

GROWTH OF MALE WHITE-TAILED DEER: CONSEQUENCES OF MATERNAL EFFECTS

KEVIN L. MONTEITH*, LOWELL E. SCHMITZ, JONATHAN A. JENKS, JOSHUA A. DELGER, AND R. TERRY BOWYER

Department of Wildlife and Fisheries Sciences, Box 2140B, South Dakota State University, Brookings, SD 57007, USA (KLM, JAJ, JAD)

South Dakota Department of Game, Fish and Parks, 3305 West South Street, Rapid City, SD 57702, USA (LES)

Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, ID 83209, USA (KLM, RTB)

Identifying maternal effects on offspring is critical to interpreting population dynamics, but the duration of maternal effects and which life-history traits they influence is not well understood. We quantified growth and development of male white-tailed deer (*Odocoileus virginianus*) originating from the Black Hills in southwestern South Dakota and from eastern South Dakota in a controlled environment with high-quality nutrition. Despite being in good nutritional condition, males from the Black Hills ceased rapid growth 41 days earlier, were 29% smaller at asymptotic body mass, and grew significantly smaller antlers than males from eastern South Dakota. Females from eastern South Dakota were 14.9 kg larger than females from the Black Hills, yet birth mass of male offspring was similar for females from the 2 regions. Male offspring of 1st-generation deer from the Black Hills attained a 30% larger asymptotic body mass and grew significantly larger antlers than their sires. Body mass and antler size of 2nd-generation males of Black Hills origin approached that of 1st-generation males from eastern South Dakota at maturity. Suppression in growth of 1st-generation males of the Black Hills and increased growth by their offspring supported an influence of maternal and grandmaternal condition during gestation on subsequent growth of offspring and highlighted the significance of nutrition during gestation. These intergenerational effects indicate that measures of animal condition and population performance might reflect past rather than current conditions, and illustrate the potential for time lags in responses of populations to improved environmental conditions.

Key words: antler growth, body mass, gestation, nutrition, *Odocoileus virginianus*, population dynamics, South Dakota, white-tailed deer

Although often considered positive and adaptive, maternal effects may influence fitness of offspring negatively if poor environmental conditions exist during ontogeny (Kirkpatrick and Lande 1989; Mech et al. 1991). A maternal effect is the direct influence of the phenotype of the mother on the phenotype of her offspring (after Bernardo 1996). Life-history theory indicates that females must balance the allocation of current reproductive expenditures with their probability of survival, as well as the potential for subsequent reproductive events to occur when better conditions exist (Adams 2005; Marshall and Uller 2007; Stearns 1992; Trivers and Willard 1973). When resources are limited, a conservative strategy

favoring survival of the mother would be most advantageous to long-lived, iteroparous mammals such as ungulates (Bårdsen et al. 2008; Festa-Bianchet and Jorgenson 1998; Therrien et al. 2007). That conservative strategy may result in the transmission of a maternal effect, which could influence population demography through mechanisms of offspring size, growth, survival, and reproductive performance (Bårdsen et al. 2008; Bernardo 1996; Mech et al. 1991; Ozoga and Verme 1982).

Identifying maternal consequences can be complex, and failure to consider multiple measures of maternal influence could preclude their detection (Bernardo 1996; Kirkpatrick and Lande 1989). Understanding the role of maternal effects is dependent upon identifying the life-history traits that are maternally affected (Benton et al. 2001). Maternal effects related to size may disappear during ontogeny by means of compensatory growth (Dale et al. 2008; Gendreau et al. 2005). In some situations, however, negative effects persist through

* Correspondent: montkevi@isu.edu

adulthood and potentially into subsequent generations (Albon et al. 1987; Mech et al. 1991). Accordingly, intergenerational persistence of maternal effects may cause current fitness to reflect past environmental conditions, further confounding interpretation of population response (Benton et al. 2001; Kirkpatrick and Lande 1989; Mousseau and Fox 1998). Despite the need to infer maternal effects when interpreting population demographics (*sensu* Bowyer et al. 2005), the duration that maternal effects influence large-mammal populations as well as which life-history traits they influence are not well studied (Gaillard et al. 2000).

White-tailed deer (*Odocoileus virginianus*) inhabiting South Dakota occupy contrasting landscapes, from the mixed-grass prairies of the eastern portion of the state, which is intensively farmed, to ponderosa pine (*Pinus ponderosa*) forests of the Black Hills in the southwest (Richardson and Peterson 1974). Although only 1 subspecies of white-tailed deer (*O. v. dacotensis*) inhabits South Dakota (Baker 1984), deer occupying the Black Hills are smaller than those in the eastern portion of the state; mean body mass of adult female deer from eastern South Dakota was 69 kg (Grovenburg 2007), whereas female white-tailed deer from the Black Hills averaged 46 kg (Osborn 1994).

We measured body mass and antler size to examine patterns of growth of initial cohorts of males (i.e., 1st generation) originating from the Black Hills and from eastern South Dakota, and their male offspring (i.e., 2nd generation). We tested for a negative maternal effect that Schmitz (2000) proposed to explain a disparity in body mass of 1-year-old white-tailed deer from the Black Hills and eastern South Dakota. If 1st-generation males from the Black Hills failed to exhibit increased growth after 1 year of age, we hypothesized that offspring (i.e., 2nd generation) of Black Hills deer, when raised with adequate nutrition in a controlled environment, would exhibit increased growth relative to their sires. Furthermore, if grandmaternal effects were minimized, morphological characteristics of 2nd-generation males of Black Hills origin should be similar to those exhibited by the original cohort of males from eastern South Dakota. We hypothesized that females from eastern South Dakota were not nutritionally stressed because these deer have access to high-quality forage, including agricultural crops (Gladfelter 1984; Richardson and Peterson 1974); therefore, growth of 1st-generation males from eastern South Dakota and their male offspring (2nd generation) should not be suppressed by maternal effects.

MATERIALS AND METHODS

Research facility.—We maintained white-tailed deer at the Wildlife and Fisheries Sciences Research Facility at South Dakota State University in Brookings, South Dakota (44°20'N, 96°47'W). Elevation was 490 m, and temperatures in the region range from -29°C in winter to 38°C in the summer, with a mean annual temperature of 8°C (Spuhler et al. 1971). Annual precipitation commonly varies from 33 to 63.5 cm, with snowfall ranging from 63.5 to 114 cm (Spuhler

et al. 1971). We confined deer to a 4-ha enclosure that included a 30×5 -m structure for shelter. We maintained deer on a diet of shelled corn, pelleted soy-hulls (12% protein), and alfalfa hay offered *ad libitum*. Deer had access to a limited supply of natural forage within the enclosure. Facilities and procedures for research on captive deer followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), and were approved by the Institutional Animal Care and Use Committee (1996) at South Dakota State University (97-A016).

Data collection.—We measured patterns in body mass and antler growth of male white-tailed deer. We used males in our analyses because of a limited sample size for females and variation in reproduction by females across years. Only a small portion of females was allowed to breed each year, which could confound interpretation of maternal influences on growth (Green and Rothstein 1991; Ozoga and Verme 1982; Stearns 1992). First-generation animals were acquired as neonates from 2 regions in South Dakota, Black Hills and eastern South Dakota. Second-generation animals were offspring produced in the research facility by 1st-generation animals from their respective areas of origin (i.e., Black Hills or eastern South Dakota).

We hand-raised animals using consistent husbandry practices throughout the study, which allowed us to control for environmental influences on diet and variability in postnatal investment by mothers. We fed neonates Advance Powdered Lamb Milk Replacer (Milk Specialties Company, Dundee, Illinois) mixed in a 4 to 1 ratio with warm water following a feeding schedule adapted from Buckland et al. (1975), which varied with the age of young deer. Before weaning, we provided young with *ad libitum* access to Omolene 300 Growth Horse Feed (Purina Feeds LLC, St. Louis, Missouri), a pelleted ration (12–16% protein), shelled corn, and alfalfa hay. From postweaning to adulthood, we maintained deer on a diet of shelled corn, pelleted soy-hulls (12% protein), and alfalfa hay offered *ad libitum* (Schmitz 2000, 2006).

We weighed 2nd-generation neonates weekly from parturition until weaning on a hanging scale accurate to 45.4 g (model 600; Hanson Scale Company, Shubuta, Mississippi). When body mass was >15 kg, we obtained weights using a walk-on scale accurate to 454 g (model 16; Adrian J. Paul Company, Duncan, Oklahoma). After weaning, deer were weighed during the 2nd week in October, the 1st week in July, and opportunistically throughout the remainder of the year.

We anesthetized males in October using a mixture of Telazol–ketamine HCl–xylazine HCl (2.37 mg/kg, 1.9 mg/kg, and 0.47 mg/kg, respectively; Telazol obtained from Wildlife Pharmaceuticals, Fort Collins, Colorado). We measured the inside spread of the main beams and then sawed antlers off approximately 2.54 cm above the corona using a hack or cable saw. We measured length of each main beam, various measures of beam circumference, and length of all tines ≥ 2.54 cm for both antlers to the nearest 0.32 cm with a 0.64-cm steel tape as described by Nesbitt and Wright (1981). Beam circumference was the sum of 4 circumference measurements: the smallest

circumference above corona and below brow tine, and between each successive pair of tines along the main beam.

Statistical analyses.—We modeled growth of male white-tailed deer from each region by generation with data on body mass acquired throughout the year from birth to 7 years old. We fit the relationship of body mass to age using the von Bertalanffy growth equation (Ricker 1979; Zullinger et al. 1984) with a 3-parameter, nonlinear model: $M(t) = A[1 - 1/3e^{-K(t - I)}]^3$, where $M(t)$ is mass at age t , A is asymptotic body mass (kg), K is a growth-rate parameter (day^{-1}), and I is age at inflection point (days). Age at the inflection point represented the age at which mass gain began to slow, and, thereby, approximated the duration of rapid postnatal growth for each group. We conducted analyses using the nonlinear model function in SYSTAT 10.0 (SPSS Inc., Chicago, Illinois) using least-squares estimation by the Gauss–Newton method with starting points for iterations set to 0 for estimation of parameters A , K , and I . We considered parameters of the von Bertalanffy growth curve statistically different if 95% confidence intervals did not overlap.

We described antler growth of white-tailed deer relative to age using multiple-regression analysis (Neter et al. 1996). Before fitting those data, we used principal component analysis to derive a single variable that explained most of the variation related to antler size (Bowyer et al. 2001; Stewart et al. 2000). Variables included in the principal component analysis were length of main beams, total tine length, beam circumference measurements, and greatest inside spread of antlers. We expected a curvilinear pattern between antler growth and age because antler size tends to decline in senescent male cervids (Bowyer et al. 2001; Goss 1983; Stewart et al. 2000). We tested the reliability of using principal component 1 (PC1) as an index to overall size of antlers by regressing that composite variable with gross nontypical score (Bowyer et al. 2001), a measure of overall antler size from the Boone and Crockett scoring system (Nesbitt and Wright 1981). We used an F -test to determine whether multiple regressions for antler size for each group differed with respect to generation and area of origin (Zar 1999).

To control for individual variability and repeated sampling of individuals, we also compared peak body mass (in October) and antler size (PC1) relative to age among cohorts using analysis of variance (ANOVA) with repeated measures (Zar 1999). For the repeated-measures analyses, we used data on antler size and body mass from 1.5 to 4.5 years of age because of limited sample size in older age classes, particularly for 2nd-generation males. Sample size in subsequent age classes declined as age progressed because animals had not yet attained that age or had died. Males in this captive population achieved 90% of peak body mass and antler size by 4.5 years old (Schmitz 2006).

To address early life-history characteristics that may confound interpretation of future growth of offspring, we tested for effect of region (i.e., Black Hills versus eastern South Dakota) on fecundity, Julian birth date, maternal mass, and total birth mass of offspring using multivariate analysis of

variance (MANOVA). Following a significant main effect in MANOVA, we used canonical correlation analysis to identify variables responsible for overall significance of the main effect (Johnson and Wichern 2002). Variables identified in the canonical analysis were then included as dependent variables in separate ANOVAs with the same main effect (i.e., region). We used a chi-square test to determine if sex ratio of offspring differed between regions (Caughley 1977:79–81). We defined prenatal investment as the proportion of total offspring mass relative to maternal mass (Knott et al. 2005; Robbins and Robbins 1979). We used t -tests to test for differences in prenatal investment and birth mass of males between regions. Before interpretation of results, we examined residual plots of each dependent variable to assess compliance with assumptions of ANOVA. First-generation males sired an average ($\pm SE$) of 3.3 ± 0.45 litters over the duration of the study, but never bred the same female in subsequent years. We adopted $\alpha \leq 0.02$ to compensate for a lack of independence among samples and to avoid a type I error (Bowyer et al. 2007). We used SYSTAT 10.0 for all statistical analyses.

RESULTS

First generation.—The von Bertalanffy growth curve explained >97% of the variation in body mass relative to age for male white-tailed deer from South Dakota (Fig. 1). Body mass of 1st-generation males from the Black Hills and eastern South Dakota increased from birth until 4.5 years of age, when asymptotic body mass was achieved (Fig. 1). The growth rate parameter was lower for 1st-generation males from eastern South Dakota than for 1st-generation males from the Black Hills (Table 1). Time of inflection in growth, however, occurred at a significantly later date (41 days) for males from eastern South Dakota than for males from the Black Hills (Table 1). Asymptotic body mass of 1st-generation males from eastern South Dakota was 41% larger and differed from mass of males originating from the Black Hills (Table 1). When we controlled for repeated sampling of individuals through 4.5 years of age, between-subject effects for annual peak body mass also were significant for 1st-generation males ($F = 10.46$, $df = 1, 8$, $P = 0.012$). First-generation males from the Black Hills did not approach body mass exhibited by 1st-generation males from eastern South Dakota, and consequently, did not exhibit increased growth after 1 year of age (Fig. 1).

Principal component 1, which reflected antler size, explained 85% of the variation in measurements of antlers for white-tailed deer and was strongly correlated ($r^2 = 0.98$) with the Boone and Crockett scoring system; eigenvectors for PC1 exhibited similar loading scores (0.87–0.95) among antler characteristics. Antler growth, as indexed by PC1, was suppressed in 1st-generation males from the Black Hills compared with 1st-generation males from eastern South Dakota (Fig. 2). Peak antler growth, as indicated by the curvilinear relationship, occurred at 5.5–6.5 years of age for 1st-generation males from the Black Hills and eastern South

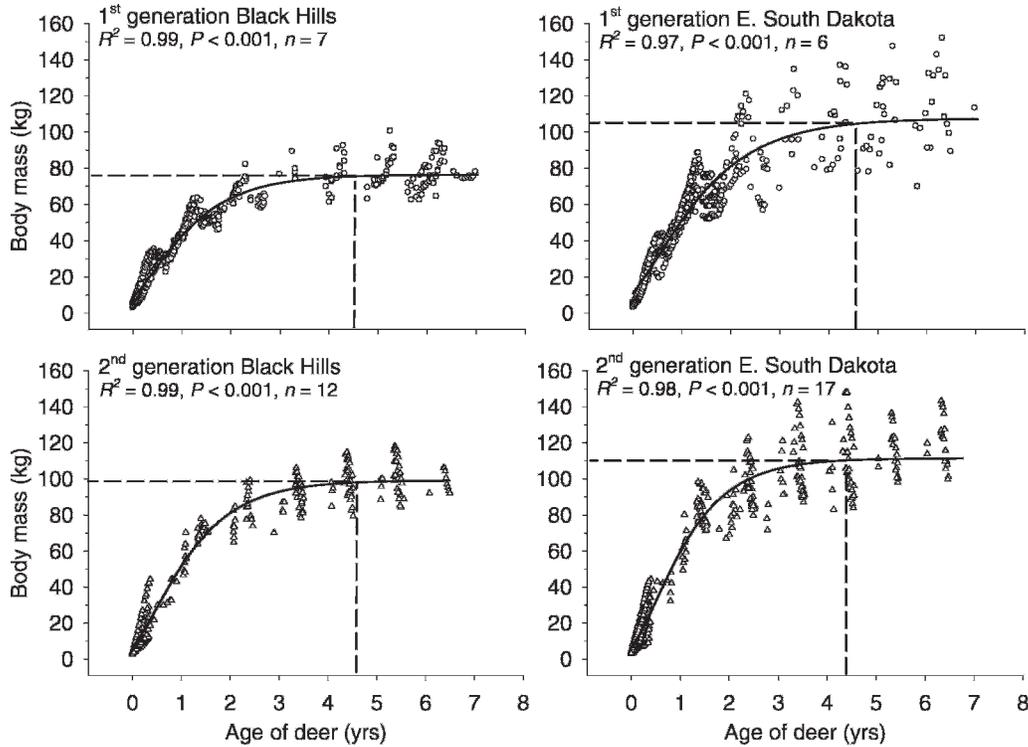


FIG. 1.—Body mass (kg) relative to age (years) of male white-tailed deer (*Odocoileus virginianus*) raised in captivity fitted with the von Bertalanffy growth curve (South Dakota, 1997–2007). Study animals were composed of original cohorts (1st generation) acquired as neonates from eastern South Dakota and the Black Hills in southwestern South Dakota during 1997–1998. Second-generation young were born in the research facility sired from 1st-generation adults. Sample size indicates number of individual deer and the dashed line represents time to asymptotic body mass (A; Table 1).

Dakota (Fig. 2). Nonetheless, peak antler size was larger for 1st-generation males from eastern South Dakota (PC1 = 1.26) than 1st-generation males from the Black Hills (PC1 = 0.23). Regression equations for antler growth relative to age differed between 1st-generation males ($F = 23.64, df = 6, 62, P < 0.001$), and regional differences in antler growth between 1st-generation males also were substantiated by repeated-measures ANOVA ($F = 26.57, df = 1, 7, P = 0.001$). First-generation males from the Black Hills exhibited both smaller body mass and antler size through maturity compared with 1st-generation males from eastern South Dakota.

Second generation.—Early life-history characteristics (Table 2) differed between offspring born to female white-tailed deer from the Black Hills and those from eastern South Dakota

(Wilks' $\lambda = 0.399, F = 11.66, df = 4, 34, P < 0.001$). Canonical correlation analysis, however, indicated that overall significance was most influenced by maternal mass, which differed between regions ($F = 48.28, df = 1, 34, P < 0.001$). Mean body mass of females from the Black Hills was 14.9 kg smaller than that of females from eastern South Dakota (Table 2). Prenatal investment (neonatal proportion of maternal mass $\pm SE$) was greater for Black Hills females (0.114 ± 0.005) than for females from eastern South Dakota ($0.099 \pm 0.003; t = 2.65, df = 36, P = 0.012$). Females from the Black Hills produced more males than females at birth, whereas females from eastern South Dakota produced more females than males (Table 2), but those patterns were not significant ($\chi^2 = 1.19, df = 1, P = 0.276$). Birth mass (\pm

TABLE 1.—Parameter estimates ($\pm SE$) for von Bertalanffy growth curves fitted to growth in body mass (kg) relative to age (days) of male white-tailed deer (*Odocoileus virginianus*) raised in captivity (South Dakota, 1997–2007). Study animals were composed of original cohorts (1st generation) acquired as neonates from eastern South Dakota and the Black Hills in southwestern South Dakota during 1997–1998. Second-generation young were born in the research facility and were sired by 1st-generation males from the same region. Different lowercase letters in each column indicate significant differences in growth parameters between groups of males based on 95% confidence intervals.

| Male white-tailed deer | n | Asymptotic body mass | | Growth constant | | Age at inflection | |
|-------------------------------------|----|----------------------|------|-----------------|--------|-------------------|------|
| | | A | SE | K | SE | I | SE |
| 1st-generation Black Hills | 7 | 76.42a | 0.59 | 0.0030a | 0.0001 | 151.16a | 3.97 |
| 1st-generation eastern South Dakota | 6 | 107.58b | 1.77 | 0.0024b | 0.0001 | 192.44b | 7.78 |
| 2nd-generation Black Hills | 14 | 99.12c | 0.80 | 0.0030a | 0.0001 | 189.67b | 5.66 |
| 2nd-generation eastern South Dakota | 18 | 111.40b | 1.01 | 0.0033a | 0.0001 | 189.73b | 5.40 |

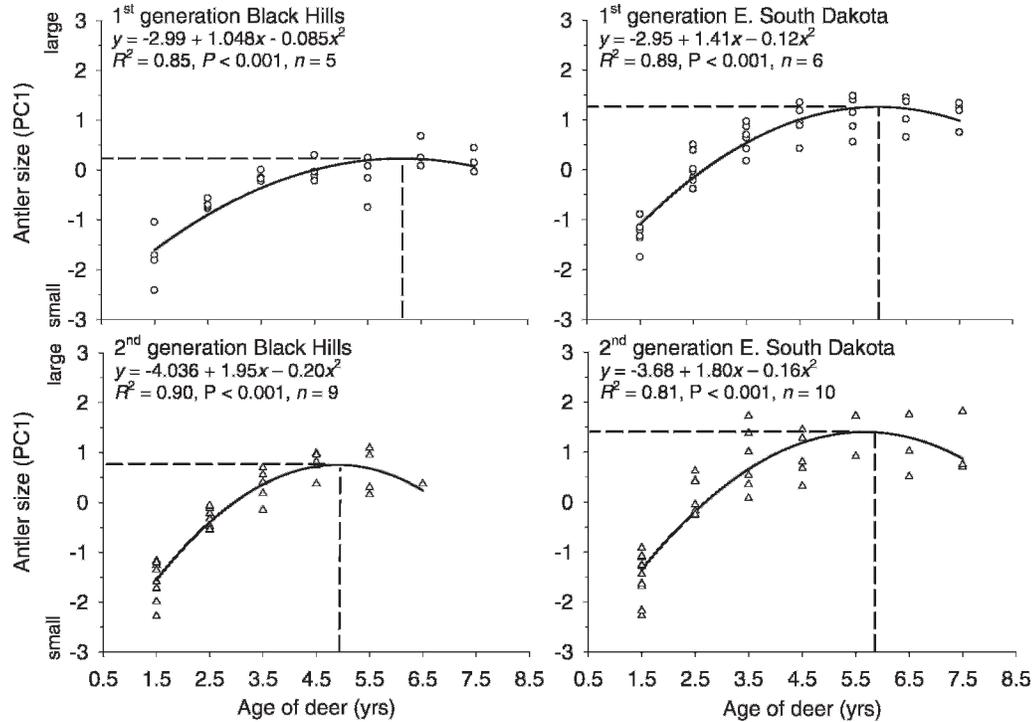


FIG. 2.—Size of antlers, as indexed by principal component 1 (PC1), relative to age (years) of male white-tailed deer (*Odocoileus virginianus*) raised in captivity (South Dakota, 1997–2007). Positive loadings correspond to larger antlers and negative loadings to smaller antlers. Study animals were composed of original cohorts (1st generation) acquired as neonates from eastern South Dakota and the Black Hills in southwestern South Dakota during 1997–1998. Second-generation young were born in the research facility sired from 1st-generation adults. Sample size indicates number of individual deer and the dashed line represents time to peak antler size.

SE) of 2nd-generation males of Black Hills origin (3.51 ± 0.12 kg) and eastern South Dakota (3.65 ± 0.10 kg) was similar ($t = 0.95$, $d.f. = 34$, $P = 0.350$).

Patterns of growth in body mass of 2nd-generation males were similar to those of their sires, with asymptotic body mass attained at 4.5 years of age (Fig. 1). Constants for growth rate of 1st- and 2nd-generation males of the Black Hills were identical (Table 1). Asymptotic body mass and point of inflection, however, differed between generations (Table 1). Second-generation males of Black Hills origin exhibited rapid

growth for 39 days longer than 1st-generation males from the Black Hills (Table 1). Second-generation males of Black Hills origin attained an asymptotic body mass 30% larger than their sires (Table 1). Repeated-measures analysis further indicated increased growth by 2nd-generation males of Black Hills origin; 1st- and 2nd-generation males of Black Hills origin differed in body mass ($F = 29.09$, $d.f. = 1, 7$, $P = 0.0001$). Second-generation males of Black Hills origin also attained greater antler size (PC1 = 0.75) than their sires (PC1 = 0.23). Despite the small sample size in older age classes, the parabolic relationship indicated that antler growth differed between 1st- and 2nd-generation males of the Black Hills ($F = 11.54$, $d.f. = 6, 56$, $P < 0.001$). Furthermore, repeated-measures ANOVA indicated that antler growth differed between generations of males from the Black Hills ($F = 10.98$, $d.f. = 1, 7$, $P = 0.013$).

Asymptotic body mass (Table 1) and antler size ($F = 5.86$, $d.f. = 6, 66$, $P < 0.001$) of 2nd-generation males of Black Hills origin remained smaller than those of 1st-generation males from eastern South Dakota (Table 1). Nevertheless, 2nd-generation males of Black Hills origin had compensated for 72% of the initial difference in asymptotic body mass that occurred between 1st-generation males and antler size approached that of 1st-generation males from eastern South Dakota (Fig. 2). Moreover, repeated-measures analysis indicated that body mass ($F = 0.251$, $d.f. = 1, 9$, $P = 0.251$) and antler size ($F = 2.63$, $d.f. = 1, 8$, $P = 0.144$) relative to age for 2nd-generation males of Black Hills origin and 1st-generation males from eastern South Dakota were similar, although that

TABLE 2.—Mean and SE of characteristics of litters born to female white-tailed deer (*Odocoileus virginianus*) that were obtained as neonates from the Black Hills and eastern South Dakota and raised in captivity (South Dakota, 1997–2007). Different lowercase letters in rows indicate significant differences between region of origin (ANOVA for variables identified with canonical correlation analysis following MANOVA except for sex ratio, which was the chi-square test).

| Litter characteristics | Region of origin | | | |
|------------------------------|------------------|------|----------------------|------|
| | Black Hills | | Eastern South Dakota | |
| | \bar{x} | SE | \bar{x} | SE |
| Young per female | 1.92a | 0.10 | 1.95a | 0.07 |
| Julian birth date (days) | 155a | 2.33 | 153a | 1.65 |
| Total birth mass (kg) | 6.52a | 0.32 | 7.14a | 0.23 |
| Maternal mass (kg) | 57.3a | 1.75 | 72.2b | 1.23 |
| Sex ratio (proportion males) | 0.58a | 0.10 | 0.45a | 0.07 |

outcome likely was influenced by smaller sample size available for repeated-measures ANOVA.

Both 1st- and 2nd-generation males of eastern South Dakota origin exhibited similar patterns of body mass (Fig. 1) and antler size (Fig. 2). Asymptotic body size, growth constant, and age of inflection for growth were similar (Table 1). In addition, annual peak body mass ($F = 0.34$, $df = 1, 10$, $P = 0.574$) and antler size ($F = 0.29$, $df = 1, 8$, $P = 0.603$) up to 4.5 years of age were similar between generations of males of eastern South Dakota origin.

DISCUSSION

Resource limitation can negatively affect growth of male ungulates (Clutton-Brock et al. 1982; Geist 1986; Simard et al. 2008), but release from that limitation is expected to result in improved growth (Ashley et al. 1998; Leberg and Smith 1993). Contrary to that prediction, male white-tailed deer acquired as neonates from the Black Hills and raised in a controlled environment on a high nutritional plane ceased rapid growth at an earlier age and remained smaller in both body mass and antler size compared with males acquired from eastern South Dakota (Figs. 1 and 2). Offspring of those Black Hills males, however, attained a significantly larger body mass and antler size than their sires (Table 1; Fig. 2). Further, 2nd-generation males of Black Hills origin were only slightly smaller in both body mass and antler size compared with 1st-generation males from eastern South Dakota (Table 1; Fig. 2). Those results support the maternal effects hypothesis and indicate that maternal condition during gestation led to lifelong consequences on growth for 1st-generation males from the Black Hills. Increased growth in both body mass and antler size exhibited by 2nd-generation males of Black Hills origin indicates a reduction in the negative maternal effect that limited growth of their sires.

One potential shortcoming of our study was that we were unable to directly assess genetic differences between deer from eastern South Dakota and the Black Hills, which might have influenced growth of deer from those regions. Nutritional limitation and intraspecific competition over long periods in the Black Hills may have led to selection of smaller body size to lower absolute nutrient demand (Sinclair and Parkes 2008), a phenomenon that has been observed on islands (Simard et al. 2008). Nonetheless, compensatory growth exhibited by 2nd-generation males of Black Hills origin makes a substantial genetic effect unlikely, and leads us to conclude that the most-parsimonious explanation for size differences between regions in South Dakota was nutrition.

We also recognize the potential for pseudoreplication because adult males sired >1 young in our sample. Nevertheless, our approach was to replicate the mating system of polygynous white-tailed deer (DeYoung et al. 2006; Ott et al. 2003). Potential bias related to pseudoreplication would be similar for each group of deer, and we controlled for individual effects by using a repeated-measures analysis (Zar 1999). Furthermore, we reduced alpha from 0.05 to 0.02 to

compensate for the potential lack of independence among samples and to minimize the potential for a type I error (Bowyer et al. 2007). We acknowledge that sample sizes were small for some of the older age classes of deer; nonetheless, we were able to detect substantial intergenerational differences in body and antler size.

If 2nd-generation males of eastern South Dakota origin also exhibited increases in either body mass or antler size beyond those exhibited by their sires, then the responsive growth by 2nd-generation males of Black Hills origin might have been a result of being raised in a nutritionally controlled environment. Growth patterns of 1st- and 2nd-generation males of eastern South Dakota origin, however, were nearly identical, supporting the hypothesis that growth of deer in eastern South Dakota was not inhibited by negative maternal effects. We hypothesize that deer from eastern South Dakota represent the potential for maximum body mass and antler size for this subspecies in the northern Great Plains. Availability of agricultural crops for food and cover throughout much of the year probably contributed to the accelerated pattern of growth of white-tailed deer from eastern South Dakota (Brinkman et al. 2004; Kramlich 1985; Nixon et al. 1991).

The role of nutrition in modifying fetal sex ratios in ungulates has been well studied (McCullough 1979; Sheldon and West 2004; Verme 1983), yet the plausibility of hypotheses forwarded to explain this phenomenon remains controversial (Cameron 2004; Trivers and Willard 1973). Both litter size and sex ratio at birth can influence subsequent growth of young because of asymmetry in maternal investment, particularly during lactation (Birgersson 1998; Hewison and Gaillard 1999; Hogg et al. 1992). Litter size and sex ratios, however, were similar between females from the Black Hills and eastern South Dakota (Table 2), and we controlled for variability in postnatal investment because all animals were hand-raised under the same husbandry practices. Females from the Black Hills likely increased prenatal investment relative to body mass in response to good nutritional condition to compensate for negative maternal effects. Similarly, Keech et al. (2000) concluded that there was a direct link between reproductive investment and nutritional condition in female moose (*Alces alces*) and survival of their young. Other studies on ungulates also have demonstrated that conditions experienced by individuals in early life have long-term effects on life-history characteristics ranging from survivorship (Kie and White 1985; Mech et al. 1991), to rate of senescence (Nussey et al. 2007), to antler or horn growth (Festa-Bianchet et al. 2000; Kruuk et al. 2002; Schmidt et al. 2001), to life-time reproductive success (Festa-Bianchet et al. 2000; Nussey et al. 2007). Nonetheless, effects of physical condition during early development in those studies included environmental influences, which might further exacerbate effects; we controlled for environmental variation and quantified the potential role of negative maternal effects on growth. Indeed, our experimental design controlled for potential effects of maternal condition on provisioning of young (Therrien et al. 2007, 2008), and for females adjusting

maternal investment in neonates in response to current environmental changes (Rachlow and Bowyer 1994).

Intergenerational effects occur when the actions of an individual affect not only its own survivorship and performance, but also that of its offspring and possibly subsequent generations (Livnat et al. 2005). Transmission of effects from environmental conditions from past generations into the phenotypic variation of subsequent generations may result in a time lag in population response (Beckerman et al. 2002; Plaistow et al. 2006). Residual effects of grandmaternal nutrition (i.e., nutritional condition of mothers of 1st-generation males from the Black Hills) on both body mass and antler size may have continued to persist in 2nd-generation males of Black Hills origin, because they did not fully attain the antler and body size exhibited by males from eastern South Dakota (Figs. 1 and 2).

Suppression of wildfire in the Black Hills of southwestern South Dakota has led to canopy closure with decreased quantity and quality of understory vegetation (Larson and Johnson 1999; Richardson and Peterson 1974; Zimmerman et al. 2006). For decades, white-tailed deer in the Black Hills have been in decline (DePerno 1998) and have suffered from poor nutritional condition (Hippensteel 2000; Osborn 1994), as a likely result from overpopulation and habitat deterioration (Leopold et al. 1947; Richardson and Peterson 1974). Nevertheless, we predict that given sufficient time after habitat improvements and subsequent reduction of density-dependent effects, white-tailed deer from the Black Hills should exhibit body mass and antler characteristics comparable to deer from eastern South Dakota. This outcome is supported by the increased growth of 2nd-generation deer from that region, and makes density dependence and habitat deterioration the most likely explanation for this phenomenon.

Consequences of maternal effects.—An intergenerational maternal effect on growth and size at maturity, which was initiated prenatally, highlights the importance of good nutrition during gestation. Most of the cost of gestation is accrued during the last one-third of gestation in white-tailed deer (Pekins et al. 1998; Robbins and Moen 1975; Robbins and Robbins 1979; Verme 1963); hence, adequate nutrition during late winter and early spring is essential unless substantial somatic reserves are present from the previous summer or autumn. Dams in poor physical condition are more likely to give birth to smaller, weaker young, which may predispose young to mortality (Bartmann et al. 1992; Sams et al. 1996), including predation (Cook et al. 1971; Keech et al. 2000; Kie and White 1985; Kunkel and Mech 1994; Nelson and Woolf 1987). Effects of birth mass may have lifelong influences on survival and reproductive success (Albon et al. 1987). We hypothesize that young that survive may experience slow growth, smaller adult body mass, smaller antlers, and consequently, lower fitness.

Environmental conditions during early gestational development of young ungulates can affect the entire cohort and produce long-lasting consequences (Albon et al. 1987; Anderson and Linnell 1997; Forchhammer et al. 2001; Rose

et al. 1998; Töigo et al. 1999). Cohort variability may be the direct result of negative maternal effects acting on growth and subsequent reproductive success of offspring. Post et al. (1997) determined that fluctuations in cohort-specific body weights of red deer (*Cervus elaphus*) were correlated with winter conditions while the cohort was in utero. Moreover, Albon et al. (1987) documented cohort variability in reproductive performance and survival of red deer that was explained by birth mass, which in turn was influenced by conditions during the last 2 months of gestation. Maternal effects may cause correlations between environmental conditions experienced during early development and fitness components exhibited later in life (Beckerman et al. 2002; Lindström 1999). Our results indicate that conditions during gestation alone can have lifelong consequences for growth and reproduction. For instance, lifelong growth of male white-tailed deer from the Black Hills was likely hampered by both maternal and grandmaternal condition during gestation, but occurred to a lesser degree in subsequent generations under controlled conditions with high-quality forages.

Antler growth and development are affected by the nutritional state of an individual as determined by population density in relation to habitat conditions (Goss 1983; Kruuk et al. 2002; Schmidt et al. 2001, 2007) and are life-history traits that may represent phenotypic quality (Bowyer et al. 2001; Solberg and Sæther 1994; Vanpé et al. 2007). We documented suppression in antler growth caused by a negative maternal effect, despite males being in good nutritional condition. Some studies have concluded that a time lag in population response to improved conditions was a direct result of the delay in recovery of vegetation (Fryxell et al. 1991; McCullough 1979). Despite recovery or substantial improvement of habitat, patterns of growth and population demographics may continue to be suppressed through negative maternal and grandmaternal effects. Biologists should consider the potential for intergenerational maternal effects that persist in young born before conditions improved and for residual maternal effects in growth of subsequent generations.

The intergenerational effects of maternal condition reported herein, and those reported by other research (e.g., Geist 1986; Mech et al. 1991), stress the importance of understanding current and historical nutritional condition of populations before using current data on weather, habitat condition, density, and predation to interpret population dynamics. Interpretation of those relationships may be confounded by maternal effects, where lags in population response to habitat improvement or release from severe density dependence may persist for multiple generations, and consequently, have a destabilizing effect on population dynamics (Benton et al. 2001; Lindström and Kokko 2002). Our results stress the importance of long-term investigations of large, long-lived mammals, particularly when attempting to describe population trajectories in highly variable environments; short-term population demographics can be misleading and yield erroneous conclusions (Kie et al. 2003; McCullough 1990). Having realistic and predictable models of population

dynamics of large ungulates relative to carrying capacity (K) is of substantial theoretical and applied value (Bowler et al. 2005; Kie et al. 2003), and we suggest that the consideration of the influence of maternal effects may provide further insights into understanding their dynamics. Moreover, accurate interpretation of predator–prey dynamics may be contingent upon understanding the response in life-history characteristics of ungulates to environmental stochasticity and density-dependent mechanisms (Beckerman et al. 2002; Bowyer et al. 2005). Clearly, more research is needed to elucidate the influence of maternal condition and investment on population dynamics and the evolution of life-history strategies in large ungulates, which may only be possible through long-term studies (Lindström 1999).

ACKNOWLEDGMENTS

Funding for this research was provided by Federal Aid in Wildlife Restoration administered through the South Dakota Department of Game, Fish and Parks (study 75123); South Dakota Agricultural Experiment Station; National Science Foundation/EPSCoR grant EPS-0091948; a Griffith Faculty Research Award presented to JAJ; the Department of Wildlife and Fisheries Sciences at South Dakota State University; and the Department of Biological Sciences at Idaho State University. We appreciate our technicians who contributed to data collection: L. A. Dixon, A. J. Fey, A. R. Monteith, and K. B. Monteith. We thank R. A. Long, K. B. Monteith, T. R. Stephenson, J. C. Whiting, and 2 anonymous reviewers for providing useful comments on this manuscript.

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Submitted 16 June 2008. Accepted 21 November 2008.

Associate Editor was Jane M. Waterman.