

Kelley M. Stewart · R. Terry. Bowyer · Brian L. Dick
Bruce K. Johnson · John G. Kie

Density-dependent effects on physical condition and reproduction in North American elk: an experimental test

Received: 16 March 2004 / Accepted: 11 November 2004 / Published online: 7 December 2004
© Springer-Verlag 2004

Abstract Density dependence plays a key role in life-history characteristics and population ecology of large, herbivorous mammals. We designed a manipulative experiment to test hypotheses relating effects of density-dependent mechanisms on physical condition and fecundity of North American elk (*Cervus elaphus*) by creating populations at low and high density. We hypothesized that if density-dependent effects were manifested principally through intraspecific competition, body condition and fecundity of females would be lower in an area of high population density than in a low-density area. Thus, we collected data on physical condition and rates of pregnancy in each experimental population. Our manipulative experiment indicated that density-dependent feedbacks affected physical condition and reproduction of adult female elk. Age-specific pregnancy rates were lower in the high-density area, although there were no differences in pregnancy of yearlings or in age at peak reproduction between areas. Age-specific rates of pregnancy began to diverge at 2 years of age between the two populations and peaked at 6 years old. Pregnancy rates were most affected by body condition and mass, although successful reproduction the previous year also reduced pregnancy rates during the current year. Our results indicated that while holding effects of winter constant, density-dependent

mechanisms had a much greater effect on physical condition and fecundity than density-independent factors (e.g., precipitation and temperature). Moreover, our results demonstrated effects of differing nutrition resulting from population density during summer on body condition and reproduction. Thus, summer is a critical period for accumulation of body stores to buffer animals against winter; more emphasis should be placed on the role of spring and summer nutrition on population regulation in large, northern herbivores.

Keywords Body mass · Body condition · *Cervus elaphus* · Lactation · Pregnancy

Introduction

Detecting density dependence is neither simple nor straightforward (McCullough 1990; Kie et al. 2003). Density-dependent processes often interact with other variables including predation, harvest, and genetics, as well as density independent factors such as climate—those interactions can make density-related processes difficult to document (McCullough 1979, 1990; White and Bartmann 1997; Bowyer et al. 1999; Aanes et al. 2000). Density dependence has been investigated in birds (Sedinger et al. 2001; Both and Visser 2003; Elmberg et al. 2003), small mammals (Aars and Ims 2002), carnivorous mammals (Fryxell et al. 1999; Macdonald et al. 2002), and large, herbivorous mammals (McCullough 1979; Kie and White 1985; Bowyer et al. 1999; Myrsterud et al. 2000; Sæther et al. 2002; Toigo et al. 2002) with varying results, because most organisms exhibit both density-dependent and density-independent characteristics.

Most aspects of the ecology of large mammals are influenced by density-dependent processes (McCullough 1979, 1999; Fowler 1981; Gaillard et al. 2000; Kie et al. 2003 for reviews). Thus, large mammals offer a quintessential model for studying density dependence

K. M. Stewart (✉) · R. Terry. Bowyer
Institute of Arctic Biology and Department of Biology
and Wildlife, University of Alaska Fairbanks,
Fairbanks, AK 99775-7000, USA
E-mail: ftkms1@uaf.edu
Fax: +1-907-4746967

Present address: R. Terry. Bowyer
Department of Biological Sciences, Idaho State University,
Pocatello, ID 83209, USA

B. L. Dick · J. G. Kie
United States Forest Service, Pacific Northwest Research Station,
1401 Gekeler Lane, La Grande, OR 97850, USA

B. K. Johnson
Oregon Department of Fish and Wildlife,
1401 Gekeler Lane, La Grande, OR 97870, USA

because of their life-history strategies, including strong competitive ability, large body size, long lifespan, low reproductive rate, and high maternal investment (McCullough 1979; Clutton-Brock et al. 1987; Rachlow and Bowyer 1994; Gaillard et al. 2000). Although numerous studies of large herbivores have demonstrated the role that density dependence plays in the dynamics and regulation of populations (Klein 1968; Caughley 1970; Kie and White 1985; Clutton-Brock et al. 1987; Singer et al. 1997; Kie and Bowyer 1999), others have failed to detect those processes (Banasiak 1961; Gasaway et al. 1983; Mackie et al. 1990). Most studies attempting to examine density-dependent mechanisms of large herbivores make comparisons across too narrow a breadth of densities with respect to ecological carrying capacity (K) or too short a time span to detect changes in fecundity, recruitment, or survival and, as a result, often fail to recognize those processes (McCullough 1990; Kie et al. 2003). Research substantiating the importance of density-dependent mechanisms in ungulate populations typically has come from long-term studies in which populations varied markedly in size with respect to K , and appropriate vital rates for populations were collected (McCullough 1979; Clutton-Brock et al. 1987; Gaillard et al. 2000). Such a design, however, cannot sort stochastic effects that occur among years from influences of density dependence (White and Bartmann 1997). Moreover, comparing densities among populations to evaluate parameters such as recruitment or survival is meaningless without knowledge of where those populations are with respect to K (McCullough 1979; Bowyer et al. 1999; Kie et al. 2003). Few studies have experimentally tested effects of high-population and low-population density of large, herbivorous mammals simultaneously in the same ecosystem, because of the difficulty of performing manipulative experiments on those large mammals (McCullough 1979; Stewart et al. 2002).

Forage availability during winter often is thought to be most critical for regulating populations of large mammals; estimates of K and habitat improvements

typically are focused on winter ranges (Banasiak 1961; Mackie et al. 1990; Raedeke et al. 2002). Conversely, other studies report that nutrition during summer is critical for building body reserves to sustain animals during winter (Mautz 1978; McCullough and Ullrey 1983; Cook et al. 2004). Pederson and Harper (1978) noted that differences in productivity of two herds of mule deer (*Odocoileus hemionus*) resulted from differences in forage availability and quality on summer ranges. Moreover, Teer et al. (1965) reported variation in counts of corpora lutea with changes in population density of white-tailed deer (*O. virginianus*), which would not have occurred if forage in spring and summer were not in short supply. Among temperate and arctic ungulates, nutritional requirements during winter cannot be met because of low-quality forage; consequently, winter nutrition is dependent on catabolism of body stores (Mautz 1978; McCullough and Ullrey 1983; Schwartz et al. 1988b; Parker et al. 1999). Nonetheless, few critical tests of the role of summer range on density-dependent processes exist because of interactions between seasons resulting from depletion of body reserves accrued in summer during winter.

We designed a manipulative experiment to examine effects of density-dependent processes in North American elk (*Cervus elaphus*) at high-population (near K) and low-population (below maximum sustained yield, MSY) densities, simultaneously in the same system. We hypothesized that differences in body condition and reproduction between high and low densities of elk would result from density-dependent processes (Table 1). If those density-dependent effects are manifested principally through intraspecific competition, based on that hypothesis we predicted that body condition and pregnancy rates of adult females would be lower in the high-density population than for the population at low density (Table 1). We also hypothesized that effects of density dependence would be exhibited by differences in nutrition obtained during spring, summer, and autumn, while experimentally holding effects of winter nutrition constant. Although such data would need to be collected

Table 1 Life-history characteristics of ungulates and hypotheses tested with this study that reflect the relative differences in a population at or below maximum sustained yield (MSY) and at carrying capacity (K), modified from Kie et al. (2003)

Life-history characteristic	Population size at or below MSY	Population size at or near K	Hypothesis tested in this study
Physical condition of adult females	Better	Poorer	Yes
Pregnancy rate of adult females	Higher	Lower	Yes
Age at first reproduction for females	Younger	Older	Yes
Yearlings pregnant	Usually	Seldom	Yes
Pause in annual production by adult females	Less likely	More likely	Yes
Corpora lutea counts of adult females	Higher	Lower	No
Weight of neonates	Heavier	Lighter	No
Litter size ^a	Higher	Lower	No
Survivorship of young ^b	Higher	Lower	No
Age at extensive tooth wear ^c	Older	Younger	No

^aNo variation in litter size of North American elk

^bIn the absence of efficient predators

^cNot applicable because animals did not remain consistently in the same study area

across a wide range of densities and include information on survivorship of young (Table 1) to fit a recruitment curve (sensu McCullough 1979), our experimental manipulation of elk density provides a critical test of whether density dependence in reproduction occurs for this large mammal.

Materials and methods

Study area

We conducted research from 1998 to 2001 on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45°12'N, 118°3'W) is situated in the Blue Mountains of north-eastern Oregon and southeastern Washington, USA, and is located 35 km southwest of La Grande, Oregon, USA. Elevations range from 1,120 to 1,500 m. Starkey encompasses 10,125 ha, and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores, including migration to traditional winter ranges (Rowland et al. 1997). We restricted collection of data to the northeast experimental area on Starkey, which encompassed 1,452 ha, and was separated from the remainder of the study area by the same type of fence (Stewart et al. 2002). The northeast study area was divided into two pastures, east (842 ha) and west (610 ha) with equal proportions of habitats, to accommodate experimental comparisons of population densities of elk. The northeast area consisted of four major habitats: (1) mesic forest dominated by grand fir (*Abies grandis*); (2) xeric forest characterized by Ponderosa pine (*Pinus ponderosa*); (3) xeric grassland dominated by a few grasses and forbs, such as onespice oatgrass (*Danthonia unispicata*) and low gumweed (*Grindelia nana*); and (4) logged forest harvested in 1991–1992, and then seeded with rhizomatous grasses including bluegrass (*Poa* sp.—Stewart et al. 2002). Predators occur infrequently on Starkey and no effort was made to control predators on our study areas.

Experimental design and statistical analyses

Elk populations were at moderate density on the study area during 1998 (east area 4.51 elk/km²; west area 5.41 elk/km²). During 1999, we began an experiment to examine effects of population density by comparing a population at high density, which was randomly assigned to the east area, and a low-density population in the west area. We selected 4.0 elk/km² for the low-density population and 20.0 elk/km² for the high-density population based on earlier work on Starkey (Rowland et al. 1997). Nonhunted populations of elk have been reported to attain densities as high as 33 elk/km² (Houston 1982; Hobbs et al. 1996). Moreover, Hobbs et al. (1996) used 31 elk/km² for their high-density treatment in an experiment examining resource compe-

tition between cattle and elk. The experiment began in May 1999. Within 1 month of the beginning the experiment, however, a gate was left open between study areas, resulting in movement of elk from the high-density to the low-density population. Thus our low-density population for that year was 6.6 elk/km² and the high-density population 10.8 elk/km². During the final 2 years of study (2000 and 2001), we maintained a high-density population at 20.1 elk/km² and low-density population of 4.1 elk/km².

Elk are maintained throughout winter in a holding area in which they are fed a maintenance diet of alfalfa hay (Rowland et al. 1997). We were unable to keep individuals in the same population each year, because of the limited area for holding animals on the winter feedground. Therefore, the experiment was reset each year. Accordingly, we offered a variable indicating where animals had been the previous year (including main study area) in addition to previous reproductive effort (either pregnancy or successfully recruiting young the previous year) in our analyses. Thus, analyses of effects of density dependence in this study are related to nutrition during late spring, summer, and autumn. Elk were released from the winter feeding area to our study sites in late April.

As elk entered the feedground during winter, they were captured and moved via a system of alleys through the handling facility for collection of data on individual animals (Rowland et al. 1997). Yearlings, young (<1 year old), and adult females (≥2 years old) were processed through the handling facility. Each animal was identified by ear tags with unique numbers. Animals that were handled initially as adults were recorded as an adult age class—their exact age was unknown. Conversely, animals handled initially as young or yearlings were recorded as known-age individuals. We restricted our analyses on reproduction and body condition to include only known-age individuals from each of our study areas.

Body mass was determined for each individual with a digital scale to the nearest 1 kg. Blood was collected from the jugular veins of adult and yearling females, and serum was analyzed (Bio Tracking, Moscow, Idaho, USA) for pregnancy-specific protein B to determine pregnancy rates (Noyes et al. 1997; Keech et al. 2000). Depth of maximum rumpfat (maxfat) was determined as an index of body condition for adult and yearling female elk via ultrasonography (Keech et al. 1998; Stephenson et al. 1998). Data on rumpfat were collected at the midpoint (midfat) between the illium and ischial tuberosity, rather than maximum fat levels during 1998; however, from 1999 to 2001 we collected data for both mid and maximum depth of rumpfat for yearling and adult females. We used linear regression to develop equations to convert midfat to maximum depth of rumpfat for 1998, to compare maximum fat levels collected on all yearling and adult female elk (Cook et al. 2001). The regression equation was: maxfat = 0.0265 + 1.2409midfat ($r^2 = 0.939$, $P < 0.0001$). All further

analyses of depth of rumpfat were performed on maximum levels of fat for 1999–2001 and the converted values of maxfat for 1998 only.

We determined annual and seasonal precipitation from a weather station on Starkey: winter (November–March), spring (April–June), summer (July–September), and autumn (October; Stewart et al. 2002). We calculated number of degree days $> 5^{\circ}\text{C}$ (number of degrees that the mean daily temperature was $> 5^{\circ}\text{C}$, summed across all days; Bowyer et al. 1998). This variable was selected because it provided an index of growth for plants in seasonal environments (Chapin 1983; Bowyer et al. 1998).

We examined treatment level effects of mean physical condition (indexed by maximal depth of rumpfat) and proportion of adult females and yearlings pregnant in each study area against population density for each year using one-tailed Spearman rank correlation (r_s) (Neter et al. 1990). We selected one-tailed tests because the direction of the relationship between population density, physical condition, and reproduction was known (Kie et al. 2003). Spearman rank correlations make no assumptions concerning the shape of the relationships between variables (Zar 1999; Bowyer et al. 2001). We also tested for density-independent factors affecting body condition using one-tailed Spearman rank correlations to compare annual precipitation and temperature for each year of study versus mean physical condition for each population density as well as examining appropriate interactions.

We examined growth of elk by fitting the von Bertalanffy equation for sigmoidal growth of body mass against age of elk (Ricker 1979; Zullinger et al. 1984; Spaeth et al. 2001) using nonlinear regression (Proc NLIN, SAS 2001). We used multivariate analysis of covariance (MANCOVA) to examine indices of body condition of individual adult female elk between high and low population densities in 1999–2001, years during which our population densities were most disparate. We followed multivariate analyses with individual analysis of covariance (ANCOVA) for each of the body-condition indices. Because populations of large herbivores are strongly age-structured, that variable is an important factor when examining differences in body mass (Kie et al. 1983; Gaillard et al. 2000; Pettorelli et al. 2001); accordingly, age was used as the covariate in those analyses.

We calculated proportion of elk pregnant for all known-aged individuals for high-density and low-density populations from 1999 to 2001. We used simple linear regression, weighted by the number of animals pregnant for each age, to examine relationships between proportion pregnant and age for high-density and low-density populations (Neter et al. 1990). We compared nonlinear regressions for the two populations using the F -test to examine regression coefficients (Neter et al. 1990). We then compared predicted values at the inflection point of the regression parabola to determine if the proportion of elk pregnant in the high-density population was lower than that of the low-density

population using a one-tailed t -test for comparison of points on regression lines (Zar 1999).

We employed stepwise logistic regression ($\alpha=0.15$ enter, 0.10 remain) to examine effects of body condition, age, environmental variables (temperature and precipitation), and previous reproduction on pregnancy of individual elk following the mating season. Our binomial dependent variable was pregnancy and independent variables included: age (years), body mass (kg), rumpfat (mm), lactational status (1 = lactating, and 0 = not lactating), precipitation (cm), temperature (degree/days) and year (1998–2001). Lactational status, measured during late autumn or early winter, was used to index effects of reproduction during the previous year on reproductive effort for the current year. Initially, seasonal and annual precipitation and temperature were offered in separate stepwise models in addition to offering the respective interaction. P -values were used to evaluate logistic regressions. If > 1 model was significant AIC was used to select the best model, and odds ratios were used to examine the contribution of specific variables selected in stepwise logistic models.

Results

During 1998, elk in both study areas were maintained at moderate population densities and exhibited similar pregnancy rates; sample sizes were similar between study sites (Table 2). Our manipulation of population density began in 1999; however, our target population densities were not achieved until we further manipulated densities of elk during 2000–2001 (Table 2). We achieved five-fold differences in density during 2000–2001, where the low-density population consisted of 4.1 elk/km² and the high-density area was 20.1 elk/km² (Table 2), variation sufficient to obtain a critical test of the role of density dependence on physical condition and reproduction in elk.

Proportion of females pregnant was negatively related to population density across 3 years (1999–2001) of our density manipulation, plus 1 year (1998) of pre-treatment data (Fig. 1). Fewer females became pregnant as population density increased. Body condition (e.g. rumpfat) of adult and yearling females was negatively correlated with population density; females in the high-density area had poorer body condition than those in the low-density area (Fig. 1). Annual precipitation (cm) did not significantly affect body condition of adult females ($r_s=0.395$, $P=0.332$); temperature (degree/days) also did not affect ($r_s=0.119$, $P=0.778$) body condition of female elk. No significant interaction occurred between precipitation and population density ($P=0.113$) or temperature and precipitation ($P=0.212$) on body condition of elk.

We fit a von Bertalanffy growth curve for age-specific growth and observed a curvilinear relationship $\{\hat{Y} = 105.8 + 95.679 [1 - 0.333e^{-1.556(x-1)}]^3, P < 0.001\}$ between body mass (kg) and age (years) for 454 adult

Table 2 Descriptive statistics for adult and yearling female elk at different population densities during 1998–2001 on the Starkey Experimental Forest and Range, Oregon, USA

Population characteristic	West study area			East study area		
	<i>n</i>	$\bar{X}$	<i>SD</i>	<i>n</i>	$\bar{X}$	<i>SD</i>
1998						
Population density (Elk/km ²)		5.41			4.51	
Previous year pregnancy ^a	16	0.69	1.854	16	0.75	1.732
Current year pregnancy ^a	17	0.53	2.058	19	0.74	1.919
Lactational status ^a	17	0.35	1.970	19	0.26	1.919
Body mass (kg)	17	180	21.8	19	198	29.6
Rumpfat (cm)	17	0.60	0.291	19	0.52	0.258
1999						
Population density (Elk/km ²)		6.56			10.79	
Previous year pregnancy ^a	20	0.45	2.225	35	0.34	2.808
Current year pregnancy ^a	24	0.58	2.415	45	0.58	3.313
Lactational status ^a	15	0.27	1.713	38	0.16	2.248
Body mass (kg)	24	182.8	25.9	45	180	29.3
Rumpfat (cm)	24	0.53	0.33	45	0.51	0.285
2000						
Population density (Elk/km ²)		4.10			20.07	
Previous year pregnancy ^a	18	0.33	2.000	110	0.44	5.201
Current year pregnancy ^a	18	0.83	1.581	111	0.51	5.266
Lactational status ^a	18	0.28	1.900	111	0.28	4.772
Body mass (kg)	18	192	31.0	111	180	30.1
Rumpfat (cm)	18	0.71	0.383	111	0.46	0.321
2001						
Population density (Elk/km ²)		4.10			20.07	
Previous year pregnancy ^a	15	0.60	1.897	104	0.49	5.098
Current year pregnancy ^a	15	0.53	1.932	106	0.47	5.140
Lactational status ^a	15	0.33	1.826	99	0.22	4.137
Body mass (kg)	15	183	21.3	106	188	28.8
Rumpfat (cm)	15	0.58	0.348	106	0.43	0.283

^aBinomial variables where 1 = pregnant or lactating 0 = not pregnant or not lactating; thus means and standard deviations were calculated using formulas for binomial variables

female elk. That curve indicated that age was an important factor when examining differences in body mass of individual animals. When age was included as a covariate (*Wilks lambda* $F_{2,312} = 5.15$, $P = 0.006$, $n = 319$), body condition of adult female elk was lower ($P = 0.002$) in the high-density ($\bar{X} = 0.47$, $SE = 0.21$), than in the low-density area ($\bar{X} = 0.61$, $SE = 0.42$) but body mass of individuals did not differ ($P = 0.464$) between high ($\bar{X} = 182.9$, $SE = 1.95$) and low ($\bar{X} = 1.86$, $SE = 3.91$) densities.

We observed a parabolic relationship between age and pregnancy rates of female elk on low-density and high-density areas, with lower pregnancy rates at young and older ages (Fig. 2). The greatest proportion of females pregnant occurred at 6 years of age for both population densities of elk; no significant difference in the overall shape of curves occurred ($P > 0.05$; Fig. 2). Nevertheless, proportion of female elk pregnant at 6 years of age in the high-density area ($\hat{Y} = 0.770$) was significantly lower ($P < 0.05$) than that of the low-density area ($\hat{Y} = 0.941$).

Our logistic model indicated that age, body mass, previous reproduction, annual precipitation, and maximal depth of rumpfat affected pregnancy of adult and yearling female elk (Table 3). Year was offered to the logistic model, but failed to enter ($P > 0.15$). Annual

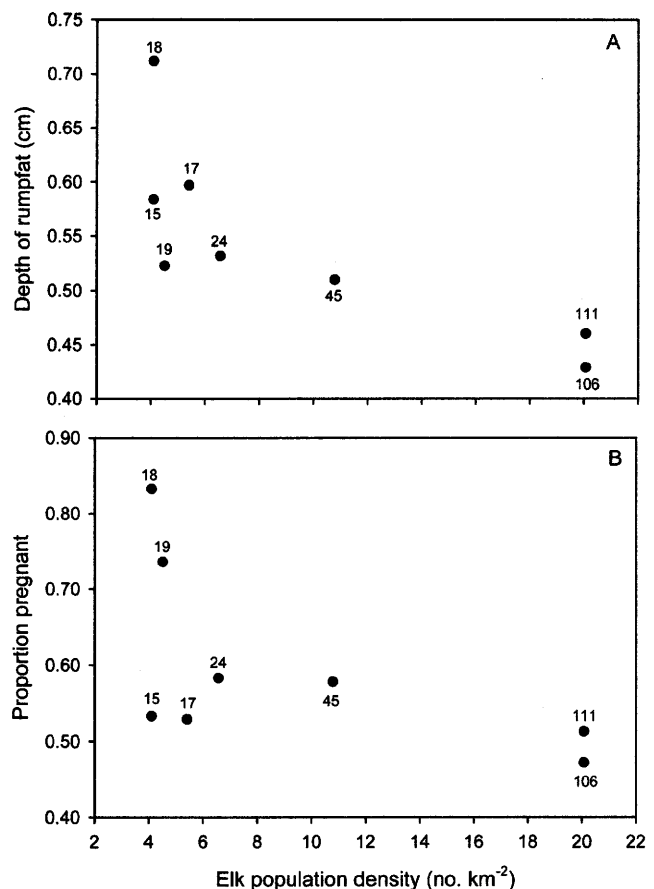


Fig. 1 Effects of population density of elk on a body condition as indicated by depth of rumpfat, and b proportion of yearling and adult female elk that were pregnant ($n = 355$) on the Starkey Experimental Forest and Range, Oregon, USA, 1998–2001. Sample sizes used to calculate mean physical condition and proportion pregnant are indicated over points in each figure. Spearman rank correlations indicated negative relationships between population density of elk and a body condition ($r_s = -0.855$, $P = 0.003$), and b proportion of females pregnant ($r_s = -0.687$, $P = 0.030$)

precipitation was the only environmental variable to enter any logistic regression ($P < 0.15$). A variable indicating which population-density treatment each animal had been the previous year was offered to our logistic models, but failed to enter ($P > 0.15$). Thus, the index of previous reproductive effort was likely more indicative of an individual's reproductive history than where the animal had been the previous year. The overriding factor affecting current-year reproduction was maximal depth of rumpfat, as indicated by odds ratios > 14 times that of other variables (Table 3). Body mass and previous reproduction were progressively less influential in affecting reproduction (Table 3).

Discussion

Density-dependent mechanisms are mediated through intraspecific competition, via per capita availability of food, and the subsequent influence of nutrition on

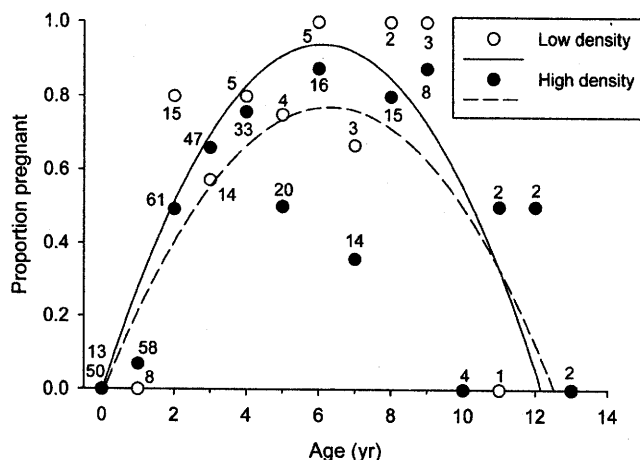


Fig. 2 Relationships between proportion of female elk pregnant and age for high-density and low-density areas, weighted by sample size, on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001

(highdensity: ($n = 332$) $P < 0.001$, $R^2_{adj} = 0.695$,
 $\hat{Y} = -0.0196 + 0.251\text{Age} - 0.0199\text{Age}^2$;
 lowdensity: ($n = 73$) $P < 0.001$, $R^2_{adj} = 0.6576$,
 $\hat{Y} = -0.008 + 0.311\text{Age} + 0.026\text{Age}^2$).

Sample sizes used in weighted regression analyses are shown next to data points—for the 0 age class 50 young were sampled for the high-density area, and 13 young for the low-density area

Table 3 Results of logistic regression to evaluate pregnancy of adult female elk, $n = 332$, at the level of the individual from 1998–2001 on the Starkey Experimental Forest and Range, northeastern Oregon, USA. Model evaluation criteria included Likelihood Ratio Test ($P < 0.001$), AIC = 287.56, with concordance 89.1%

Variable	df	Parameter estimate	SE	P-value	Odds ratio ψ
Intercept	1	-14.75	1.962	< 0.001	–
Age	1	-0.15	0.089	0.098	0.86
Body mass	1	0.07	0.010	< 0.001	1.09
Lactation status	1	-0.91	0.416	0.029	0.91
Rumpfat	1	2.51	0.816	0.002	60.84
Annual precipitation	1	0.05	0.017	0.003	1.09

reproduction and recruitment of young into the population (McCullough 1979; Sæther and Haagenrud 1983; Schwartz and Hundertmark 1993; Keech et al. 2000). We predicted that density-dependent effects would be evidenced by differences in body condition and pregnancy rates of females between our manipulated populations of elk. Indeed, our results supported those predictions, and indicated that elk at high-population density were in much lower physical condition and had lower pregnancy rates than elk maintained at low density (Fig. 1). Similarly, Lubow et al. (2002) reported strong density-dependent effects on recruitment and survival of juvenile elk as population density approached K , likely in response to declines in physical condition of adult females. Our results are consistent with other data on effects of population density on body condition in ungulates; females in poorer physical con-

dition are less likely to reproduce (McCullough 1979; Adamczewski et al. 1997). Nonetheless, results of previous research include effects of both winter and summer conditions.

We observed neither differences in reproduction among yearlings, which was low or nonexistent in both study areas, nor differences in pregnancy of old (> 9 years) individuals (Fig. 2). Our data indicated that at 2 years of age, however, pregnancy rates between the two populations began to diverge (Fig. 2). Indeed, pregnancy rates among prime-aged (ages 4–9) elk were much lower in the high-density area compared with the low-density area—the greatest difference between densities was at 6 years old (Figs. 1, 2). Numerous studies have reported density dependence in adult fecundity and increasing age at first reproduction for large herbivores (McCullough 1979; Kie and White 1985; Van Vuren and Bray 1986; Clutton-Brock et al. 1987; Houston and Stevens 1988; Kirkpatrick and Turner 1991). Our low-density population may not have been sufficiently low for yearlings to obtain sufficient resources and, hence, the improved physical condition necessary to initiate reproduction. We note, however, that we were limited to a moderate density by the necessity of obtaining an adequate sample for comparison. Moreover, changes in body mass with age fitted an asymptotic distribution, with adult body mass attained at about 2 years of age for females. Those growth curves did not differ among populations; reproduction of yearlings would likely require a critical body mass necessary to begin reproduction at a younger age in the low-density population (*sensu* Cameron and Ver Hoef 1994). This outcome is not surprising because elk were not placed in high or low-density areas consistently and winter conditions were identical for all animals.

Twinning rates in moose (*Alces alces*) are highly correlated with decreasing age at first reproduction (Keech et al. 2000; Boer 1992), and numerous studies have examined changes in litter size with concurrent changes in population density (Kie and White 1985; Gaillard et al. 2000). Elk rarely have more than one offspring (Bubenik 1982); thus, we could not examine differences in litter size between populations. Our data also indicated that elk > 9 years of age began to exhibit senescence in pregnancy, although sample sizes for those age classes were low—this outcome needs further investigation (Fig. 2). Nonetheless, senescence in reproduction has been reported for individual cervids in “old” age classes (Gaillard et al. 2000; Ericsson et al. 2001; Mysterud et al. 2001; Loison et al. 2002).

Feedback processes associated with density dependence are mediated through nutrition; thus individuals in populations near K tend to be in poor physical condition and often exhibit low rates of reproduction, delayed reproduction, and low survivorship (McCullough 1979; Kie et al. 1980; Skogland 1984; Bowyer et al. 1999; Kie et al. 2003). Moreover, intraspecific competition for resources may force adult females to make tradeoffs between parental investment in current offspring and

future reproductive efforts (McCullough 1979; Clutton-Brock 1984). Factors affecting pregnancy among individual female elk in our study included age, physical condition (body mass and depth of rumpfat) and previous reproductive effort (Table 3). Those animals in poorer physical condition that had recruited an offspring the previous year were less likely to become pregnant than those individuals on a higher nutritional plane; this represents a reproductive pause. Physical condition of individuals was the most important factor determining whether individuals became pregnant; those variables that contributed most strongly to reproductive effort were body mass and fat levels (Table 3). Our results are consistent with studies of muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) in northern environments where body mass, nutritional condition, and lactational status strongly affected reproduction (Cameron et al. 1993; Gerhart et al. 1997; White et al. 1997). Moreover, maternal fat reserves also are related to body mass in neonatal cervids, with subsequent effects on life-history characteristics, including survivorship (Gaillard et al. 1997; Bowyer et al. 1998; Keech et al. 1999; Barten et al. 2001). Thus, increasing population density, which resulted in lowering of fat reserves and pregnancy in our study also provides a link to survivorship of young (Keech et al. 2000).

We initially were surprised that population density failed ($P > 0.15$) to enter logistic models; however, if effects of population density act through intraspecific competition and decreased physical condition, effects of density were already included in the model (i.e., density was a lurking variable). Failure of population density to enter the logistic model also indicated that socially mediated reduction in reproduction was unlikely, because those measures of condition explained effects of population density on reproduction. If population density had entered the model, that variable likely would indicate that something else related to differing densities (e.g., social stress) was not explained by condition, reproductive effort, and density-independent factors (e.g., precipitation).

Annual precipitation (a density-independent variable) affected pregnancy rates of individual elk, most likely from its influence on plant growth and foraging conditions among years (Lenart et al. 2002). Nonetheless, density-dependent factors overrode effects of density-independent factors in this montane ecosystem. Indeed, seasonal temperature and seasonal precipitation failed to enter any of our logistic models. Our results indicated, however, that annual precipitation had effects on pregnancy at the level of the individual rather than the level of the population (i.e., linear regression examining precipitation and body condition was not significant). Measurement at the level of the individual may be necessary to detect subtle effects of processes such as previous reproduction and annual rainfall. Density-independent interactions with density-dependent processes may be more pronounced where effects of density are accumulated through time and where poor

physical condition may be aggravated by successive winters resulting in depleted range conditions, a topic in need of additional study.

Elk on Starkey were maintained on a feed ground during winter; thus, effects of different population densities in our study are specific to spring, summer, and autumn. Foraging conditions in winter were controlled by our experimental design. Because elk from both populations were maintained on the same diet throughout winter, we were able to control for effects of winter and focus on differences in nutrition from spring, summer, and autumn ranges, something that is not possible without our experimental approach. Our results indicated strong effects of density dependence on animal condition and pregnancy rates resulting from differences in spring, summer, and autumn nutrition rather than from metabolism of body stores during winter.

Our results support the hypothesis that summer nutrition is critical for building body stores; those animals in the high-density population exhibited lower body condition and reproduction than those at low density. Energy stores are determined by quality of the summer range, while depletion is a function of winter range quality and length of winter (Mautz 1978; Schwartz et al. 1988a,b; Parker et al. 1999). Indeed, animals that are nutritionally stressed and are unable to build adequate body reserves during summer are probably more affected by winter than those animals on a high plane of nutrition during summer (Mautz 1978). We hypothesize that interactions among climate and population density on fecundity and survival are most likely expressed during winter and that young and senescent individuals may be more sensitive to weather severity during winter than prime-aged animals (sensu McCullough 1979).

Our experimental approach to examining density dependence allowed us to compare effects of population density with the same climatic conditions for each population density across years. We detected strong density dependence in elk expressed by changes in body condition and reproduction with increasing density. We demonstrated effects of differing nutrition during summer on body condition and reproduction; summer is the most important period for accumulation of body stores to buffer animals against winter. Moreover, our results also support the hypothesis that effects of density dependence and measures of K must be viewed as year-round phenomena, rather than during a single season. We suggest that more emphasis be placed on the role of spring and summer on density-dependent processes and thereby population regulation in elk and other northern ungulates.

Acknowledgements We appreciate the assistance of Starkey Project personnel. R.G. White, M. Vavra, K.J. Hundertmark, J.S. Sedinger, and P.S. Barboza provided helpful comments on the manuscript. E. Rexstad provided valuable expertise in statistical analysis. This study was funded by the United States Forest Service, the Institute of Arctic Biology at the University of Alaska Fairbanks, and the Rob and Bessie Welder Wildlife Foundation.

This is Rob and Bessie Welder Wildlife Foundation contribution number 627. All aspects of this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks and the Starkey Project, and were in keeping with protocols adopted by the American Society of Mammalogists for field research involving mammals (Animal Care and Use Committee 1998).

References

- Aanes R, Sæther BE, Oritsland NA (2000) Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* 23:437–443
- Aars J, Ims RA (2002) Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. *Ecology* 83:3449–3456
- Adamczewski JZ, Flood PF, Gunn A (1997) Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). *J Zool (London)* 241:245–269
- Animal Care and Use Committee (1998) Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J Mammal* 79:1416–1431
- Banasik CF (1961) Deer in Maine. *Maine Game Div Bull* 6:1–159
- Barten NL, Bowyer RT, Jenkins KJ (2001) Habitat use by female caribou: tradeoffs associated with parturition. *J Wildl Manage* 65:77–92
- Bartmann RM, White GC, Carpenter LH (1992) Compensatory mortality in a Colorado mule deer population. *Wildl Monogr* 121:1–39
- Boer AH (1992) Fecundity of North American moose (*Alces alces*): a review. *Alces Suppl* 1:1–10
- Both C, Visser ME (2003) Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *Am Nat* 161:326–336
- Bowyer RT, Van Ballenberghe V, Kie JG (1998) Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *J Mammal* 79:1332–1344
- Bowyer RT, Nicholson MC, Molvar EM, Faro JB (1999) Moose on Kalgini island: are density-dependent processes related to harvest? *Alces* 35:73–89
- Bowyer RT, McCullough DR, Belovsky GE (2001) Causes and consequences of sociality in mule deer. *Alces* 37:371–402
- Boyce MS (1989) The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, New York
- Bubenik AB (1982) Physiology. In: Thomas J W, Toweill DE (eds) *Elk of North America: ecology and management*. Stackpole, Harrisburg, pp 125–179
- Cameron RD, Ver Hoef JM (1994) Predicting parturition rate of caribou from autumn body mass. *J Wildl Manage* 58:674–679
- Cameron RD, Smith WT, Fancy SG, Gerhart KL, White RG (1993) Calving success of female caribou in relation to body weight. *Can J Zool* 71:480–486
- Caughley G (1970) Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* 51:54–72
- Chapin FS III (1983) Direct and indirect effects of temperature on arctic plants. *Polar Biol* 2:47–52
- Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. *Am Nat* 123:212–229
- Clutton-Brock TH, Albon SD, Guinness FE (1987) Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *J Anim Ecol* 56:857–871
- Cook RC, Cook JG, Murray DL, Zager P, Johnson BK, Gratson MW (2001) Development of predictive models of nutritional condition for Rocky Mountain elk. *J Wildl Manage* 65:973–987
- Cook JG, Johnson BK, Cook RC, Riggs RA, Delcurto T, Bryant LD, Irwin LL (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildl Monogr* 155:1–61
- Elmberg J, Nummi P, Poysa H, Sjöberg K (2003) Breeding success of sympatric dabbling ducks in relation to population density and food resources. *Oikos* 100:333–341
- Ericsson G, Wallin K, Ball JP, Broberg M (2001) Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82:1613–1620
- Fowler CW (1981) Density dependence as related to life history strategy. *Ecology* 62:602–610
- Fryxell JM, Falls JB, Falls EA, Brooks RJ, Dix L, Strickland MA (1999) Density dependence, prey dependence, and population dynamics of martens in Ontario. *Ecology* 80:1311–1321
- Gaillard JM, Boutin JM, Delorme D, VanLaere G, Duncan P, Lebreton JD (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* 112:502–513
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393
- Gasaway WC, Stephenson RO, Davis JL, Shepherd PEK, Burris OE (1983) Interrelationships of wolves, prey, and man in interior Alaska. *Wildl Monogr* 84:1–50
- Gerhart KL, Russel DE, VanDewetering D, White RG, Cameron RD (1997) Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. *J Zool* 242:17–30
- Hobbs NT, Baker DL, Bear GD, Bowden DC (1996) Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecol Appl* 6:200–217
- Houston DB (1982) *The Northern Yellowstone elk*. Macmillan, New York
- Houston DB, Stevens V (1988) Resource limitation in mountain goats: a test by experimental cropping. *Can J Zool* 66:228–238
- Keech MA, Stephenson TR, Bowyer RT, Van Ballenberghe V, Ver Hoef JM (1998) Relationships between blood-serum variables and depth of rump fat in Alaskan moose. *Alces* 34:51–57
- Keech MA, Boertje RD, Bowyer RT, Dale BW (1999) Effects of birth weight on growth of young moose: do low-weight neonates compensate? *Alces* 35:51–57
- Keech MA, Bowyer RT, VerHoef JM, Boertje RD, Dale BW, Stephenson TR (2000) Life-history consequences of maternal condition in Alaskan moose. *J Wildl Manage* 64:450–462
- Kie JG, Bowyer RT (1999) Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *J Mammal* 80:1004–1020
- Kie JG, White M (1985) Population dynamics of white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge, Texas. *Southwestern Nat* 30:105–118
- Kie JG, Drawe DL, Scott G (1980) Changes in diet and nutrition with increased herd size in Texas white-tailed deer. *J Range Manage* 33:28–34
- Kie JG, White M, Drawe DL (1983) Condition parameters of white-tailed deer in Texas. *J Wildl Manage* 47:583–594
- Kie JG, Bowyer RT, Stewart KM (2003) Ungulates in western forests: habitat relationships, population dynamics, and ecosystem processes. In: Zabel C, Anthony R (eds) *Mammal community dynamics in western coniferous forests: management and conservation*. The Johns Hopkins University Press, Baltimore, pp 296–340
- Kirkpatrick JF, Turner JW (1991) Compensatory reproduction in feral horses. *J Wildl Manage* 55:649–652
- Klein DR (1968) The introduction, increase, and crash of reindeer on St. Matthew Island. *J Wildl Manage* 32:350–367
- Lenart EA, Bowyer RT, Ver Hoef J, Ruess RW (2002) Climate change and caribou: effects of summer weather on forage. *Can J Zool* 80:664–678
- Loison A, Toigo C, Appollinaire J, Michallet J (2002) Demographic processes in colonizing populations of isard (*Rupicapra pyrenaica*) and ibex (*Capra ibex*). *J Zool (London)* 256:199–205
- Lubow BC, Singer FJ, Johnson TL, Bowden DC (2002) Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. *J Wildl Manage* 66:757–775

- Macdonald DW, Newman C, Stewart PD, Domingo-Roura X, Johnson PJ (2002) Density-dependent regulation of body mass and condition in badgers (*Meles meles*) from Wytham Woods. *Ecology* 83:2056–2061
- Mackie RJ, Hamlin KL, Pac DF, Dusek GL, Wood AK (1990) Compensation in free-ranging deer populations. *Trans No Am Wildl Nat Res Conf* 55:518–526
- Mautz WW (1978) Sledding on a bushy hillside: the fat cycle in deer. *Wildl Soc Bull* 6:88–90
- McCullough DR (1979) The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor
- McCullough DR (1990) Detecting density dependence: filtering the baby from the bathwater. *Trans No Am Wildl Nat Res Conf* 55:534–543
- McCullough DR (1999) Density dependence and life-history strategies of ungulates. *J Mammal* 80:1130–1146
- McCullough DR, Ullrey DE (1983) Proximate mineral and gross energy composition of white-tailed deer. *J Wildl Manage* 47:430–441
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2000) Relationships between sex ratio, climate, and density in red deer: the importance of spatial scale. *J Anim Ecol* 69:959–974
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2001) Effects of age, sex and density on body weight of Norwegian red deer: evidence of density dependent senescence. *Proc R Soc London B* 268:911–919
- Neter J, Wasserman W, Kutner MH (1990) Applied linear statistical models, 3rd edn. Richard D. Irwin, Homewood
- Noyes JH, Sasser RG, Johnson BK, Bryant LD, Alexander B (1997) Accuracy of pregnancy detection by serum protein (PSPB) in elk. *Wildl Soc Bull* 25:695–698
- Parker KL, Gillingham MP, Hanley TA, Robbins CT (1999) Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildl Monogr* 143:1–48
- Pederson JC, Harper KT (1978) Factors influencing productivity of two mule deer herds in Utah. *J Range Manage* 31:105–110
- Pettorelli N, Gaillard JM, Van Laere G, Duncan P, Kjellander P, Liberg O, Delorme D, Maillard D (2001) Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proc R Soc London B* 269:747–753
- Rachlow JL, Bowyer RT (1994) Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *J Mammal* 75:328–337
- Raedeke KJ, Millspaugh JJ, Clark PE (2002) Population characteristics. In: Toweill DE, Thomas JW (eds) North American elk: ecology and management. Smithsonian Institution Press, Washington D.C., pp 449–513
- Ricker WE (1979) Growth rates and models. *Fish Physiol* 8:679–743
- Rowland MM, Bryant LD, Johnson BK, Noyes JH, Wisdom MJ, Thomas JW (1997) The Starkey project: history, facilities, and data collection methods for ungulate research. USDA For Serv Tech Rep PNW-GTR 396:1–62
- Russell DE, Gerhart KL, White RG, Van De Wetering D (1998) Detection of early pregnancy in caribou: evidence for embryonic mortality. *J Wildl Manage* 62:1066–1075
- Sæther BE, Haagenrud H (1983) Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. *J Mammal* 64:226–232
- Sæther BE, Engen S, Filli F, Aanes R, Schroeder W, Andersen R (2002) Stochastic population dynamics of an introduced Swiss population of ibex. *Ecology* 83:3457–3465
- SAS (2001) SAS system for windows. Version 8.2. SAS Institute, Cary
- Schwartz CC, Hundertmark KJ (1993) Reproductive characteristics of Alaskan moose. *J Wildl Manage* 57:454–468
- Schwartz CC, Hubbert ME, Franzman AW (1988a) Energy requirements of adult moose for winter maintenance. *J Wildl Manage* 52:26–33
- Schwartz CC, Regelin WL, Franzmann AW (1988b) Estimates of digestibility of birch, willow, and aspen mixtures in moose. *J Wildl Manage* 52:33–37
- Sedinger JS, Lindberg MS, Chelgran ND (2001) Age-specific breeding probability in black brant: effects of population density. *J Anim Ecol* 70:798–807
- Singer FJ, Harting A, Symonds KK, Coughenour MB (1997) Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J Wildl Manage* 61:12–25
- Skogland T (1984) Toothwear by food limitation and its life history consequences in wild reindeer. *Oikos* 51:238–242
- Spaeth DF, Hundertmark KJ, Bowyer RT, Barboza PS, Stephenson TR, Peterson RO (2001) Incisor arcades of Alaskan moose: is dimorphism related to sexual segregation? *Alces* 37:217–226
- Stephenson TR, Hundertmark KJ, Schwartz CC, Van Ballenberghe V (1998) Predicting body fat and body mass in moose with ultrasonography. *Can J Zool* 76:712–722
- Stewart KM, Bowyer RT, Kie JG, Cimon NJ, Johnson BK (2002) Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J Mammal* 83:229–244
- Teer JG, Thomas JW, Walker EA (1965) Ecology and management of the white-tailed deer in the Llano Basin of Texas. *Wildl Monogr* 15:1–62
- Toigo C, Gaillard JM, Gauthier D, Girard I, Martinot JP, Michallet J (2002) Female reproductive success and costs in an alpine capital breeder under contrasting environments. *Ecoscience* 9:427–433
- Van Vuren D, Bray MP (1986) Population dynamics of bison in the Henry Mountains, Utah. *J Mammal* 67:503–511
- Verts BJ, Carraway LN (1998) Land mammals of Oregon. University of California Press, Berkeley
- White GC, Bartmann RM (1997) Density dependence in deer populations. In: McShea WJ, Underwood HB, Rappole JH (eds) The science of overabundance: deer ecology and population management. Smithsonian Institution, Washington, DC, pp 120–135
- White RG, Rowell JE, Hauer WE (1997) The role of nutrition, body condition, and lactation on calving success in muskoxen. *J Zool* 243:13–20
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River
- Zullinger EM, Ricklefs RE, Redford KH, Mace GM (1984) Fitting sigmoidal equations to mammalian growth curves. *J Mammal* 65:607–636