defined as an animal's energetic state (Jones and Purvis 1997), and can be visualized as the proportion of reversible mass to irreversible mass.

In this thesis an in-depth review of the ecological and evolutionary significance of body size and growth patterns is made, focusing on specific case studies where relevant. A method is then established for studying intraspecific growth rate differentiation at the population level that is suitable for use with harvest records, an abundant yet limited data source for some vertebrates. This

may prove to be a useful indicator of habitat quality as well as phenotypic quality. The model organism for this study is the white-tailed deer, *Odocoileus virginianus*. As a keystone herbivore, this animal is of considerable conservation importance (Waller and Alverson 1997). Although phenotypic quality is best represented by body condition, total body mass has such a sizable impact on life-history traits, particularly juvenile survival (Gaillard et al. 1997; Loison et al. 1999), reproductive age (Saether and Haagerud 1985; Williamson 1991; Langvatn et al. 1996), litter size, (Hewison 1996) and longevity (Gaillard et al. 2000), that for large herbivores including ungulates, mass alone (body size) is often used as a proxy for phenotypic quality (Pettorelli et al. 2002). Within ungulate species, longevity increases with body mass (Gaillard et al. 2000). Blackburn et al. (1999) contend that, for ungulates, body mass is the most appropriate measure of phenotypic quality. Thus, for this study, body mass serves as the body size metric for white-tailed deer.

Chapter II is a literature review of body size and growth; the ecological and evolutionary significance of body size, patterns in growth that enable body size differentiation, and the mechanisms of body size differentiation. It begins with a discussion of the ecological relevance of body size between species; size is a determinant of an organism's metabolic rate (Garland and Carter 1999). Large size is associated with higher ability to acquire resources, higher reproductive success, and higher over-winter survival abilities (Lindstedt and Boyce 1985; Jones and Purvis 1997; Mysterud et al. 2001; Savage et al. 2004;

3

McNab 2010), while smaller size better suits an organism to long-term food shortage (Jones and Purvis 1997). Ecogeographic trends are then reviewed: Bergmann's rule; the tendency for body size to increase with latitude (Scholander et al. 1950; James 1970; Geist 1987; 1998; Ashton et al. 2000; Ashton and Feldman 2003; Meiri 2007; Entling et al. 2010), Cope's rule; the tendency for body sizes to increase through time (Stanley 1973; McNab 2010; Albert and Johnson 2011), and the observed decrease in body sizes upon entrance into deserts and islands (Yom-Tov and Nox 1986; Yom-Tov and Geffen 2006). These patterns are all likely driven by resource availability (Geist 1987; 1998; Huston and Wolverton 2009; McNab 2010; Huston and Wolverton 2011). Within this context, the studies of intraspecific and interspecific body size differentiation are reviewed.

The interspecific approach is useful for linking natural selection to species distributions. The following studies are reviewed: 1) Linstedt and Boyce's (1985) study of relative metabolic requirements, in which they found larger species to possess higher fasting endurance. 2) Jones and Purvis's (1997), in which they find no support for Brown's (1993) hypothesis that for mammals there is an optimal body size for maximizing reproductive output. 3) Albert and Johnson's (2011) phylogenetic analysis of the right-skewed distribution common to most animal clades, which shows that for fish, body size diversification occurred early in evolutionary history and the right-skewed body size distribution does not reflect a current shift towards large body size.

4

The intraspecific approach is useful because it can give insights into an organism's ecology. Within a species, larger individuals usually have higher feeding efficiency, reproduction, mate competition, and superior predator avoidance; however, large individuals are more vulnerable to fluctuations in food resources over long time durations. Some organisms undergo environmentally mediated shifts in niche between life-history stages. These shifts may occur at specific body sizes, and their timing may be informative in terms of the organism's ecology and its environment (Persson and Bronmark 2002). Within-population variability in traits that are associated with resource indicate that different individuals reflects individual specialization within the population's niche, which enables larger populations than could otherwise occur (Roughgarden 1972; Van Valen 1972; Lyman and O'Brien 2005). Thus, natural selection should favor phenotypic plasticity in body size. Phenotypic plasticity in body size is a necessary variable in the iteroparous reproductive strategy for many organisms (Geisel 1976; Jones and Purvis 1997; McNab 2010). Because resource supply rates vary, adjusting overall metabolic requirements to maximize reproductive output given variation in resource supply rates is often achieved by varying body size accordingly (Geisel 1976). Life-history evolution theory and energetics theory relevant to this topic are reviewed. Of particular importance is the influence of food availability on both population density and body size (Kie et al. 1983; Kruuk et al. 1999; Gaillard et al. 2000; Lesage et al. 2001). Population density limits an individual's food availability (Lesage et al. 2001; Agetsuma

5

2007; Rodriguez-Hidalgo et al. 2010; Huston and Wolverton 2011).

Consequently, population density correlates negatively with body size such that

rates of resource demand are roughly equivalent (the energetic equivalence rule)

(Damuth 2007).

The roles of environmentally mediated changes in body size in phyletic

diversification are also reviewed, including Lyman and O'Brien's (2005) study of

changes in morphological diversity along gradients in precipitation. Changes in

morphological function associated with changes in size over evolutionary time

are also discussed (e.g. Hanken and Wake 1993).

Differentiation in body size is realized through differentiation in growth

patterns (birth weight, growth rate, and ontogenetic growth period) (Southwood

1988; Sand et al. 1995; Zeddrosser et al. 2006; Solberg et al. 2008). Growth

patterns are also ecologically relevant as they are indicative of adaptations to

environmental conditions. Growth rate as a life-history variable reviewed

because it is particularly relevant; growth rate immediately following birth is the

strongest determinant of mortality (Zullinger et al. 1984; Pontier et al. 1989).

Differentiation of adult size by variation in maturation period is also discussed, as

this may underlie differentiation of adult body size in some situations (Stearns

1976; Bruce et al. 2002). Despite its advantages, growth may be associated with

trade-offs concerning mature function, peak cellular efficiency, immune function,

and resistance to physiological stressors (Mangel and Stamps 2001).

Growth rate may prove to be a useful indicator of habitat quality for organisms in which it responds to environmental conditions. Numerous functions have been derived to which data points can be empirically fit to generate growth curves (France et al. 1996). Most of these functions have the flexibility to estimate multiple parameters, such as birth weight, growth rate, and length of the maturation period (Leberg et al. 1989; France et al. 1996; Bolker 2008). No single function performs optimally in all situations. The most suitable function depends on the data to which is it fitted and on the research objectives (Leberg et al. 1989; Bolker 2008). Four of the most common functions, the monomolecular equation, the von Bertalanffy equation, the Gompertz equation, and the Richards equation are reviewed. The methods by which they were derived, their parameters, and their assumptions are discussed.

Because sexual dimorphism is present in most mammals, and differences in size between males and females have evolutionary and ecological significance, sexual dimorphism is discussed, focusing on ungulates. For ungulates, the origins of sexual dimorphism are related to the emergence of polygynous mating systems, which follow a move from a closed to an open habitat (Pérez-Barbaría et al. 2002). Within a species, the degree of sexual dimorphism correlates positively with body size, a phenomenon known as Rensch's rule (Fairbairn and Preziosi 1994; Fairbairn 1997; Blanckenhorn 1999; Fairbairn 2005; Szdkély et al. 2004). For sexually dimorphic species that follow Bergmann's rule, the degree of dimorphism correlates to latitude (Blanckenhorn

et al. 1999). For these reasons studies of size and growth patterns should separate males from females.

Having established the ecological and evolutionary relevance of body size and growth patterns as life-history variables, the white-tailed deer (*Odocoileus virginianus*) is suggested as a model organism for studying environmentally mediated body size differentiation in mammals because of their dramatic phenotypically plastic response to high population density (Geist 1998; Purdue et al. 2000; Wolverton et al. 2007; 2009), particularly when near *K* carrying capacity (Kie et al. 1983; Lesage et al. 2001; Simard et al. 2008). This response is sexually dimorphic, affecting males more than females (Purdue et al. 2000; Lesage et al. 2001; Comer et al. 2005), which reflects different mating behaviors and different habitat preferences (Leberg et al. 1993; Blanckenhorn 2007). Because of this, and because males and females differ in the lengths of their maturation periods (Shaw et al. 2006), males and females should be studied separately.

Males with higher birth weights tend to gain more mass from one age class to the next at all ages, indicating higher growth rate. Schultz et al. (1995) suggested that birth weight may be a useful indicator of physiological status or condition. If this is the case, then population-averaged growth rates may serve as a useful indicator of phenotypic quality and habitat quality. Growth rate has the advantage that it is not biased by differences in age structure. Growth curves can be empirically fit to age-specific weights using any of the growth functions

reviewed in Chapter II, although given the commonality of harvest records for this species, an equation that can estimate a rate parameter given low-precision age estimates may prove to be valuable.

Chapter II concludes with a discussion of the importance of studying phenotypic plasticity in body size for white-tailed deer specifically, as this trait enables them to avoid starvation under high population density, but with consequences for survival and adult recruitment for many plant species (Russell and Fowler 1999). Deer herbivory causes changes in plant mortality as well as browse lines (Russell et al. 2001), and has also been observed to drive bottom-up cascades that impact some animal species (Waller and Alverson 1997; Côté et al. 2004).

Chapter III establishes specific methodology for analyzing population-level growth rate in white-tailed deer that was developed specifically for use with harvest records. This species has been studied in considerable detail, and it has been clearly demonstrated that differences in food availability drive differentiation in adult body size. The relationships between population density, food availability, growth rate, and body size are studied for a single population on the Fort Hood military base in central Texas, USA. Harvest records for this population date back to the year 1971. It has previously been demonstrated that population density has steadily declined during this time, and adult body sizes have risen in response (Wolverton et al. 2007; 2009). The mechanism(s) behind realizing this body size increase remain an open question. The research

hypothesis for this study that white-tailed deer differentiate adult body size in response to differences in food availability by adjusting ontogenetic growth rate. Dressed body mass is used as the body size metric (dependent variable), and age classes are used as the independent variable. Using nonlinear least squares curve fitting, these bivariate data points are empirically fit to a logarithmic function for each year in the study period for the purpose of interannual comparison of the growth rate parameter. Because age estimates are expected to be less accurate for older individuals (Gee et al. 2002), maturation period cannot be evaluated with these harvest records. However, adjustment of growth rate does not exclude the possibility of adjustment of the length of the maturation period. To evaluate model performance, the same procedure is repeated using the monomolecular, Gompertz, and Richards equations. Because these methods estimate multiple parameters (such as birth weight or adult weight and inflection point in addition to growth rate), they should ideally be used on datasets with a truly interval-scale independent variable. Therefore, they were expected to have less power to detect interannual differences in growth rate. In order to compare the performances of the four functions, a Pearson's correlation was calculated with year as the independent variable and the growth rate parameter as the dependent variable. Results of the curve fitting procedures as well as the correlation between year and growth rate were both graphed for visual comparison. All growth curves showed a visible increase in growth rate over time. White-tailed deer increase body weight in

10

response to lowered population density by increasing ontogenetic growth rate. From visual inspection of these graphs, the strongest growth rate adjustment appears to be during the first two years of life. The increase in growth rate parameter over time is most strongly detected by the logarithmic curve. It was moderately detected by the monomolecular equation. This equation includes growth rate parameter as well as an estimate of adult mass and is the simplest of the established methods tested here. Growth rate increase was weakly detected by the Richards equation, which includes the same parameters but with additional exponential terms, and not detected by the Gompertz equation, which also includes an inflection point. It is apparent that increased model complexity, as well as error in estimation of parameters such as adult weight and inflection point, weaken the accuracy of growth rate estimations for this dataset.

These analyses demonstrate that adjustment of growth rate is a key mechanism behind the white-tailed deer's reaction norm to dietary stress. Adjustment of growth rate under high predatory pressure is an intuitive result; high mortality risk causes a younger age structure to emerge, and during times of low density high growth rate would be highly advantageous as it would allow individuals to leave more offspring sooner in life. This study provides a simple, effective technique for estimating growth rate from data sources that are unsuitable for more complex modeling techniques. Harvest records may be unsuitable for making age-specific weight predictions. They are often criticized as imprecise, error-laden or poor quality. However, they are common and tend

to be large sample sizes. Growth rate indicates phenotypic and thus habitat quality, and the logarithmic equation performs well on harvest records despite these limitations. These results also give direction to future research on taxonomic turnover; under what conditions does selective pressure act on the individual's genotype.

CHAPTER II

ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF BODY SIZE AND
GROWTH PATTERNS

Body size is a relevant characteristic in population dynamics and life

histories of mammals and other vertebrates because of the role that it plays in

reproduction and survivorship. Variation in body mass within a clade may

explain as much as 90% of the variation in many other traits, including metabolic

rate (Garland and Carter 1994). Survivorship, which is predictable by mass-

specific metabolic rate (Savage et al. 2004), is largely determined by an

organism's ability to acquire food and avoid predation. In marine fishes, for

example, an individual's probability of mortality diminishes with age in a

predictable manner that scales with mass-specific metabolic rate (Savage et al.

2004). Between species, large body size is advantageous for acquiring

resources whereas smaller species convert energy to offspring more efficiently

(Jones and Purvis 1997). For many animals, for example ungulates, large body

size determines success in reproduction, mate competition in males, and over-

winter survival (Lindstedt and Boyce 1985; Mysterud et al. 2001; McNab 2010).

Despite the myriad advantages of large size, there are some situations in which

small size is advantageous. Smaller species have an advantage in energy

conservation and are better suited to chronic food limitation (Jones and Purvis

1997). Geist (1998) describes this dichotomy for ungulates as resulting from two different types of selection: 1) Efficiency selection produces smaller species relative to their clades that have lower maintenance costs. These are characterized by generalist diets, high reproductive rates, and phylopatry. This produces what he calls a maintenance phenotype. 2) Dispersal phenotypes have low reproductive rates, relatively larger body sizes, specialized diets, and large home ranges.

<div align="center">Ecogeographic Trends in Body Size</div>

Bergmann's rule describes a positive correlation between body size and latitude (James 1970). This correlation is empirical and does not provide a mechanistic explanation (Meiri 2007). Carl Bergmann (1947) proposed that an organism's internal heat production to its surface area heat loss favors larger body sizes in cooler climates and smaller body sizes in warmer climates (James 1970). However, this explanation is inadequate for several reasons. For animals that follow Bergmann's rule, the relationship between size and latitude tends to reverse above 60 degrees N. In some clades, the relationship between body size and latitude is negative (Mayr 1956; Ashton et al. 2000; Meiri et al. 2004). Bergmann's rule is seen in many ectotherms, which indicates that the trend is ancestral to endothermy (Ashton and Feldman 2003; Entling et al. 2010). Phylogenetic reconstructions reveal that exceptions to Bergmann's rule are nonrandom and are thus more likely to have arisen independently (De Quieroz and Ashton 2004).

There are other observed trends in body size, and these may provide some insight into the causes of body size differentiation. For mammals, body size tends to increase through time, a trend known as Cope's rule (McNab 2010). It is thought that this is driven by the selective advantages of large body size (Stanley 1973; McNab 2010). Mammalian body size often decreases upon entrance into desert environments (Yom-Tov and Nox 1986; Yom-Tov and Geffen 2006) and when species invade islands (Foster 1964; Van Valen 1973). Some authors argue that resource availability underlies all of these trends (Geist 1987; 1998; McNab 2010). McNab (2010) dubs this explanation the "resource rule." Huston and Wolverton (2009; 2011) linked Geist's ideas directly to the global distribution of evolutionary and ecologically relevant net primary production (eNPP), or growing season, which they term "Geist's rule" or the "eNPP rule."

Because Bergamnn's rule is the most widely known and studied ecogeographic rule pertaining to body size, much of the evidence for the resource rule comes from studies of the correlation between body size and latitude. Rosenzweig (1968) observed that ambient temperature and latitude are both good predictors of body size in carnivores, but temperature performs no better than latitude as a predictor of size, which implies that it is not the ultimate driver. He found that actual evapotranspiration, used as a proxy for primary productivity, to be superior correlate, particularly in areas of low productivity (but see discussion in Huston and Wolverton 2011). Numerous environmental variables correlate with latitude, notably productivity and seasonality, both of

which influence nutritional availability. Body size differentiation should thus

reflect gradients of these variables. Seasonality is predicted to favor larger body

size due to fasting endurance (Lindstedt and Boyce 1985) until it reaches a

threshold past which body size becomes limited (Geist 1987; Wolverton et al.

2009). Limitations of food availability often reduce growth rate and adult body

size (Arnett and Gotelli 1999). This predicts that body size should decrease at

high latitudes, as noted by McNab (1971) and Geist (1987). The tendency of the

majority of North American mammals to vary body size in accordance to

gradients of seasonality and primary productivity confirm these predictions.

Approaching 50° to 60° N, body sizes for mammal species increase as

productivity increases. Above 60° N, seasonality limits productivity and body

sizes decrease (Geist 1998; Huston and Wolverton 2011). Body size is typically

proportional to seasonality, or the length of the annual growing season. This

occurs during most of the "seasonal productivity pulse" (Geist 1987:2).

Ecogeographic trends can be studied within species or between species.

The interspecific approach is useful for linking natural selection to species

distributions. For example, Lindstedt and Boyce (1985) tested the effects of

large body size on fasting endurance because it is enhanced by a lowered

relative metabolic requirement. This is advantageous in seasonal environments.

By dividing energy reserves after their rate of use for terrestrial mammals, they

found to possess higher fasting endurance than smaller species.   The authors

concluded that this effect contributes to Bergmann's Rule between species and

predicted that it would be even more pronounced within species. As another example, most animal clades, including mammals and fish, show a right-skewed body size distribution, meaning that the modal mass is less than the mean, even on a log-scale (Brown 1993; Jones and Purvis 1997; Albert and Johnson 2011). This may be evidence of small size conferring selective advantages, higher diversification rates at small sizes, high risk of extinction for large species, or disproportionate responses to environmental processes between small and large animals (Albert and Johnson 2011). Brown (1993) hypothesized that there is an optimal body size with respect to reproductive power (~100g). He based this hypothesis on the assumption that energy available for reproduction is surplus to energy needed for maintenance, and on the general allometric relationships that energy acquisition reproduction demonstrate with body size; large species have an advantage at acquiring resources but small species are more efficient at energy conversion. He predicted that variables affecting reproductive output should not scale linearly with body size; rather, there should exist an optimum at which their slopes change sign. Jones and Purvis (1997) tested this prediction with published literature values for the order Chiroptera (bats) because Brown's proposed optimum size is intermediate to this order's size range. They used ordinary least squares regression to estimate the allometric slopes of several life-history variables to body size and found no evidence of Brown's prediction. This lead them to conclude that, for the order chiroptera, the life history variables they tested and body size broadly show the same relationships as with larger

mammals. Between smaller and larger species of this clade, allometric

relationships between life history variables and body size do not differ. So why

are size distributions right-skewed for most clades? Albert and Johnson (2011)

suggested that the right-skewed distribution reflects transition to larger size,

different evolutionary processes may be in action at opposite ends of the size

spectrum, or perhaps the same environmental processes affect taxa at the ends

of the size spectrum differently. Albert and Johnson tested these hypotheses

with size and stratigraphic data for 465 fish species. Using two chordate

outgroups and log-transformed total body length (cm) as the size measurement,

they performed a phylogenetic analysis and tested Cope's rule by determining

the direction, proportion, and magnitude of size changes. Two major phases in

fish size diversification were detected: 1) A rapid expansion associated with a 10-

fold increase in arithmetic average size from the Lower Cambrian to the Upper

Silurian (542-417 mya). Body size showed negative skewness during this time

period. 2) A much slower, much longer phase of size evolution from the Lower

Devonian to Recent (416-0 mya). The analysis indicates that the features of

body size diversity such as its average, range, and standard deviation became

established early in vertebrate history (23% of their current age), thus the

negative skewness is not likely reflective of a current transition to large size.

They also found that this negative skew becomes symmetrical when body size

distributions are converted to a power-log scale ($\ln[\text{size}]^b$), rather than a log scale

($\ln[\text{size}]$). This suggests that the negative skew results from high magnitude in

changes to large size, rather than from the frequency. This may indicate that evolutionary processes are equivalent at either end of the size spectrum when measured on the appropriate scale, but the authors caution that according to current understanding, power laws are predicted to act upon linear and not logged sizes; therefore, this must be regarded as phenomenological. Inferring mechanism from the observance of power-law behavior may be misleading because power-law behavior may be generated by many different mechanisms (Bolker 2008).

<center>Intraspecific vs. Interspecific Study of Body Size</center>

When correlating body size to nutritional availability, there are some difficulties associated with the interspecific approach. There is no standardized metric for body size. Different measurements are often employed between taxa (Blackburn et al. 1999). Interspecific patterns in animal body sizes within communities are difficult to detect reliably because, between species, taxonomic effects on body size may obfuscate the effects of environment and community assembly (McNab 2010; Huston and Wolverton 2011). Because intraspecific population densities may affect body size, mean species body size requires scaling to population size, and it is very difficult to census body size for an entire community. Differences in relative abundances between large and small species may thus generate artifactual patterns (Meiri and Thomas 2007). Species richness may influence body size patterns, which can also be difficult to separate from the effects of nutrition. Species richness predicts body mass more strongly

<center>19</center>

than latitude in New World birds (Blackburn and Gaston 1996), and body size variances are higher where species diversity is low (Meiri and Thomas 2007). Spatial scale and site selection may also bring their own set of challenges. Overall, species with widespread distributions are more common than species with smaller distributions (Blackburn and Gaston 1998). Because population density affects body size, intraspecific population density differences may affect average body size estimates at the community level. It may be challenging or impossible to separate these effects from the influence of primary productivity. These challenges may be surmountable by studying body size differentiation within one species, within one geographic range, and within a timescale during which assuming a relatively constant species richness is reasonable.

Body size differentiation within a species is of ecological relevance. Large size is typically advantageous, with some notable exceptions. Among vertebrates species, large body size endows individuals with a higher feeding efficiency, and differences in dietary preferences may exist between larger and smaller individuals. For example, Barbraud et al. (1999) found female snow petrels of higher body growth are able to bear larger young. For many species, large males have an advantage competing for females (Monteith et al. 2009; Huston and Wolverton 2011) and are able to spend less time feeding and more time breeding during breeding seasons (Geist 1987). Sexual selection may also act on large size. Large size in females may be advantageous because their relative metabolic rate is lower, which raises their tolerance to short-term dietary

stress (Gaillard et al. 2000). Larger females are usually able to reproduce

earlier in life (Zedrosser et al. 2006), produce more and larger offspring, which

grow faster and have higher survivorship, although for vertebrates offspring

survivorship and lifespan (living through more breeding attempts) may influence

variation in fitness more strongly than fecundity. Large size is also advantageous

for predator avoidance (Geist 1987; Zedrosser et al. 2006). Despite the myriad

advantages of being larger, phenotypic variation in body size is often maintained

within species. This is because environmental conditions can vary between

different areas and selection can act in opposing directions. Intraspecific

competition can also force small individuals into marginal areas (Barbraud et al.

1999). For males close to the maximum attainable body size the increase in

genetic fitness that large size brings may come with the cost of being more

vulnerable to fluctuations in food availability, as has been observed in iguanas

(Owensmith 1993; Wilelski and Wrege 2010). If resources are limiting or

disturbances are frequent over long time durations, then smaller individuals are

more able to maintain high body condition (Geist 1998; Wolverton et al. 2009).

Variation in characteristics associated with differential resource use (such

as size) may also occur between different life history stages. For some species,

surpassing given thresholds in body size is accompanied by changes in dietary

niche. Persson and Brönmark (2002) studied this phenomenon in pikeperch.

Between the juvenile and adult life stages, these fish switch from planktivory in

pelagic zones to piscivory in the benthos. To make this transition, fish must

achieve enough growth and survive in the juvenile stage. This depends on their competitive abilities against fish species that constitute future prey. Individuals that are more specialized as piscivores make this switch earlier in life, which requires a faster growth rate. Increasing competitive ability during the juvenile stage may be at the expense of competitive ability as piscivorous adults. This constitutes an ontogenetic tradeoff between being a specialist with respect to one dietary niche and being a generalist with respect to multiple dietary niches. Population densities in the piscivore stage depend on success as competitors in the planktivorous stage. Unfavorable conditions for pikeperch at this stage, such as high competition, may reduce growth rates, which in turn may impair adult recruitment. On the other hand, high competitive abilities for pikeperch in the planktivorous stage limits prey availability for pikeperch in the piscivorous stage. In the piscivorous niche, pikeperch growth is dependent upon and mirrors prey growth (Persson and Brönmark 2002).

Ecophenotypic Plasticity in Body size

If an effective limit to assimilated energy exists, then assimilated energy must be divided three ways: Between growth, reproduction, and maintenance (Geisel 1976; Jones and Purvis 1997; McNab 2010). This constitutes a tradeoff: A large increase in one will necessarily diminish the other two. Reproduction requires metabolic energy in addition to what is needed for maintenance be converted into offspring (Brown 1993; Jones and Purvis 1997). If a reduction of available energy occurs at any age and energy invested in growth remains

constant, then the age-specific death rate "must be equal to some intrinsic death rate multiplied by some decreasing function of reproductive effort" (Geisel 1976:61). If energy availability varies over the course of an organism's lifespan, then having a long reproductive period may increase genetic fitness over reproducing early. In unstable or rapidly changing environments, it is advantageous for organisms to have multiple, equally weighted opportunities to reproduce. Iteroparity, reproducing several times over multiple seasons, is a strategy to increase the probability that reproduction coincides with favorable environmental conditions. Environmentally-dependent phenotypic plasticity in body size is thus a necessary variable in reproductive strategy for many iteroparous organisms; if resources are scarce, minimizing overall metabolic requirements by achieving a smaller adult body size increases probability of surviving long-term shortage, thus increasing the chances that an individual's reproduction coincides with favorable environmental conditions and resource abundance (Geisel 1976).

Natural selection should also favor plasticity with respect to body size because climate, which affects primary productivity levels, varies at both geological and ecological timeframes (Lesage et al. 2001). Any level of body mass must be maintained by adequate metabolic inputs, and a key way to adjust consumption in accordance to variation in rates of resource availability is to vary body size accordingly. Because of this, food availability, population density, and body size are inextricably related (Kie et al. 1983; Kruuk et al. 1999; Gaillard et

al. 2000; Lesage et al. 2001). A population's per area energy use is a product of population density and the metabolic requirements of the individuals in that population. This holds for a wide variety of animals, across a range of average body sizes that span several orders of magnitude, and across trophic levels, morphologies, and niches (Damuth 2007). Thus, food availability influences population densities as well as body size. A population's rate of increase depends on the metabolic rates of individuals and the rates of resource supply (Savage et al. 2004). A population's average metabolic rate determines the rate of resource demand, and also how a population's energy is divided between survivorship, growth, and reproduction (Savage et al. 2004). Because body size and body temperature determine metabolic rate, the dependence of population growth on mass and temperature explains most of the variability in population growth rates (Savage et al. 2004). Poikilotherms depend on ambient temperature to thermoregulate, hence their body size maxima are larger in warmer environments than in cooler environments (Savage et al. 2004; Albert and Johnson 2011). Additionally, while homeotherms demonstrate a rapid decay in growth at sexual maturity, poikilotherms typically grow indeterminately, and their growth is temperature dependent. Adult body size thus tends to be more plastic and reproductive output tends to be more variable for poikilotherms than for endotherms (Albert and Johnson 2011). Homeotherms thermoregulate metabolically, which enables them to maintain relatively constant body temperature regardless of environmental temperature, and so most variability in

24

their metabolic rates is the result of differences in body size alone (Savage et al. 2004; Albert and Johnson 2011). Carrying capacity and population density should thus be negatively related to body size. Density dependent responses in body size are thought to occur when populations are near K carrying capacity (Zedrosser et al. 2006). Between species, for many animals, population densities negatively correlate with body size, at a rate around -0.75 (which is the reciprocal of the rate at which metabolic rates increase with body size), such that all population's rates of resource demand are roughly equivalent. This is known as the energetic equivalence rule (see Damuth 2007 and references therein).

For mammalian herbivores such as ungulates, competition for browse occurs at high population density during the growing season. This should reduce adult body size by reducing ontogenetic growth (Lesage et al. 2001). This negative relationship between population density body size has been demonstrated in a variety of environmental contexts for white-tailed deer (see review in Huston and Wolverton 2011:357-359). High population density may also limit pregnancy rates, which has also been observed in red deer (*Cervus elaphus*) (Rodriguez-Hidalgo et al. 2010) and Japanese serow (*Naemorhedus crispus*) (Agetsuma 2007). Because pregnancy rates correlate positively with body size, these effects may be directly related. Loison et al. (1999:25) identified both a "lower threshold [of body size] below which all individuals died and an upper threshold, above which all individuals survived," and Moen and Severinghaus (1981) also suggested that, for white-tailed deer, there exists a

lower threshold of body size, below which individuals cannot survive. Within

species, body size differences between populations may result from phenotypic

responses of differences in food availability because of localized genetic

differentiation, or both (Barbraud et al. 2009).

Intraspecific variation in characteristics associated with differential

resource use may also occur between adult individuals within populations.

Precipitation is a determinant of primary productivity for ecosystems and

positively correlates with mammalian species richness (See Lyman and O'Brien

2005 and references therein). Higher energy availability to a system enables

more consumers to divide it. When all members of a population are

morphologically similar, an individual uses more of the population's niche. When

individuals are differentiated with respect to one or more characteristics, each

individual uses a smaller part of the population's niche, for which it is specialized

(Lyman and O'Brien 2005). If individuals in a population show much

differentiation in a trait that is of ecological relevance (such as body size), this

indicates individual differences in resource acquisition (Roughgarden 1972;

Lyman and O'Brien 2005). This enables larger populations to persist than could

otherwise (Van Valen 1965; Lyman and O'Brien 2005).

Environmentally mediated changes in body size also influence

demographic characteristics involved in phyletic diversification (e.g. reproductive

rates, population growth, population density, individual organismal vagility, and

gene flow) (Albert and Johnson 2011). Species adapt to differences in

environmental condition and to changes in environments by changing body size, and this may also give way to phyletic diversification (Hanken and Wake 1993; Albert and Johnson 2011). For example, Lyman and O'Brien (2005) tested the hypothesis that for arid areas, increased in precipitation positively correlates with morphological diversity within taxa. They focused on a number of phenotypes (but not genotypes) including body size, and size class richness lent support to this hypothesis. They concluded that ecophenotypic responses within species result from small climatic changes, and taxonomic turnover results from climate changes that are large enough to exceed the limits of plasticity. Miniaturization, which is a common life history strategy in both freshwater and marine fish (Albert and Johnson 2011), often results in novel morphologies and the emergence of higher taxa (Hanken and Wake 1993). Miniaturization is typically achieved through a reduction in growth rate but sometimes occurs via adjustment of the growth period. Diminution in size is typically associated with structural simplification, which can facilitate changes in function. This is often the route to the adoption of parasitism (Hanken and Wake 1993). For a given clade, associated with extremes in body size occur in individuals at extremely large or small sizes, and the amount of phenotypic modifications required at either extreme are approximately equivalent (Albert and Johnson 2011)

Variation in adult body mass may be achieved via adjustment of growth rate, birth weight, or maturation period (Southwood 1988; Sand et al. 1995; Solberg et al. 1998). Such patterns in growth are in themselves ecologically

relevant. They are adaptations to environmental conditions, and as such show dramatic variation between species (Pontier et al. 1989). Within species of large mammals, females with faster growth rates usually reproduce earlier, produce more and higher quality offspring, and have higher predator avoidance than smaller females, as has been observed in ungulates as well as in brown bears (Zeddrosser et al. 2006 and references therein). As a life-history variable, growth rate immediately after birth is the strongest determinant of environmental mortality risk (Zullinger et al. 1984; Pontier et al. 1989). Slow growth, long maturation periods, and long interbirth intervals are all associated with increased probability of population declines (see Govindarajulu et al. 2011 and references therein). Life history theory predicts that increasing populations should select for achieving reproductive status earlier. When population size is stable, adult mortality should exceed juvenile mortality and successful reproduction should therefore positively correlate with size, age, social status, and adult mortality. Under these conditions selection should favor lengthened ontogenetic growth periods (Stearns 1976).

For some vertebrate species, body size may positively correlate with age at maturity but not growth rate, although the two are not mutually exclusive. Additional opportunities for growth are sometimes realized by increase in the length of the maturation period (Bruce et al. 2002). Early maturation should be selected in environments in which mortality risk is high. Low mortality rates relax these pressures (Stearns 1992; Bruce et al. 2002). This has been confirmed in

reptiles and amphibians (see references in Bruce et al. 2002). Similarly, Sand et al. (1995) found body size differentiation in moose to be the result of increased maturation period and not growth rate, although Solberg et al. (2008) found differences in adult mass between males and females to be attributable to both combined. Adult moose in northern Sweden grew for two more years than southern Swedish moose. They showed no correlation in juvenile mass with latitude or adult body mass. Most of the variation in adult body mass was attributed to length of maturation period and rate of growth after the juvenile stage. However, they found no differences in adult skeletal dimensions between their study sites, indicating that the observed differences in mass were due to differences in reversible mass, and hence reflected differences in body condition and not in growth.

For mammals, patterns in growth may differ considerably between locations as growth patterns indicate adaptations to environment (Pontier et al. 1989). Within a single population, individuals may demonstrate a range of possible growth rates that all generate the same fitness because trade-offs exist between growth and mortality (Mangel and Stamps 2001). Despite the advantages of large body size at all ages, animals that grow faster sometimes have higher probabilities of mortality than animals that grow more slowly because of tradeoffs associated with faster growth. Examples include tradeoffs between growth rate and mature function, as peak efficiency is compromised in cells and tissues that are investing in growth and division; compromises between growth

rate and somatic development; growth rate and immune function, because of the energetic costs of immune system maintenance and coping with immunological stressors; and growth rate and resistance to physiological stressors (Mangel and Stamps 2001).

Growth rate may be a useful indicator of habitat quality for species in which it is environmentally mediated. In this case, average population-level growth rates are of interest. Many different procedures have been employed for estimating growth curves in animals; most have the flexibility to estimate multiple parameters such as birth mass, growth rate, and adult mass, and some utilize more biologically indeterminate terms such as inflection points. Use of growth functions is largely empirical. Values of their parameters are usually obtained by generating curves of best fit to data points (France et al. 1996). It is generally advantageous use a function whose terms are biologically meaningful (whose parameters represent an underlying mechanism or phenomenon), although functions that include indeterminate parameters may have the advantage of increased flexibility that enable them to generate a superior fit (Leberg et al. 1989; Bolker 2008). However, simpler models tend to make more accurate predictions unless a critical mechanism is ignored. This is because gaining accuracy by including more detail can result in loss of precision from error in estimating each of those details. This is known as the bias-variance tradeoff (Bolker 2008). Typically, one derives a growth curve function by integrating a differential equation in which "rate is a function of state." This "allows meaning to

be associated with the parameters..." (France et al. 1996:165). Some of the

more common methods are discussed here.

Commonly Used Growth Functions:

The Monomolecular Equation

The monomolecular curve was developed as a form of the law of

diminishing returns to describe the live weight of an animal as a function of its

food consumption by Spillman and co-workers at the United States Department

of Agriculture (France et al. 1996). Its assumptions are that growth is constant,

growth is independent of an organism's weight (W), growth is irreversible, and

that growth rate is proportional to substrate level (S). The rate of change of an

organism's weight over time (**t**) is defined as:

$dW/dt = \mu S$ *Equation 2.1*

where **μ** is a constant. Replacing substrate level **S** with the difference between

present weight (W) and final weight (W_f), Equation 1 becomes:

$dW/dt = \mu(W_f - W)$.   *Equation 2.2*

Setting W to its initial value (W_0) and integrating Equation 2 yields:

$W = W_f - (W_f - W_0)e^{-\mu t}$ *Equation 2.3*

W_f represents adult weight and is a horizontal asymptote. μ is the growth rate

parameter that dictates the steepness and shape of the curve; it describes the

rate at which growth slows over time. This is a simple growth function that

models growth without an inflection point; the rate of increase decays

31

continuously with time (France et al. 1996; Lopez et al. 2000; Solberg et al.

2008), which is typical of precocious mammals (Solberg et al. 2008).

The Von Bertalanffy Equation

The Von Bertalanffy equation is a forerunner of the Richards equation

(France et al. 1996), and is frequently used to model body growth metrics, such

as body length in fish and amphibians (e.g. Cloerne and Nichols 1978; Hjelm et

al. 2000; Bruce et al. 2002) and head circumference in brown bears (Zedrosser

et al. 2006). Like the monomolecular curve, this function models growth with

continuous decay in growth rate and no inflection point. The model assumes that

at the time of birth (t_0), body size (L) is at its minimum (L_{min}), which is a constant;

that growth rate is at its highest when body size is at its smallest ($dL/dt = L'_{max}$),

and that there is an upper bound to body size (L_{max}) (Cloern and Nichols 1978).

The rate of change in body size over time is thus defined:

$dL/dt = L'_{max} - b*(L - L_{min})$ *Equation 2.4*

Integration of this equation yields:

$L(t) = L_{max} - (L_{max} - L_{min})*exp[-b(t - t_0)]$ *Equation 2.5*

(Cloerne and Nichols 1978; France et al. 1996). Note that the final form of the

Von Bertalanffy equation is very similar to the monomolecular curve. The

difference is in the exponential term ($t - t_0$). and in some applications they may

take on the same form. If the time interval used begins at t - 0, then they are the

same function. This equation has been adapted in a number of ways; for

example, Cloern and Nichols (1978) adapted it to include seasonal variation in growth rate. There is also a sigmoidal form of this equation. Let $t-t_0 = x$:

$$L(t) = L_{max}{}^v - (L_{max}{}^v - L_{min}{}^v)*exp[-bx]^{1/v} \qquad \text{Equation 2.6}$$

where $0 < v < 1/3$ (Porter et al. 2010).

The Gompertz Equation

The Gompertz equation is a function that describes sigmoidal growth (with an inflection point). It assumes that growth is proportional to body weight, growth decays over time according to first-order kinetics, growth is irreversible, and substrate is not limiting. Let us begin with two separate rates: the rate of growth, μ, and the at which the growth rate decays through time, D, such that:

$$dW/dt = \mu W \qquad \text{Equation 2.7}$$

and

$$d\mu/dt = -D\mu \qquad \text{Equation 2.8}$$

Note that Equation 2.7 is the second derivative of change in weight over time. Integration of Equation 2.7 with the initial condition $\mu = \mu_0$ at $t = 0$ and substituting $dW/dt = \mu W$ gives:

$$dW/dt = \mu_0 W e^{-Dt} \qquad \text{Equation 2.9}$$

Integration of this equation at $t = 0$ and $W = W_0$ yields:

$$W = W_0 exp[\mu_0(1-e^{-Dt})]/D \qquad \text{Equation 2.10}$$

This curve approaches a horizontal asymptote (W_f) as t approaches infinite, such that:

$$W_f = W_0 exp(\mu_0/D) \qquad \text{Equation 2.11}$$

(France et al. 1996)**.** The point of inflection, *I*, occurs at W_f/e (France et al. 1996; Porter et al. 2010) The Gompertz function can now be rewritten as:

$W = W_{f*}exp(-exp(-\mu*(a-I)))$ *Equation 2.12*

(Zullinger et al. 1984). This function has been very popular in modeling growth in poultry (see references in Porter et al. 2010), but it has the limitation of a fixed inflection point (Porter et al. 2010).

The Richards Equation

The Richards Equation was originally derived from the von Bertalanffy equation (von Bertalanffy 1957), and thus carries the same assumptions. It was originally used to model plant growth (Richards 1959). It is useful in its generality as it encompasses the previous functions, but it owes its generality to an additional parameter, *n*, that is empirically determined and has no specific biological meaning (France et al. 1996). *n* determines the location of the inflection point and spans the range [-1,1]. Unlike the Gompertz equation, which has a fixed inflection point, the Richards equation demonstrates a movable inflection point that can occur at any fraction of the asymptotic (adult) weight. The rate of change of weight over time is modeled as:

$dW/dt = \mu W(W_f^n - W^n)/nW_f^n$ *Equation 2.13*

μ, W_f, and *n* are constant values. μ and *W* are positive. When *n* = -1, the equation becomes the monomolecular function (the point of inflection disappears). When *n* = 1 it becomes the logistic function. The Gompertz

34

equation can be derived at $n = 0$ (Porter et al. 2010). Integrating Equation 9 at

the initial condition $W = W_0$, $t = 0$, we obtain:

$$W = W_0 W_f / [W_0^n + (W_f^n - W_0^n) e^{-\mu ts}]^{1/n} \qquad \text{Equation 2.14}$$

Alternatively, the integrated form of the Richards equation can be written with n

replaced as *1-m*, and μ replaced as *2/T*(1 + m)*, where *T* is the length of the

ontogenetic growth period:

$$Wt = [W_f^{(1-m)} - \{W_f^{(1-m)} - W_0^{(1-m)} * e^{(-2*t/T)*(1+m)}\}]^{1/(1-m)} \qquad \text{Equation 2.15}$$

(Leberg et al. 1989; Maehr and Moore 1992). The parameter *m* now determines

the location of the inflection point as well as the growth rate. Equation 15 is an

even more flexible form of the Richards equation; at $m = 0$, it becomes the

monomolecular curve, at $m = 2/3$ it becomes a sigmoid version of the Von

Bertalanffy equation, at $m = 1$ it becomes the Gompertz equation, and at $m = 2.0$

it becomes the logistic function (Leberg et al. 1989).

    Other functions are sometimes borrowed and/or adapted from other areas

of biology to model growth; for example, the logistic curve can be used in this

manner (France et al. 1996), and Lopez et al. (2000) adapted the Michaelis-

Menten equation to model growth. The Michaelis-Menten equation was originally

derived to analyze allosteric enzyme kinetics (Segal 1975) from an equation

proposed by Hill (1913) to describe oxygen binding to hemoglobin. No model is

superior to all others in every respect; the most suitable model depends on the

dataset(s) to which the curve is fit and on the research objectives. For example,

in modeling salamander growth, Bruce et al. (2002) found the Gompertz equation

to provide superior fit to a variety of functions, which included the Von Bertalanffy equation. Lopez et al. (2000) found the adapted Michaelis-Menten equation to outperform the Gompertz equation and to perform equivalently to the Richards equation when tested on age specific body weights for 83 animal species. Zullinger et al. (1984) found the Gompertz and von Bertalanffy equations to outperform logistic function for 331 mammal species. Porter et al. (2010) tested the Richards equation, the Von Bertalanffy equation, Gompertz equation, and the Morgan equation (not reviewed here) on growth in turkey hens. They found the Morgan and Von Bertalanffy equations to outperform the Gompertz equation while Richards equation failed to converge. The choice of functions is often made by inspection of data plots (France et al. 1996) or by comparison of the performances of multiple models (e.g. Leberg et al. 1989; Lopez et al. 2000; Bruce et al. 2002; Porter et al. 2010).

Most studies of growth in the wild use data gathered from cohorts (e.g. Lopez et al. 2000; Maehr and Moore 1992; Zedrosser et al. 2006). This has the advantages of the resulting curves being representative of the entire ontogenetic periods of the individuals in the cohort and the precise ages of the individuals being known rather than estimated. Cohort data are thus less error-prone and less variable than population-level data, as population-level data are typically from harvests, ages are estimated and often reported in classes (Leberg et al. 1989; Gee et al. 2002), and curves generated from them are a compromise of a multitude of separate growth trajectories. Because of this, Bruce et al. (2002)

warn that using group data to model individual growth leads to increasingly biased age-specific mass predictions as age increases. However, sometimes population-level average growth rates are of interest where age-specific mass predictions are not needed. In this case, harvest records may be a simple, cost effective alternative to following numerous cohorts.

The use of population-level data from harvests to estimate average growth rates and maturation periods is not without precedent. Sand et al. (1995) used data from the regular hunting seasons to estimate population-level growth rates for moose for 14 separate populations using the Gompertz equation. Hunters recorded the dates, localities, masses, and collected the lower jawbones. Age was estimated to the nearest half-year by counting the annual cementum layers of the first molar, ontogenetic development, and tooth wear combined. Similarly, Solberg et al. (2008) used population-level harvest data to estimate sex-specific growth curves using the monomolecular equation for comparison of male and female growth trajectories. Sexual dimorphism is a very common feature in mammals. Interpreting sex-specific patterns in growth requires consideration of the ecological and evolutionary significance of the nature of sexual dimorphism in size.

Sexual Dimorphism in Mammalian Body Size

Males of most mammal species exhibit sexual dimorphism in body size, with males tending towards larger size than females (Pérez-Barbaría et al. 2003 and references therein). Differences in growth patterns are often studied

between sexes of the same species are of interest as they may reflect differences in habitat use (Leberg et al. 1993), and may also provide answers as to the evolutionary origins of an organism's mating system, as is the case for ungulates. There are three groups of explanations for the origins of the observed degree of sexual dimorphism in ungulate body mass: 1) Sexual dimorphism arises from mate competition in males, or that females select among males (the sexual selection hypothesis). 2) Large body mass increases the probability of polygyny, which increases the intensity of sexual selection; and 3) Sexual dimorphism arises as a result of males and females occupying different ecological niches (Pérez-Barbaría et al. 2002). Pérez-Barbaría et al. (2002) tested the origins of sexual dimorphism in ungulates by constructing a phylogeny based on morphological and paleontological data. They analyzed habitat type occupied by each species in their study, the mating system of each species, and the degree of sexual dimorphism exhibited by each species. They found that dimorphism arose after the occupation of open habitats. Ungulates were most parsimoniously monomorphic when first moving into open habitats, as polygynous mating system is more likely to arise in open habitats. This is evident because there is a strong correlation between polygyny and sexual dimorphism in body size, and rates of evolution towards higher dimorphism are faster in polygynous species. Patchy distributions of food resources, characteristic of open habitats, may lead to more intense competition as large males will

aggregate around productive patches and defend them. Polygynous mating systems then speed evolution towards higher sexual dimorphism in body size.

Rensch's rule predicts that, between species within a clade, sexual dimorphism correlates to body size; that is, the larger individuals of a given species, the greater the magnitude of differences in size between males and females (Blanckenhorn et al. 1999). Some authors have suggested that Rensch's rule results from sexual selection of large males combined with genetic correlations in size (Fairbairn and Preziosi 1994; Fairbairn 1997; Szdkély et al. 2004; Fairbairn 2005). This predicts that, within species, as mean body size increases along a productivity gradient, variance around mean body size will also increase, and that the larger sex will be more variable in body size (Blanckenhorn et al. 1999). Blanckenhorn et al. (1999) found that, within sexually dimorphic species, male body masses increase more steeply with latitude than female species, which lends support to this idea. Thus, for dimorphic species, studies of body size and growth patterns should consider males and females separately.

White-Tailed Deer as a Model Organism for Intraspecific Growth Patterns:

Barbraud et al. (1999) claim that the main problem with studies on body size in relation to life-history traits is that body size ranges within species are usually too small for quantitative analysis. White-tailed deer (*Odocoileus virginianus*) are a particularly suitable model organism for studying intraspecific body size differentiation and underlying growth patterns in mammals. They demonstrate a dramatic level of phenotypic plasticity in response to differences in

diet quality (Geist 1998; Lesage et al. 2001; Wolverton et al. 2007; 2009). Birth

weights have been shown to vary geographically according to Bergmann's rule

(Nelson and Woolf 1985). In southern Illinois, an area of high agricultural and

forest productivity, day-old fawns are estimated to average 2.9 kg and range from

2.5 to 3.3 kg (SD 0.3 kg) while in Oklahoma fawns are reported to weigh about 2

kg (4.41 lb.) (Bartush and Garner 1979). Schultz and Johnson (1995) detected

an influence of mass at birth on mass at mature ages. Leberg et al. (1993) found

the length of the growth period increased as body size decreased. This may be a

common feature in ungulates, as variability in maturation time related to food

availability has also been detected in moose (*Alces alces*) (Sand et al. 1995;

Solberg et al. 2008). High population densities place a limit on adult body size

due to intraspecific competition. This tendency affected males more strongly

than females and correlated negatively with population density (Purdue et al.

2000; Lesage et al. 2001; Comer et al. 2005).

It is likely that density dependence in adult body size occurs when

populations are near *K* carrying capacity (Zedrosser et al. 2006), as is often the

case with white-tailed deer. In North America, their populations underwent a

drastic decline due to hunting in the late 19th century. Their historic range is east

of the Rocky Mountains. By the early 20th century they had been extirpated from

much of their former ranges (Côté et al. 2004). Strict hunting regulations in the

1930s allowed them to increase and reclaim their former range, and now

currently expanding further west (Russell et al. 2001). By the mid-Twentieth

century, wolf extirpation from most of North America's boreal forests and prohibited deer hunting in many areas (McDonald et al. 2007), deer population growth increased dramatically and often reached or exceeded carrying capacity (Leopold et al. 1947). By the 1980s deer overbrowsing had severely suppressed tree regeneration, and consequently, deer physical condition had visibly deteriorated (McDonald et al. 2007). Populations remain dense in many areas, and competition for browse as a result of high population density often leads to a drastic reduction in body size (Kie et al. 1983; Lesage et al. 2001; Simard et al. 2008). This response allows population densities to remain high when food is scarce (Simard et al. 2008). Not only does this make deer especially suitable for studying density-dependent body size responses, but is also of wildlife management concern.

Much of the observed body-size variability in white-tailed deer is the direct result of food availability, which is evident from the common interaction between population density and body size (Wolverton et al. 2009), and from the observation that individuals with different allozyme genotypes do not tend to follow different patterns in growth (Leberg et al. 1993). Leberg et al. (1993) modeled population growth using the Richards equation to examine the sex-specific relationships between growth and population density. They found significant differences in growth patterns of deer between swamp and upland habitats and detected variation among cohorts in both sexes. For males, as population density increased, the length of the growth period increased and the

asymptotic mass (adult mass) decreased. They explained this as resulting from the energy requirements of mate competition and a higher tendency for males to use marginal habitats. Correlations of changes in body mass among age classes with population density were greater than those with total population density. The authors hypothesize that because faster growth requires more energy food shortages may impact males more severely than females. Large males may be less efficient competitors than females, and males may use less productive habitats and consume less nutrition.

High population densities often limit adult body size due to intraspecific competition, and this effect is particularly strong in white-tailed deer due to their high level of phenotypic plasticity (Kie et al. 1983; Geist 1998; Purdue et al. 2000; Lesage et al. 2001; Comer et al. 2005; Wolverton et al. 2007; 2009). This tendency affects males more than females, (Purdue et al. 2000; Lesage et al. 2001; Comer et al. 2005). This is likely because more calories are needed for rutting activities and because males more frequently inhabit marginal habitat than females. Leberg et al. (1993) observed sexual dimorphism in this species to correlate negatively with population density, in accordance with the general observations of Blanckenhorn et al. (2007). Therefore, males of this species, being the larger and more variable sex, should make for greater ease of observation of body size responses to differences in food availability or quality. Due to their larger sizes and corresponding lower relative metabolic requirements, males should require proportionally less reversible mass during

42

the rut (Clutton-Brock et al. 1982). If this is the case, then there is a trade-off between energetic investment in the current rut and body reserves for overwinter survival (Lesage et al. 2001).

For deer, phenotypic plasticity in body size is a key mechanism behind tolerance ranges to dietary stress. An individual's reaction norm, the "range of potential phenotypes that a single genotype could develop if exposed to a specified range of environmental conditions" (Stearns and Koella 1986:893), directly determines its tolerance range to environmental stressors. It is only when all individuals of a population are at their maximum size potential or the entire population is subject to the same selective pressures that natural selection acts on body size (Geist 1987).

The precise mechanism behind body size differentiation between white-tailed deer populations remains an open question. For deer, birth weight appears to be an important factor associated with later development. Schultz and Johnson (1995) detected a positive correlation between fawn mass and mass at maturation. For deer to realize their full body size potential, browse must be abundant and high quality during ontogenetic growth (Verme and Ullrey 1984). For white-tailed deer, fawns are fully weaned by two months following birth. High quality browse must also be available between birth and weaning because females in better nutritional condition produce richer milk, which increases growth rates in young (Geist 1987) and during gestational development (Loison et al. 1999; Pettorelli et al. 2002). In other words,

productivity during the growing season is a determinant of deer body size (Huston and Wolverton 2011).

Shultz et al. (1995) found positive relationships between body mass at specific ages and body mass at subsequent ages throughout the entire ontogenetic growth period, and for males they found a positive correlation between birth weight and growth rate. They conducted a study on the male offspring of captive females. Day-old fawns were weighed. After weaning, fawns were released into paddocks and cohorts were followed. One male from each cohort was reweighed shortly after they shed their antler velvet at 1.5 years of age and 2 years of age, and all males were reweighed shortly after they shed their antler velvet at 2.5 years of age. They used general linear models to determine effects of birth date, body mass at birth, and the interaction of these two terms on age-specific masses and on adult body mass. There was no association of birth date on body mass, but deer born heavier were heavier at all age classes. Males with higher birth masses gained more mass between birth and 1.5 years of age, indicating higher growth rates. They concluded that an optimal body mass at birth may exist due to the physiological costs of producing large offspring to females. Based on these results, the authors suggest that body mass may be a useful indicator of physiological status or condition, especially within the same sex and age class. These results suggest that there may be a positive relationship between birth weight and adult weight, and that deer differentiate body size according to development conditions by adjusting their

ontogenetic growth rates, although this does not exclude adjustment of the maturation period. From these results, and on the observation that reproductive success in red deer is linked to early growth (Clutton-Brock et al. 1982), Shultz et al. (1995) concluded that birth weight for male white-tailed deer may be a useful metric for early growth, survivorship, and reproductive potential. If this is the case, then for this species population average growth rate estimates may also serve as an indicator for overall reproductive potential at later ages, as well as for phenotypic quality. Since these variables are dictated by environmental conditions, growth rate may also serve as an indicator of habitat quality, with the advantage that it would require no consideration of a population's age structure. Data on age-specific body mass for white-tailed deer are readily available in the form of harvest records. A method of estimating growth rates that is suitable for use with harvest record data, in which age estimates are often reported in ordinal-scale classes, would be a valuable tool in wildlife management for deer as well as their habitats.

Lesage et al. (2001) tested the effects of population density and winter severity on white-tailed deer by tracking growth within cohorts between different hunting regions. Growth was tracked between areas of high density/severe winters, high density/mild winters, low density/severe winters, and low density/mild winters. The low density hunting regions produced deer that were larger than the high density hunting regions. They found a reduction in growth in deer in the high density/severe winter hunting region, but the low-density/severe

winter hunting region produced some of the largest deer in North America. From

this it was concluded that the observed differences in growth pattern resulted

from intraspecific forage competition and not climatic differences. They tested

the performances of the Von Bertalanffy equation, the logistic equation, and the

Gompertz equation. For their data, the Von Bertalanffy equation to generated

the best fit. They found variation in sexual dimorphism between the high-

density/mild winter hunting area and the high-density severe winter hunting

areas. This suggests that dietary stress affect males and females differently.

They also found that sexual dimorphism (larger males) in this species is the

result of males having a longer ontogenetic growth period. For males, faster

growth occurs where growth periods are longer, which is determined by food

availability.

Phenotypic plasticity, in combination with a tendency to switch to less

preferred plant species when preferred species are scarce, enables them to

avoid starvation, often at the expense of the plant community (Weckerly 1994;

Waller and Alverson 1997; Taillon et al. 2006). Mammalian herbivory causes

pronounced changes in plant morphology. The most common is the production of

abundant lateral stems in woody plants as a result of terminal meristem removal.

Another common effect is browse line (Russel et al. 2001). Deer have been

shown to reduce survival rates of some plant species and may inhibit adult

recruitment (Russell and Fowler 1999). If deer lower the probability of survival

for individual plants in a population, they may also alter that population's growth

rate. Impacts on the plant community have been shown to cause cascading

effects on some animal species, including birds, mammals, and insects (Waller

and Alverson 1997; Côté et al. 2004). Dense deer populations have been shown

to eliminate the replacement of a number of tree species compared to protected

areas (Kie et al. 1983). Enclosure studies have also shown that deer can reduce

species richness of the regenerating tree community (Stromayer et al.1997). In

the context of early successional habitat, deer may affect the rate as well as the

direction of succession, giving rise to alternative stable states of lower plant

diversity (Côté et al. 2004; Stromayer et al.1997). Thus, deer management is

important not only for the economic and aesthetic importance of deer, but also for

the management of the ecosystems that they inhabit.

CHAPTER III

EFFECT OF POPULATION DENSITY ON JUVENILE GROWTH RATE IN
WHITE-TAILED DEER

Introduction

The geographic distributions of and ecological mechanisms underlying body
size variability in large mammals are subjects of much interest in animal ecology
(Rosenzweig 1968; McNab 1971; 1983; Meiri et al. 2004; Rodríguez et al. 2006;
McNab 2010; references cited in Huston and Wolverton 2011). Much of the
literature on animal body size focuses on Bergmann's rule, but there is little
agreement among ecologists concerning what mechanisms cause differences in
animal body within and between species (Meiri and Thomas 2007; Huston and
Wolverton 2011). McNab (2010) describes the literature on Bergmann's rule and
body size as "chaotic," and he argues that many studies are undertaken at
geographic and taxonomic scales that will not elicit understanding of the
underlying biological mechanisms that drive variability in body size. Huston and
Wolverton (2011) conclude, along with many other ecologists (e.g., Meiri et al.
2007), that there is much to be gained by studying intraspecific variability in body
size at multiple spatial scales. A meaningful way to examine intraspecific
patterns in body size is to study variability of ontogenetic growth rate in
populations or sub-populations of a species inhabiting areas with variable food

48

quantity and quality. (Maehr and Moore 1992; Sand et al. 1995; Solberg et al. 2008).

The white-tailed deer (*Odocoileus virginianus*) is a species that is studied in great detail in terms of the relationships among body size, growth rate, habitat quality, and population density at several spatial scales (Kie et al. 1983; Simard et al. 2008, Tremblay et al. 2005; Wolverton et al. 2009). Clearly these studies demonstrate interesting patterns indicating that food availability dramatically influences growth rate and body size in this species. The white-tailed deer is a highly phenotypically plastic species in terms of body size (Geist 1998), which accounts for much of its variability in size and growth. In order to more clearly understand the mechanisms underlying these patterns, however, it is useful to closely examine the relationship between food availability and growth rate during distinctive ontogenetic periods. Under what conditions does large body size develop? Does large body size in among members of a population or subpopulation develop mainly in the early periods of growth, and does the growth period last longer in some populations than in others? These questions about growth are answered in a variety of ways for white-tailed and other cervids at a variety of spatial and temporal scales (Kie et al. 1983; Reimers et al. 1983; Jacobson 1984; Strickland and Demarais 2000; Mysterud et al. 2001; Schmidt et al. 2001; Jones et al. 2008); here the relationships among population density, food availability, growth rate, and body size are examined for a single population

for which detailed harvest records have been kept for several decades in Fort Hood, Texas.

Background

Large body size may confer a number of selective advantages depending on environmental conditions. Larger individuals are more starvation resistant due to a reduction in the relative energy requirement, which is advantageous in seasonal environments (Geist 1987; Lindstedt and Boyce 1985). Larger females are able to produce more and larger offspring, which grow faster and have higher chances of survival, and larger males typically have an advantage in competition for mates (Monteith et al. 2009; Huston and Wolverton 2011). Larger individuals often have an advantage in predator avoidance (Geist 1987) and in acquiring resources. Smaller species, on the other hand, have an advantage in energy conservation (Jones and Purvis 1997).

Carl Bergmann (1847) originally proposed that thermoregulation drives body size differentiation within clades; that is, he argued that the ratio of an organism's internal heat production to its surface area heat loss favors larger body sizes in cooler climates and smaller body sizes in warmer climates (James 1970). The correlation between larger body size and cooler climate is well documented within and between species, with notable exceptions: In some clades, the reverse of Bergmann's rule manifests (Mayr 1956; Ashton et al. 2000; Meiri et al. 2004). This relationship and its converse are no more than empirical generalizations, however (Meiri 2011). Heat conservation is an unlikely

explanation on a number of grounds (Scholander et al. 1950; Geist 1987; 1998).

The positive relationship between body size and latitude tends to reverse below

60° north latitude (McNab 1971; Geist 1987; Huston and Wolverton 2009; 2011),

and smaller species follow the trend less often than biophysical modeling

predicts (Ashton et al. 2000). Phylogenetic reconstructions reveal that

exceptions to Bergmann's rule tend to cluster together within mammals and

squamates and most likely arose independently (Queroz and Ashton 2003).

Thus, the tendency for body sizes to increase with latitude most parsimoniously

arose before endothermy. In fact, the presence of Bergmann's rule in many

ectotherms is evidence against thermoregulation as the mechanism (Ashton and

Feldman 2003; Entling et al. 2010).

There are other observed ecogeographic trends in body size. Cope's rule

is the tendency in mammalian body size tends to increase through time (McNab

2010), which is typically explained by selective advantages of large body size

(Stanley 1973; McNab 2010). Mammalian body size often decreases upon

entrance into desert environments (Yom-Tov and Nox 1986; Yom-Tov and

Geffen 2006) and when species invade islands (Foster 1964; Van Valen 1973).

McNab (2010) argues that resource availability drives all of these patterns and

dubs this explanation the resource rule. However, Geist (1987; 1998) developed

this idea earlier, linking latitudinal patterns in body size to the global distribution

of growing season length and soil fertility. Huston and Wolverton (2009; 2011)

linked Geist's ideas directly to the global distribution of evolutionary and

ecologically relevant net primary production (eNPP), or growing season, which they termed Geist's rule or the eNPP rule for body size.

Because Bergamnn's rule is the most widely known and studied ecogeographic rule pertaining to body size, much of the evidence for the resource rule comes from studies regarding the correlation between body size and latitude. A number of environmental variables correlate with latitude, notably productivity and seasonality, both of which influence nutritional availability. Seasonality is predicted to favor larger body size due to fasting endurance (Lindstedt and Boyce 1985) until it reaches a threshold past which body size becomes limited (Geist 1987; Wolverton et al. 2009). Limitations of food availability often reduce growth rate and adult body size (Arnett and Gotelli 1999). This predicts that body size should decrease at high latitudes, as noted by McNab (1971) and Geist (1987). Rosenzweig (1968) observed that temperature and latitude are both good predictors of body size in carnivores, but temperature performs no better than latitude, which implies that it is not the proximate driver. He found that actual evapotranspiration, used as a proxy for primary productivity, to be superior correlate, particularly in areas of low productivity (but see discussion in Huston and Wolverton 2011).

Granting that there is much disagreement over whether ecogeographic trends should be studied interspecifically or intraspecifically, there are some clear advantages to the intraspecific scale when correlating body size to nutritional availability. There may be issues regarding the use of different body size metrics

between different taxa (Blackburn et al. 1999). Between species, there are logistic difficulties in separating environmental influences on body size from those of taxonomy (McNab 2010; Huston and Wolverton 2011) and community assembly; patterns in animal body sizes within communities are difficult to detect reliably. Mean species body size requires scaling to population size, and it is very difficult to census a character such as body mass for an entire community. Differences in relative abundances between large and small species may thus generate artifactual patterns (Meiri and Thomas 2007). Species richness may influence body size patterns; Blackburn and Gaston (1996) found species richness to predict body mass more strongly than latitude in New World birds, and body size ranges are higher where species diversity is low (Meiri and Thomas 2007). Spatial scale and site selection may also interact to confound analyses. Within a given site, species with widespread distributions tend to be more common than species with smaller distributions, and all species are rare in some parts of their distributions (Blackburn and Gaston 1998). Because population density affects body size, intraspecific population density differences may affect average body size estimates at the community level. It may be challenging or impossible to separate these effects from the influence of primary productivity. A possible solution to this challenge is to examine the influence of food availability within one species, within one geographic range, and within a timescale during which assuming a relatively constant species richness is reasonable. The near universality of interaction between population density and

body size (Damuth 1981; Calder 1984; Damuth 1987; 1991) indicates that food

availability per individual affects ontogenetic growth. Geist (1987) claims that for

mammals, "Body size is so sensitive to nutrition (size differences due to

environment quickly mask those due to genetics) that only when all members of

a population have grown to maximum size, or are subject to an identical

environmental regime, is selection for size effective." If this is the case, then

phenotypic plasticity in body size is a critical determinant of tolerance ranges to

dietary stress. The precise mechanism(s) behind realizing such differentiability is

an open question.

White-tailed deer (*Odocoileus virginianus*) are particularly well suited to

this type of analysis. They demonstrate a dramatic level of phenotypic plasticity

in response to differences in diet quality (Geist 1998; Lesage et al. 2001;

Wolverton et al. 2007; 2009). Birth weights have been shown to vary

geographically according to Bergmann's rule (Nelson and Woolf 1985): In

southern Illinois, an area of high agricultural and forest productivity, day-old

fawns are estimated to range from 2.5 to 3.3 kg (5.51 to 7.23 lb) while in

Oklahoma fawns are reported to weigh about 2 kg (4.41 lb) (Bartush and Garner

1979). Schultz and Johnson (1995) detected an influence of mass at birth on

mass at mature ages, and Leberg et al. (1993) found the length of the growth

period to increase as body size decreases. Variability in maturation time related

to food availability has also been detected in moose (*Alces alces*) (Sand et al.

1995; Solberg et al. 2008). High population densities place a limit on adult body

54

sizes due to intraspecific competition. This tendency affects males more strongly

than females and correlates negatively with population density (Purdue et al.

2000; Lesage et al. 2001; Comer et al. 2005). Such adaptability makes for

relative ease of observation of body size responses that may generalize to other

mammalian taxa. Body size differentiation may be achieved by one or any

combination of three possible strategies: Differentiating birth weight,

differentiating growth rate, and differentiating maturation period, depending on

the fitness tradeoffs associated with each (Southwood 1988; Sand et al. 1995;

Solberg et al. 1998). Data on age-specific body masses for white-tailed deer are

readily available in the form of harvest records.

Materials and Methods

This study tests the hypothesis that phenotypic plasticity in adult body

mass is achieved by varying juvenile growth rate in white-tailed deer. Harvest

records were obtained from the Fort Hood military base in Central Texas

(31°7'48" North, 97°46'49" West). Wildlife management on the base has

meticulously kept records on white-tailed deer harvests, including relatively fine-

scale data on the location of the kill, age, sex, dressed body weight, and antler

characteristics. Dressed body weight was used as the body size metric.

Records begin in the year 1971. Spotlight surveys and age structure shifts

towards younger individuals indicate that population density on the base has

steadily decreased since records have been kept (Wolverton et al. 2009), and

body sizes on the base have increased accordingly (Wolverton et al. 2007;

55

2009). Ages were estimated by tooth wear (Severinhaus 1949) and assigned to

age classes represented by the corresponding integer plus half year (i.e.

fawns=0.5, yearlings=1.5, 2.5, etc.). Because males and females demonstrate

differing levels of phenotypic plasticity in body size and have maturation periods

of differing lengths (Shaw et al. 2006), this study is limited to bucks. Growth

curves were estimated via non-linear least squares curve fitting (NLS) for every

year from 1971 to 2002. To minimize the influence of interannual differences in

ontogenetic growth rate due to maternal effects, each growth curve includes only

individuals estimated to have been born in the same year. Individuals for each

growth curve were thus selected by the following equation:

$$I = \sum_{i=0}^{i=4} Bt + i, a + i$$

Equation 3.1

where I = all individuals selected for the growth curve, t = year corresponding to

the start of the growth curve (year of birth), a=age class, starting at 0.5 (fawn),

and $B_{t,a}$ = individual bucks included. Outliers were excluded for the year 1971 (3

lb. 2.5 yr.), 1972 (0 lb. 1.5 yr.), and 2002 (11 lb. 2.5 yr.). Error from age

estimation is expected to be low in the first three age classes (0.5-2.5), and less

than 30% in the 3.5 age class. The 4.5 age class was included to capture the

entire growth period for males, although error is expected to be high as tooth

wear becomes increasingly error prone as age increases (Gee et al. 2002). Deer

that utilize supplemental feeders are almost exclusively older males, beyond the

4.5-year age class (Bartoskewitz et al. 2003), and because there are some feeders in the area older deer may have body masses that are artificially elevated independently of the effects of population density and habitat quality. For these reasons, age classes beyond 4.5 years were excluded.

Methods for estimating population-level growth curves for mammals are well established (Richards 1959; Maehr and Moore 1992; Leberg et al. 1993; Sand et al. 1995; France et al. 1996; Gaillard et al. 1997; Frie et al. 2003; Garel et al. 2006; Solberg et al. 2008). A variety of curve fitting procedures for assessing ontogenetic growth rate, estimate birth weights, estimate adult weights, and evaluate maturation periods exist. Because these methods estimate multiple population-level parameters, they require ratio scale data for both the independent and dependent variables. Ratio scale age estimates are rarely available from harvest record data. The most common method of estimating age for white-tailed deer is that of Severinghaus (1949): Estimation based on tooth eruption and wear. This method is prone to error from differences in dietary composition, interobserver subjectivity, and high variability in tooth wear between individuals (Gee et al. 2002). Values assigned represent the midpoints of age classes and are not a continuous variable. Age estimates by the Severinghaus technique are thus ordinal scale and must be treated accordingly. Therefore, curves built by fitting harvest record data are unsuitable for making predictions such as birth weight or asymptotic weight. Growth rate estimates obtained from fitting curves that contain these parameters may be too

57

variable to detect inter-annual variability. Thus, this study employed a simpler

method. Although there is evidence that changes in population density may

affect the length of the maturation period (Leberg et al. 1993), lack of confidence

in assignments of older age classes renders these data unsuitable for evaluating

the length of the maturation period. Harvest record data in which age

estimations are error prone (or unknown) are suitable for analysis of growth rate

only.

 There is a great deal of variability in white-tailed deer body sizes in the

yearling age class due to differing maturation rates and rapid growth. In addition,

a positive relationship between body mass at birth and body mass into the 1.5

year and 2.5 year age classes exists, and higher masses at birth (hence at 1.5

years) may positively correlate with adult body mass (Schultz et al. 1995). Birth

weights can vary, and this variation exerts influence on body weight at later ages.

After birth, white-tailed deer growth is rapid and levels off without an inflection

point, a pattern common in precocious mammals (France et al. 1996; Solberg et

al. 2008). In order to fit a continuous function to this pattern using a single

parameter, a monotonic increasing function with a monotonic decreasing

instantaneous rate of change is needed. Let r = the overall growth rate

throughout the ontogenetic period. Let M_a = mass at age a. The instantaneous

growth rate, *dM/da,* is calculated by dividing r by the individual's age, which

produces a monotonically decreasing function (*equation 2*).

dM/da = r/a   *Equation 3.2*

The integrated form of this function is as follows:

$$M_a = r \cdot \ln(a) + c \qquad\qquad\qquad\qquad\qquad Equation\ 3.3$$

The parameter r, estimated by NLS, determines the shape and the steepness of

the curve. This is used to compare interannual variability in ontogenetic growth

rate. The constant of integration, c, was also estimated by NLS and determines

the height of the curve above the x-axis. Deer body sizes at all age classes

influence the value of c but because it is additive it does not influence the shape

or steepness of the curve. This equation was adequate for the purposes of this

study because we make no predictions of age-specific body mass; curves were

simply fit to data points to compare interannual variability. Because a logarithmic

curve displays a vertical asymptote at the y axis, there is no y intercept (birth

weight) to affect the slope of the curve; fitting the data points determined the

slope entirely. The horizontal asymptote (adult weight) is not a term within the

equation, so neither did its estimation affect the slope. Least squares procedures

tend to underestimate slopes when there is error in the independent variable

(Jones and Purvis 1997); however, because this condition was consistent

throughout the study period the data are still suitable for interannual slope

comparisons. A consistent increase in values of r through the study period

indicate increased growth rate in response to increased nutritional availability,

while increases in values of c through the study period are indicative of overall

increases in body size, which is already demonstrated (Wolverton et al. 2009).

Statistical Analyses

A Pearson's correlation test was calculated between **r** values and year to demonstrate the strength of the increase in growth rate through time. To demonstrate the need for this simplified technique, analyses were repeated using the monomolecular equation (Equation 4; Natanson et al. 2006), the Gompertz equation (Equation 3.5) (Zullinger et al. 1984), and the Richards equation (*equation 3.6*) (Leberg et al. 1989).

$$M_a = M_\infty - (M_\infty - M_0)*exp(-K*a) \qquad\qquad Equation\ 3.4$$

$$M_a = M_\infty * exp(-exp(-K*(a-I))) \qquad\qquad Equation\ 3.5$$

$$M_a = [M_\infty^{(1-m)} - \{M_\infty^{\ (1-m)} - M_0^{\ (1-m)}\}*exp(-2*a/T)*(1+m)]^{1/(1-m)} \qquad\qquad Equation\ 3.6$$

K in Equation 3.4 and Equation 3.5 are growth rate constants, I in Equation 5 is the age at the point of inflection, m in Equation 3.6 is the Richards shape parameter, and T in Equation 3.6 is the estimated length of the maturation period, which was held at a constant 4.5 years according to the findings of Monteith et al. (2009). Adult body masses (M_∞), growth rate constants, and I were estimated using NLS. Resulting curves were graphed for comparison to the results of *Equation 3,* and interannual changes in K and m were tested by Pearson's correlation. M_0 was held at a constant 1 kg, ~ 1/2 of the literature values of birth weights (Nelson and Woolf 1985) because dressed body weight for fawns is about half of live fawn weight. W_∞ was compared to median body sizes for adults to determine if these estimates were reasonable. This is an important consideration because for Equations 4-6 because asymptotic mass

60

affects the values of the slope parameters. All analyses are performed using R version 2.9.2 (2009-08-24).

Results

With some year to year stochastic variation (especially prior to the mid-1980s), the steepness of the curves generated by Equation 3 showed a clearly discernible increase through time (Figure 1). Note that changes in weight distributions were the greatest for the first two age classes. Deer make the strongest growth rate adjustments to environmental conditions during the first two years of life. Growth rate parameter values (r) increased throughout the study period (Figure 2a). A Pearson's correlation test was calculated to determine the strength of this increase. A significant result was obtained ($F(1,30)$=133.8, multiple r^2=0.82, P=1.39E-12). Deer increase adult body size in response to increased nutritional availability by increasing their juvenile growth rates.

To demonstrate the need for this simplified procedure, body size data were fitted to Equations 4-6 by NLS. These equations generated curves that are very similar to those of *equation 3* (Figure 3a-3d). Pearson's correlation tests were calculated for K **(Equations 4 and 5)** and m **(Equation 6)** over time. A significant result was obtained for Equation 4 ($F(1,30)$=36.4, multiple r^2=0.55, P=1.27E-6). The monomolecular equation detected a significant trend in changes in growth rate (K) over time for these data, albeit with less explanatory power than Equation 3 due to higher variability in estimates of K (Figure 2b). A significant result was not obtained for Equation 5 **(**$F(1,30)$ = 1.661, multiple r^2 =

61

0.052, P = 0.21). The growth rate parameter within the Gompertz equation was too variable to detect interannual increases through time in this dataset (Figure 2c). A significant result was obtained for Equation 6 ($F(1, 30)$ = 11.22, multiple r^2 = 0.2479, P = 0.0022). The Richards equation detected a weak increase through time for this dataset due to high variability in estimation of m (Figure 2d). Table 1, Table 2, and Table 3 demonstrate the accuracies of Equation 4, Equation 5, AND Equation 6, respectively, in estimating adult (asymptotic) weight by comparison to median dressed body weight of the 4.5 age class. This is relevant because error in estimation of this parameter affects the estimates of the growth rate parameters. The error columns reflects the difference between asymptotic mass and median dressed body mass. We must bear in mind that median body mass is not a perfect estimate of population mean, but if asymptotic estimates are as reliable as medians, the number of cases in which the error is negative should be comparable to the number of positive cases. Equation 4 returned a negative value in 12/32 cases (Table 1), which suggests that this equation tends to overestimate adult mass. Error estimates are relatively low in most cases, but is as high as 13.86% of the median body mass. Equation 5 returned negative values for 18/32 cases (Table 2), which is reasonable. However, this equation failed to detect an increase in rate over time, and error estimates are as high as 15.77% of the median. Equation 6 returned a negative value for all years except one (Table 3), indicating that the Richards equation consistently underestimates adult body mass for these data, and by as much as 22.97% of the median.

Discussion

Despite the limitations of harvest record data in estimation of population level growth parameters due to an ordinal scale explanatory variable (age class), these analyses clearly show that white-tailed deer increase ontogenetic growth rate in response to increases in nutritional availability. This differentiation occurs primarily in the early juvenile stages of life. This does not exclude adjustment of birth weight and maturation period as mechanisms, which have already been shown. The former is a manifestation of the same phenomenon as adjustment of juvenile growth rate, as differences in fawn weight reflect differences in growth rate prior to birth. This lends support to the idea that maternal effects play a role in determining growth rate and adult body mass for white-tailed deer.

These results are of ecological and evolutionary significance, as they provide insight into a powerful life-history mechanism. Schluter (2000) proposes a positive relationship between specialization and rates of evolution, while generalized morphological characteristics evolve more slowly. Charnov (1993) and Kozlowski and Weiner (1997) propose that body size is strongly related to traits that shape evolutionary rates (population density, metabolic rate and speed of life history). Cooper and Purvis (2010) found consistent positive correlations between body size within clades and rates of evolution. White-tailed deer are relatively small among cervids, and as dietary niche generalists they are very resilient to evolution (Geist 1998). Adaptability in body size within this species is a critical part of its generalist strategy; phenotypic plasticity in body size endows

63

this organism with a high tolerance range for dietary stress. This high tolerance

range has enabled deer to inhabit a very diverse array of habitats and has

rendered them to remain relatively unchanged over evolutionary time. These

analyses demonstrate that adjusting rate of growth is a key mechanism behind

this tolerance range. Such insight into the inner workings of this response gives

direction to further studies on species turnover; under what conditions does

morphological adaptation fail to shield the genotype from selective pressure?

How is phenotypic plasticity involved?

　　We must remember that these curves are abstractions; they are crude

estimations of population-level central tendency in a characteristic that is difficult

to measure in individual wild animals. The strong correlation demonstrated with

increase through time is particularly telling; increase in time is simply a correlate

of decrease in population density, which is a correlate of increased nutritional

availability (the explanatory variable of interest). With this in mind, and given the

limitations of harvest record data, for adjustment in growth rate over time to be

detectable it must be ecologically significant, and for the correlation to have an r^2

value of 0.82 it must be particularly strong, the possibility of adjustment in birth

weight and maturation period notwithstanding. Selection for adjustment in

growth rate makes intuitive sense; higher predatory pressure causes a younger

age structure to emerge within a population of a prey species. During times

when population density is low, large-bodied phenotypes have a selective

advantage over small-bodied phenotypes, and if low population density is the

result of high probability of mortality, achieving large body size quickly and leaving larger offspring sooner is realized more readily. This confers a much stronger fitness advantage than growing for a longer period of time.

Keyser et al. (2005) warns wildlife managers not to expect immediate physical condition responses in white-tailed deer to changes in population density, because recruitment responds more quickly. McNulty (1997) found support for the hypothesis that phylopatry of females tends to stymie recolonization of depopulated areas, and that low population density would likely persist for several years, perhaps over a decade. White-tailed deer were previously extirpated from Fort Hood, reintroduced in the middle of the twentieth century, and rose to irruptive population levels before hunting was allowed on the base. Maternal effects have been shown to influence deer body sizes through two generations (Monteith et al. 2009), and deer have relatively long reproductive spans. This can cause considerable time lags in population responses to environmental conditions, which may be time lagged themselves because vegetation may take time to recover from overherbivory. These phenomena may have interacted to generate the high variability in r values seen in Figure 2a prior to the mid-1980s, although without records prior to 1971 and without environmental data this cannot be tested.

Management Implications

Understanding phenotypic plasticity is important for the management of white-tailed deer in particular as well as management of their habitats.

Competition for browse as a result of high population density often leads to a

drastic reduction in body size (Kie et al. 1983; Lesage et al. 2001). This renders

the species very resilient to resource limitation, and as a result, deer in the

absence of predation may cause drastic shifts in plant community composition

and reductions in species richness before food shortages limit population density

(Russel and Fowler 1999; Rooney 2001; Russell et al. 2001; Russell and Fowler

2004; Simard et al. 2008). This is of particular management concern for deer

and for their habitats. Deer overherbivory can lead to cascades that impact

songbirds and lepidopterans (Waller and Alverson 1997), and dense white-tailed

deer populations in early successional stages may lead to establishment of

alternate stable states (Seagle 1993; Stromayer et al. 1997). Keyser et al.

(2006) suggested that relationships between physical parameters and

environment, in their case body size and antler measures, are useful in making

herd-management decisions regarding population density and physical condition.

The same may hold true for growth rate parameter estimates, which have the

advantage of being independent of the effects of age structure of the population

and can be easily reconstructed from harvest record data.

This study provides a simple and effective method for estimating growth

curve parameters from data sources that are not necessarily well suited to more

complex modeling techniques. Of course, for datasets in which the independent

variable and dependent variable are both ratio scale, more complex methods are

highly preferred as they are able to evaluate multiple parameters and interannual

variability therein. However, these methods are not advised for harvest record data for which age is estimated by tooth wear, by unknown methods, or is otherwise represented by age classes. Fitting the monomolecular, Gompertz, and Richards equations to the same data points weakened the power to detect changes in growth rate through time, and if used with other sets of harvest record data with higher short-term interannual variability they may result in failure to detect patters that are present. All parameter estimations introduce opportunities for additional error, and if the growth rate parameter interacts with these estimates, they will further increase its error (Bolker 2008). It is noteworthy that, for the methods tested here, the more complex the equation in terms of parameter estimates, the lower the power to detect changes in growth rate. The simplest of the established methods is the monomolecular equation, which estimates a growth rate parameter and adult body mass. The Richards equation contains essentially all of the same terms as the monomolecular equation but includes additional exponential variables, and it demonstrated less power in detecting interannual variation in growth rate than the monomolecular equation. The Gompertz equation estimates three parameters (growth rate, adult mass, and inflection point) and failed to detect any significant change in growth rate. Monteith et al. (2009) used form of the Von Bertalanffy equation that includes an inflection term to model growth in a captive-reared cohort of white-tailed deer, under the assumption that deer growth undergoes a positive exponential phase very early in life. This equation fit an inflection point between the ages of 151 to

190 days. The Gompertz equation used here found age at inflection to be from 0.25 to 0.63 years (91 to 225 days) old. While comparable, this is a much wider range. This no doubt reflects error in inflection estimates that stems from the lack of precise birth weights. Error in the inflection point estimates in turn leads to error in the other growth parameters. This may account for the Gompertz equation's failure to even detect a growth rate increase that is visually apparent. Given that inflection occurs at roughly the same age as the midpoint of the first age represented in harvest records (0.5 years), it is neither necessary nor advised to evaluate this parameter with harvest record data.

In this instance, the value of the birth weight estimate was held constant based on published values for white-tailed deer neonatal weights in Oklahoma (Bartush and Garner 1979) across all years. It is unknown how representative these values really are, and it is unlikely that birth weights remained constant during the study period. Asymptotic mass parameters deviate sizably from the median of the highest age class for some years, which no doubt affected the values of growth rate parameters and diminished the models' explanatory power. A solution to this would be to use mean or median adult body mass values for each year rather than estimating this parameter via NLS, but sample averages are not perfect representations of the populations they represent, so this still needlessly introduces error into the slope parameter estimation. Also, this would be cumbersome as compared to repeatedly applying the exact same equation.

Harvest data are at times questioned as error laden or of poor quality compared to data generated from pure research in wildlife biology. However, harvest datasets are common and tend to be large samples. A solution to potential problems of data quality is to analyze harvest data at ordinal scale. The method proposed here fits a curve to data points using a single direct parameter and is not subject to these issues, and on this dataset, it has performed well. The shape of growth curves can tell the manager a lot about the ecology of a population. Not only can harvest data, thus be used to assess demography, but aspects of growth and body size can better be studied on a population by population basis for purposes of serving quality deer management, sustainable harvest, and/or other management goals.
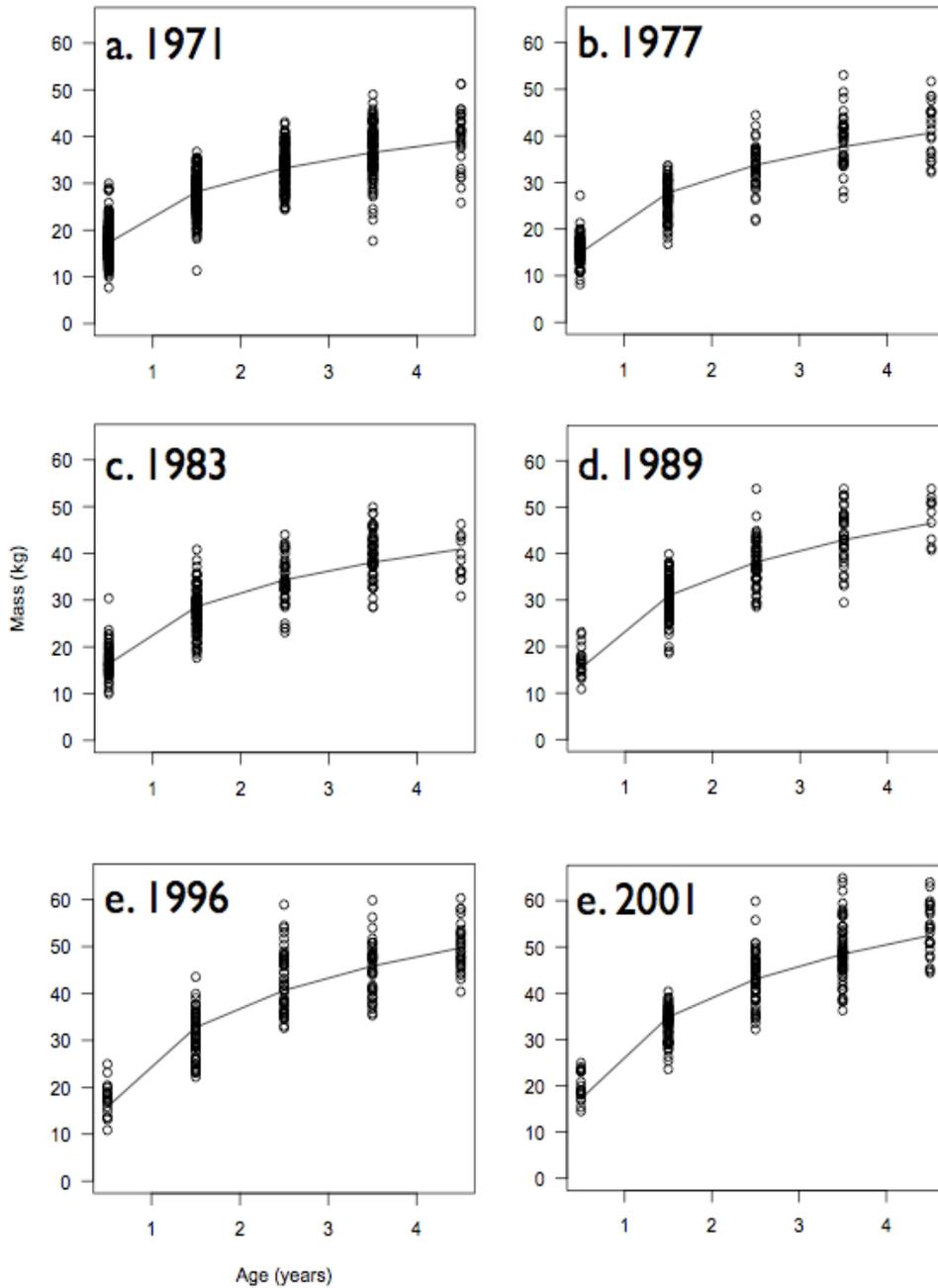
Fig. 1 Logarithmic growth curves of every sixth year of the study period. A clear increase in growth rate (steepness of the curve) throughout the study period is visually evident.
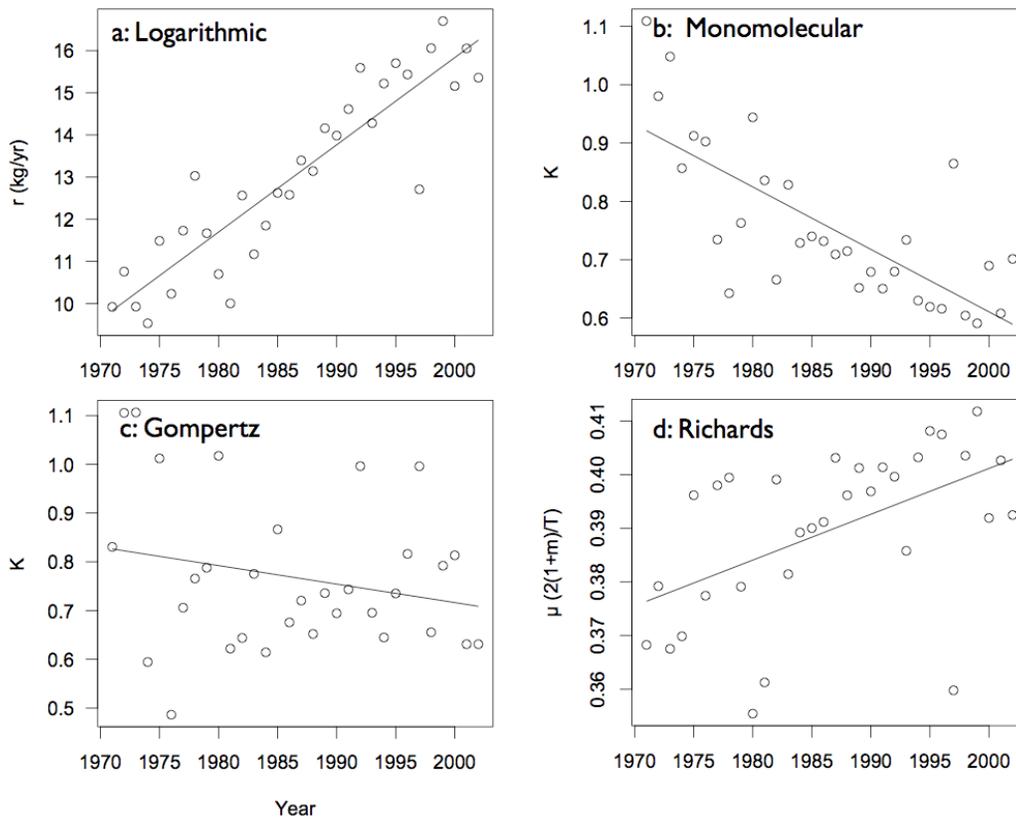
Fig. 2a Increase in r values (Equation 3.3, kg*yr^{-1}) from 1971 to 2002. Because this is the only parameter estimated by the logarithmic equation, this method results in lower residual variability and has the highest power to detect interannual changes in growth rate. A highly significant trend is detected ($F(1,30)$=133.8, multiple r^2=0.82, P=1.39E-12).

Fig. 2b Decrease in K values (Equation 3.4, dimensionless, monomolecular equation) from 1971 to 2002. This equation has moderate power to detect interannual changes, although its use results in higher residual variability than Equation 3 ($F(1,30)$=35.72, multiple r^2=0.55, P=01.26E-6).

Fig. 2c K values (Equation 3.5, dimensionless, the Gompertz equation) from 1971 to 2002. This equation did not detect a significant trend through time ($F(1,30)$ = 1.31, multiple r^2 = 0.033, P = 0.31), although an increase is visually evident in Fig. 1.

Fig. 2d μ values (Equation 3.6, dimensionless, the Richards equation) from 1971 to 2002. This equation detects a weak significant increase through time ($F(1, 30)$ = 11.22, multiple r^2 = 0.25, P = 0.0022).

71
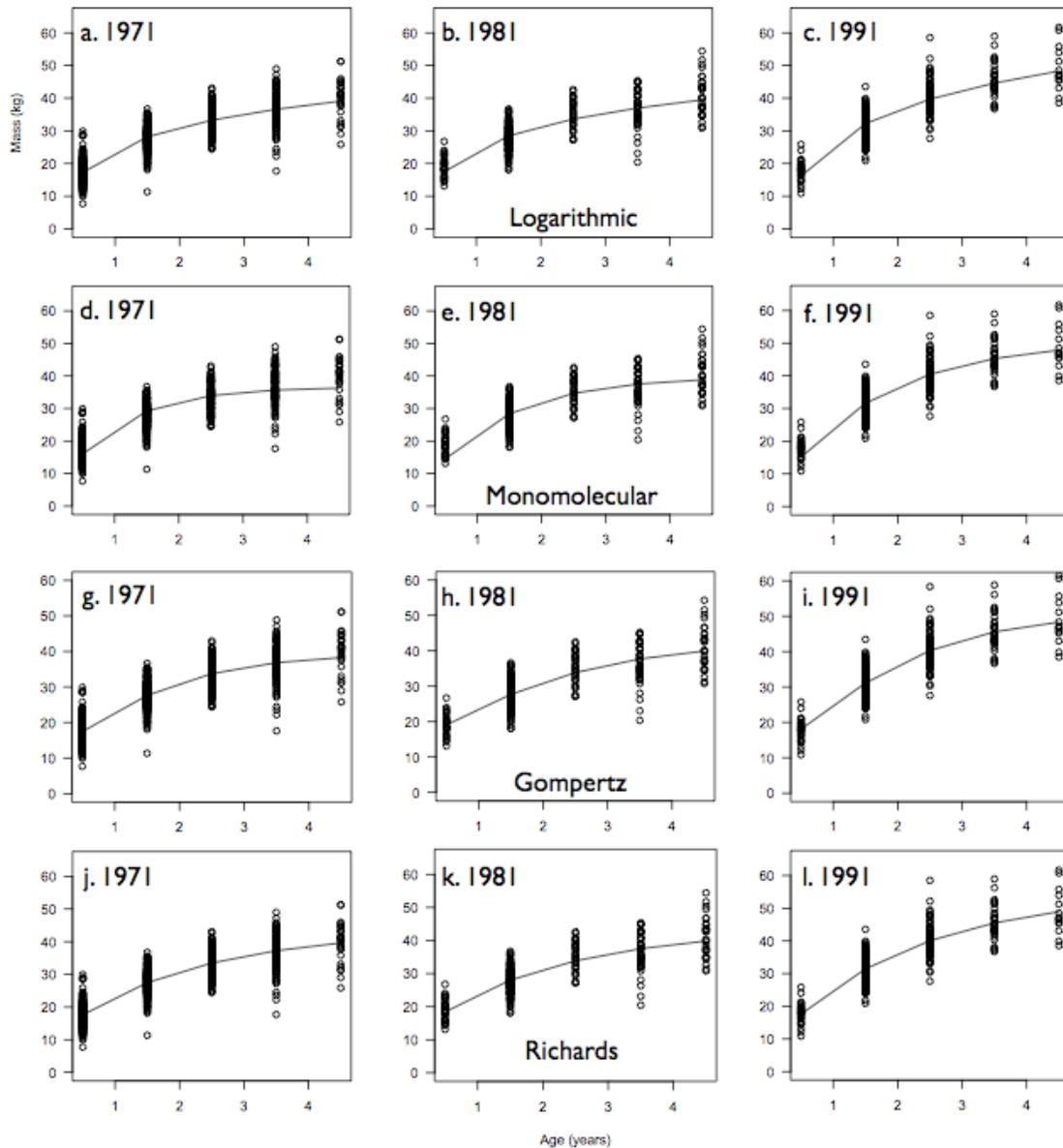
Fig. 3 Growth curves generated by NLS curve fitting of *equations 3.3-3.6* **(**Fig. 3a**:** Equation 3.3*,* Fig. 3b**:** Equation 3.4*,* Fig. 3c**:** Equation 3.5*,* and Fig. 3d: Equation 3.6*)***.**

Body mass estimates: Equation 3.4

Year	Asymptotic Mass (M_∞, kg)	Median Adult Mass (kg)	Error (kg)	Percent Error
1971	36.28	16.45	4.99	12
1972	37.19	16.87	3.63	9
1973	35.37	16.04	0.45	1
1974	37.19	16.87	5.90	14
1975	37.64	17.07	4.54	10
1976	38.10	17.28	3.17	7
1977	41.27	18.72	0.91	2
1978	43.99	19.95	-0.45	-1
1979	42.18	19.13	2.27	5
1980	40.82	18.51	2.27	6
1981	39.46	17.89	0.91	2
1982	43.54	19.74	3.63	7
1983	40.36	18.31	-2.72	-8
1984	43.08	19.54	0.91	2
1985	43.08	19.54	2.27	5
1986	45.80	20.77	0.45	1
1987	46.71	21.18	0.45	1
1988	46.26	20.98	1.36	3
1989	48.07	21.80	1.81	3
1990	48.53	22.01	2.72	5
1991	50.34	22.83	-3.17	-7
1992	50.79	23.04	-0.45	0
1993	49.43	22.42	2.72	5
1994	51.70	23.45	-0.45	-1
1995	53.51	24.27	-1.81	-4
1996	52.61	23.86	-3.17	-5
1997	45.80	20.77	4.08	7
1998	52.61	23.86	-2.72	-5
1999	53.97	24.48	-0.45	-2
2000	51.25	23.24	0.00	0
2001	55.78	25.30	-1.81	-3
2002	53.97	24.48	-0.91	-2

Table 1 Adult body mass estimated by NLS fitting to Equation 3.4. The error column is the difference between median adult mass and asymptotic mass, and the percent error column is the error's percentage of the median. The proportion of negative to positive entries (12/32) suggests that this method tends to overestimate adult weight, which affects the rate parameter.

Body mass estimates: Equation 3.5

Year	Asymptotic Mass (M_∞, kg)	Median Adult Mass (kg)	Error (kg)	Percent Error
1971	39.46	41.27	1.81	4
1972	37.64	40.82	3.17	8
1973	35.8	35.8	0.00	0
1974	43.08	43.08	0.00	0
1975	39.00	42.18	3.17	8
1976	47.62	41.27	-6.35	-15
1977	43.99	42.18	-1.81	-4
1978	43.99	43.54	-0.45	-1
1979	43.08	44.44	1.36	3
1980	40.82	43.08	2.27	5
1981	42.63	40.36	-2.27	-6
1982	45.80	47.17	1.36	3
1983	42.18	37.64	-4.54	-12
1984	47.62	43.99	-3.63	-8
1985	43.54	45.35	1.81	4
1986	49.43	46.26	-3.17	-7
1987	48.98	47.17	-1.81	-4
1988	50.79	47.62	-3.17	-7
1989	48.98	49.89	0.91	2
1990	50.79	51.25	0.45	1
1991	51.25	47.17	-4.08	-9
1992	48.53	50.34	1.81	4
1993	52.15	52.15	0.00	0
1994	54.4	51.25	-3.17	-6
1995	54.0	51.70	-2.27	-4
1996	51.25	49.43	-1.81	-4
1997	45.80	49.89	4.08	8
1998	53.51	49.89	-3.63	-7
1999	52.61	53.51	0.91	2
2000	51.25	51.25	0.00	0
2001	57.60	54.0	-3.63	-7
2002	54.9	53.06	-1.81	-3

Table 2 Adult body mass estimated by NLS fitting to Equation 3.5. The proportion of positive to negative entries in the error column (18/32) suggests that overestimates and underestimates occur at comparable frequencies, although this method did not detect a significant change in the rate parameter over time.

Body mass estimates: Equation 3.6

Year	Asymptotic Mass (M_∞, kg)	Median Adult Mass (kg)	Error (kg)	Percent Error
1971	43.99	19.95	-2.72	-7
1972	44.90	20.36	-4.08	-10
1973	43.08	19.54	-7.26	-20
1974	42.63	19.33	0.45	1
1975	46.71	21.18	-4.54	-11
1976	43.99	19.95	-2.72	-7
1977	46.26	20.98	-4.08	-10
1978	47.62	21.60	-4.08	-9
1979	47.17	21.39	-2.72	-6
1980	46.26	20.98	-3.17	-7
1981	43.99	19.95	-3.63	-9
1982	47.62	21.60	-0.45	-1
1983	45.80	20.77	-8.16	-22
1984	48.07	21.80	-4.08	-9
1985	48.98	22.21	-3.63	-8
1986	51.25	23.24	-4.99	-11
1987	51.70	23.45	-4.54	-10
1988	51.70	23.45	-4.08	-9
1989	52.61	23.86	-2.72	-5
1990	53.97	24.48	-2.72	-5
1991	54.88	24.89	-7.71	-16
1992	56.24	25.50	-5.90	-12
1993	55.33	25.09	-3.17	-6
1994	56.24	25.50	-4.99	-10
1995	58.05	26.33	-6.35	-12
1996	56.69	25.71	-7.26	-15
1997	52.15	23.65	-2.27	-5
1998	56.24	25.50	-6.35	-13
1999	58.05	26.33	-4.54	-8
2000	56.24	25.50	-4.99	-10
2001	59.41	26.94	-5.44	-10
2002	59.41	26.94	-6.35	-12

Table 3 Adult body mass estimated by NLS fitting to Equation 3.6. All but one entry is negative, and the error's percentage of the median tends to be higher than for the other methods tested. This demonstrates that this equation has a strong tendency to underestimate adult body mass for this dataset.

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