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Variation in mass and lactation among cohorts of white-tailed deer *Odocoileus virginianus*

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Age-specific body mass and % lactation are indices commonly used to monitor status of cervid populations relative to carrying capacity. However, prior-year body condition and reproductive status may influence these indices and alter their interpretation. We examined variation in body mass and % lactation among cohorts of female white-tailed deer *Odocoileus virginianus* to determine: 1) patterns of variation among age classes, 2) if cohorts compensated in subsequent years for restricted somatic development, and 3) the relationship between body mass and % lactation within cohorts. Body mass and % lactation of young deer were more variable than for older deer, potentially making them a more sensitive indicator of population status relative to carrying capacity. The lack of correlation in body mass of cohorts across years implies that cohorts can compensate for restricted somatic development during subsequent years in the environments we studied. Body mass and % lactation were positively correlated in 1.5-year cohorts, suggesting that age of primiparity was affected by body condition. However, mean cohort body mass did not influence % lactation in older cohorts. Our data support that older cohorts (≥ 3 years old) have greater resiliency to changes in density or to environmental events as these cohorts demonstrated less annual variation in body mass and % lactation than did younger cohorts. Annual changes in morphometrics and fecundity of younger-aged cohorts may be the best indicator of animal density relative to carrying capacity, or of environmental events that influence carrying capacity.

Key words: body mass, cohort correlation, cohort variation, lactation, Mississippi, Odocoileus virginianus, white-tailed deer

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Variation in body mass and condition has been shown to influence fecundity in many ungulates (Verme 1969, Albon et al. 1983, Sæther & Haagenrud 1983, Cameron et al. 1993, Hewison 1996, Festa-Bianchet et al. 1998), and changes in cohort reproductive success can have profound implications on the population dynamics of large herbivores (Albon et al. 1992, Gaillard et al. 2003). The severity of a cohort effect (i.e. below average body mass or reproductive success) on population demographics depends on its duration. Albon et al. (1992) suggested that habitat quality and animal density can exacerbate the cohort effect by prolonging its extent. They reported that cohort effects persisted (i.e. no compensation) in a red deer *Cervus elaphus* population in marginal habitat, whereas another population in better habitat compensated following restricted growth and fecundity as juveniles. Post et al. (1997) also reported persistent density-independent variation in red deer cohorts. They determined that variation in adult morphology could be linked to winter climatic condition when cohorts were *in utero*. Mech et al. (1991) related generational variation in white-tailed deer *Odocoileus virginianus* cohorts to winter conditions experienced by their grandmothers. The effects of animal density on food abundance may also cause lingering cohort effects. Work by Pettorelli et al. (2002) with roe deer *Capreolus capreolus* supports this supposition as they documented the effects of density on juveniles persisting into adulthood. Because cohort variation can have profound effects on population dynamics, monitoring annual variation is critical to effectively manage cervid populations.

Gaillard et al. (2000) concluded from an inter-specific comparison of large herbivores that survival and fecundity are more variable for juveniles than for adults. Factors that affect food quantity and quality may influence young white-tailed deer, because this is the period of greatest somatic development (Strickland & Demarais 2000). Changes in density or environment would be expected to affect young animals to a greater degree than adults. The resiliency of adults to changes in density was demonstrated in roe deer by Andersen & Linnell (2000), where adult females maintained their body condition while population size tripled.

Although a positive association between body mass and fecundity of ungulates has been documented (Verme 1967, Albon et al. 1983, Sæther & Haagenrud 1983, Gaillard et al. 1992, Cameron et al. 1993, Hewison 1996, Festa-Bianchet et al. 1998,

Anderson & Linnell 2000), using body mass as a correlate for fecundity may be problematic. Clutton-Brock et al. (1982) and Verme (1967) documented the negative influence of previous reproduction on current reproduction in red and white-tailed deer, respectively. Females that weaned offspring one year had lower fecundity rates the following year. Thus, body mass affects reproduction, and reproduction affects body mass, making causality between mass and reproductive success unclear (Festa-Bianchet et al. 1998).

Understanding the relationship between density, body mass and reproduction is especially important for development of harvest strategies. Based on the density-dependent model of population growth described by McCullough (1979), managers use variation in population morphometrics, such as body mass, as an indicator of population change and recommend harvests accordingly. Indeed, researchers have documented changes in mass following harvests that were consistent with the density-dependent model (e.g. Jacobson 1992, Ashely et al. 1998). However, annual variation in body mass may reflect changes in reproductive rate or environment rather than changes in population density.

The ability to interpret changes in body mass and reproduction of female cohorts may become more important as the prevalence of antler regulations designed to minimize the harvest of young males increases (Demarais et al. 2005). Use of body mass and antler size of younger-aged bucks to guide harvest management may no longer be possible on many state-managed properties. More information regarding female cohort variation is needed to establish patterns that can be used for deer population management.

Because changes in relative body mass are linked to survival (Bartman et al. 1992, Singer et al. 1997, Cook et al. 2004) and fecundity (Hewison 1996, Sæther & Haagenrud 1983, Verme 1967) in many cervids, and can be used to guide harvest management, our goal was to describe patterns in white-tailed deer cohort variation and compensation using body mass and lactation data spanning 12-16 years from three populations in Mississippi (Fig. 1). Our specific objectives were to:

- 1) test the predictions of Gaillard et al. (2000) that younger deer should be more variable than prime-aged deer in mass and lactation;
- 2) establish if white-tailed deer cohorts exhibit compensation for retarded body development

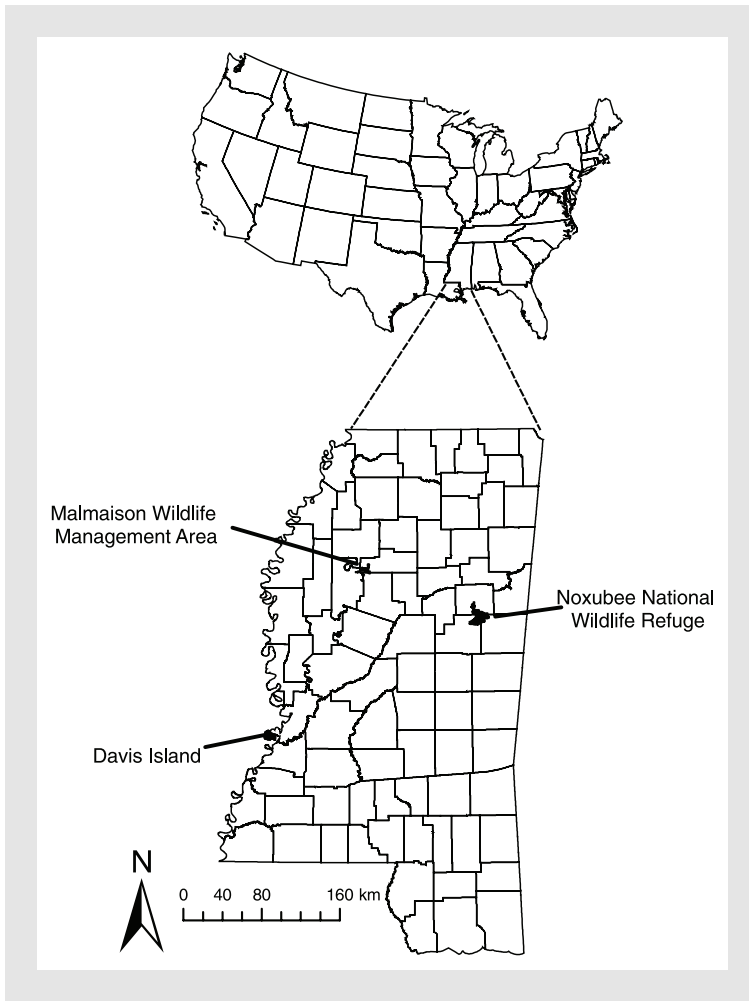


Figure 1. Location of the Malmaison Wildlife Management Area (3,838 ha; 1991-2002), Noxubee National Wildlife Refuge (19,425 ha; 1989-2003) and Davis Island, Mississippi (6,880 ha; 1986-2002), study areas.

(i.e. body mass) by testing if cohort means from year t are correlated to means at year $t + 1$, $t + 2$, or $t + 3$;

- 3) determine if mean body mass and % lactation of cohorts are correlated within and among years.

Study areas

We studied deer from Noxubee National Wildlife Refuge (NWR) during 1989-2003, Davis Island, Mississippi, during 1986-2002, and Malmaison Wildlife Management Area (WMA) during 1991-2002 (see Fig. 1). These three populations were selected because they had adequate time series of cohorts.

pasture (3%), riverine swamp (4%) and wetlands (3%).

Methods

At each study area deer were hunter-harvested during October-January. Harvested animals were eviscerated and lactation status (yes/no) was recorded by either the hunting party or WMA or NWR personnel. We recognize that % lactation is a coarse measurement of reproduction and recruitment. Using a binomial datum (lactation = 0 or 1) as a surrogate for reproductive success, which in white-tailed deer is multinomial (reproductive success = 0, 1, 2 or 3 fawns), does not reflect subtle changes in

Only cohorts with ≥ 10 deer samples were used for analyses.

The 19,425-ha Noxubee NWR is located in Noxubee, Oktibbeha and Winston counties in the Interior Flatwoods soil resource region (Pettry 1977). About 81% of Noxubee NWR is forest, comprised of bottomland hardwoods (18%), upland hardwoods (6%) and pines *Pinus* spp. (46%). Other habitat types include wetlands (5%) and low herbaceous vegetation (5%). Davis Island is a 6,880-ha privately-owned hunting cooperative in Warren County. The island is located in the Delta soil resource region (Pettry 1977) in the alluvial floodplain of the Mississippi River, where it is subject to annual flooding. Davis Island is about 77% forest, comprised primarily of bottomland hardwoods (73%) and some upland hardwoods (4%). The remaining habitat types are riverine swamp (5%), range (3%) and wetlands (3%). Malmaison WMA covers 3,838 ha located in Carroll, Grenada and Leflore counties and is part of the Delta and Loess Hills soil resource regions (Pettry 1977). Malmaison is about 77% forest, comprised primarily of bottomland hardwoods (68%) with some upland hardwoods (8%) and pine (1%). Other habitat types include

individual fecundity. However, we believe the metric can accurately index annual changes in cohort reproductive success. All deer were aged by Mississippi Department of Wildlife, Fisheries & Parks' biologists or by personnel from Mississippi State University using tooth wear and replacement criteria described by Severinghaus (1949). For analysis we assumed that all deer were aged correctly and that our samples of hunter-harvested females were representative of the female populations. We grouped deer in the age classes 0.5, 1.5, 2.5 and 3.5 or ≥ 3.5 depending on the analysis (see below).

We calculated mean cohort body mass and % lactation, as cohort means were the experimental unit for analysis, not individual deer. However, because individual deer were harvested throughout a 3-month hunting season we controlled for the potential effect of harvest dates on annual means. We used analysis of covariance (ANCOVA) to model the relationship between harvest date and mass of individual deer. Based on this linear relationship we standardized least-squares cohort means to a harvest date of 1 December for subsequent analyses. Depending on the analysis, we used ANCOVA to adjust annual cohort means for harvest dates or harvest dates and population.

To address objective 1, we compared annual variability in body mass of cohorts. We used ANCOVA (Littell et al. 1996) to generate annual body mass means for the 0.5, 1.5, 2.5 and ≥ 3.5 age classes that were adjusted for the effects of harvest date and population. We considered cohort and population as categorical variables, and harvest date as a continuous variable (we used a number that represented harvest date, much like the Julian date). We also included the interactions harvest date*population and harvest date*cohort in the ANCOVAs, but removed them if they were not significant ($P > 0.1$).

Table 1. Least-squares means (\bar{x} ; adjusted for harvest date and study population) and coefficients of variation (CV) for eviscerated body mass (in kg) and % lactation for cohorts of 0.5, 1.5, 2.5 and ≥ 3.5 -year-old female white-tailed deer harvested in Mississippi, USA, during 1986-2003. Within mass or lactation variables, CVs with the same letter are not significantly different ($P > 0.05$).

Variable	N	\bar{x}	CV
0.5 Mass	18	20.4	5.4 ^a
1.5 Mass	18	34.1	3.1 ^b
2.5 Mass	18	38.0	1.7 ^c
≥ 3.5 Mass	18	40.4	1.4 ^c
% 1.5 Lactation	18	9.9	47.6 ^a
% 2.5 Lactation	18	69.8	11.3 ^b
% ≥ 3.5 Lactation	18	76.1	9.2 ^b

so that we did not over-parameterize the models. We never included the population*cohort interaction because we did not have samples from all populations during the same years. From these ANCOVA models we generated annual body mass means for each factor level of cohort and for each age class, adjusted for harvest date and population.

We used the same general methodology to calculate annual estimates of % lactation for the 1.5, 2.5 and ≥ 3.5 age classes with ANCOVA. Because the incidence of lactation declines markedly 5-6 months after parturition (Wolf & Harder 1979), we censored ≥ 2.5 -year-old females harvested after 15 December, and 1.5-year-old females harvested after 31 December, about five months after the average parturition date for those age classes in the study populations. In one instance, the maximum likelihood algorithm failed to converge; therefore, we used % lactation unadjusted for harvest date. Lastly, we arcsin transformed all % data (Zar 1999) for all statistical comparisons, but report the untransformed % values in the results.

We used the annual body mass means and % lactation values generated by the ANCOVA models to evaluate differences in the coefficient of variation (CV) for each age class. A CV was generated for each age class, and we used the F statistic (Zar 1999:141) to determine if CVs for body mass and % lactation of younger deer were more variable than for older deer (Gaillard et al. 2000; objective 1).

To determine if variation in cohort body mass persisted in the subsequent year(s) (objective 2), we correlated mean eviscerated mass of 0.5, 1.5, 2.5 and 3.5-year cohorts among years. We did not use the inclusive ≥ 3.5 -year age class for this analysis to reduce the probability of comparing deer from non-consecutive cohorts (e.g. comparing 2-year cohort in year t to an age class composed of 3-, 4-,

Table 2. Correlation between adjusted least-squares means of eviscerated body mass from cohorts of 0.5, 1.5, 2.5 and 3.5-year-old female white-tailed deer harvested in Mississippi, USA, during 1986-2003. Mean body mass of cohorts from year t was correlated to mean body mass of those cohorts the following year (t+1), two years later (t+2), or three years later (t+3).

Correlation	r	P	N
0.5 Mass _t - 1.5 Mass _{t+1}	0.271	0.115	37
0.5 Mass _t - 2.5 Mass _{t+2}	-0.195	0.285	34
0.5 Mass _t - 3.5 Mass _{t+3}	-0.129	0.502	31
1.5 Mass _t - 2.5 Mass _{t+1}	0.064	0.715	37
1.5 Mass _t - 3.5 Mass _{t+2}	-0.337	0.059	34
2.5 Mass _t - 3.5 Mass _{t+1}	0.141	0.421	37

Table 3. Correlation between adjusted least-squares means of eviscerated body mass and % lactation from cohorts of 0.5, 1.5, 2.5, 3.5 and ≥ 3.5 -year-old female white-tailed deer harvested in Mississippi, USA, during 1986-2003. Mean body mass of cohorts from year t was correlated to % lactation of those cohorts within year (t) or the following year ($t + 1$).

Correlation	r	P	N
0.5 Mass _t - 1.5% Lactation _{t+1}	0.116	0.508	37
1.5 Mass _t - 1.5% Lactation _t	0.413	0.009	41
1.5 Mass _t - 2.5% Lactation _{t+1}	-0.118	0.505	36
2.5 Mass _t - 2.5% Lactation _t	0.089	0.602	39
2.5 Mass _t - 3.5% Lactation _{t+1}	0.035	0.848	35
≥ 3.5 Mass _t - $\geq 3.5\%$ Lactation _t	0.007	0.965	41
≥ 3.5 Mass _t - $\geq 3.5\%$ Lactation _{t+1}	0.099	0.570	37

5-, ..., year-old deer in year $t + 1$). Again, we used ANCOVA to adjust cohort means for harvest date, but we did not adjust these cohort means for population. Because the annual variability within each study population (i.e. site-specific annual variation) was critical to this analysis, we did not generate annual means averaged across the populations. Instead, we controlled for the effect of study population on cohort body mass using partial correlation coefficients (Littell et al. 2002, Zar 1999). Thus, cohort means from all three study populations were pooled for the correlation analysis, but we removed the effect of population. Mean body mass of fawn (0.5-year-old) cohorts from a particular year (t) and study population were correlated with the mass of yearling (1.5-year-old) cohorts one year later ($t + 1$), to 2.5-year cohorts two years later ($t + 2$), and to 3.5-year cohorts three years later ($t + 3$). Mass of yearling (1.5-year-old) cohorts were correlated with 2.5-year cohorts one year later ($t + 1$), and to 3.5-year cohorts two years later ($t + 2$). Finally, mass of 2.5-year cohorts was correlated with 3.5-year cohorts one year later ($t + 1$). When extreme values were identified, we used regression diagnostics for removing influential outliers (Belsley et al. 1980, Freund & Littell 2000:70). We hypothesized that body mass of cohorts in year t would be positively correlated to cohort body mass in subsequent years ($t + 1, t + 2, t + 3$).

Table 4. Correlation between % lactation from cohorts of 1.5, 2.5, 3.5 and ≥ 3.5 -year-old female white-tailed deer harvested in Mississippi, USA, during 1986-2003. Percentage lactation of cohorts from year t was correlated to % lactation of those cohorts the following year ($t + 1$).

Correlation	r	P	N
1.5% Lactation _t - 2.5% Lactation _{t+1}	0.039	0.826	36
2.5% Lactation _t - 3.5% Lactation _{t+1}	0.255	0.162	34
$\geq 3.5\%$ Lactation _t - $\geq 3.5\%$ Lactation _{t+1}	0.055	0.755	37

Table 5. Correlation between % lactation and adjusted least-squares means of eviscerated body mass for cohorts of 1.5, 2.5, 3.5 and ≥ 3.5 -year-old female white-tailed deer harvested in Mississippi, USA, during 1986-2003. Percentage lactation of cohorts from year t was correlated to mean body mass of those cohorts the following year ($t + 1$).

Correlation	r	P	N
1.5% Lactation _t - 2.5 Mass _{t+1}	-0.077	0.661	37
2.5% Lactation _t - 3.5 Mass _{t+1}	0.166	0.356	35
$\geq 3.5\%$ Lactation _t - ≥ 3.5 Mass _{t+1}	0.217	0.210	37

Lastly, to compare body mass and % lactation (objective 3), we correlated mean body mass of cohorts from a particular study population in year t to % lactation of cohorts in year t and $t + 1$. We also compared % lactation of cohorts in year t to % lactation of cohorts in year $t + 1$, and % lactation of cohorts in year t and to mean body mass of cohorts in year $t + 1$ to determine if reproduction may be associated with annual variability in cohort mass and lactation. We hypothesized that body mass in year t would be negatively related to % lactation in year t and positively related to % lactation in year $t + 1$, % lactation in year t would be negatively related to % lactation in year $t + 1$, and % lactation in year t would be negatively related to body mass in year $t + 1$. We added the inclusive ≥ 3.5 -year age class for these analyses to determine if annual variation in mass and lactation of this age class could be explained by prior-year condition. We incorporated the same methodology for conducting correlation analyses as mentioned above (i.e. partial correlation to control for study population). Also,

Table 6. Mixed-model analysis of covariance testing the effects of lactation status, population, and lactation status*population interaction (with harvest year as a random effect and deer harvest date as a covariate) on eviscerated body mass of 1.5, 2.5 and ≥ 3.5 -year-old female white-tailed deer harvested in Mississippi, USA.

Age class	Effect	df	F	P
1.5	Lactation status	1, 1546	13.07	<0.001
	Population	2, 1546	66.54	<0.001
	Lactation status*population	2, 1546	2.38	0.093
	Harvest date	1, 1546	63.34	<0.001
2.5	Lactation status	1, 1367	6.76	0.009
	Population	2, 1367	161.52	<0.001
	Lactation status*population	2, 1367	2.81	0.060
	Harvest date	1, 1367	20.66	<0.001
≥ 3.5	Lactation status	1, 456	24.44	<0.001
	Population	2, 1456	177.14	<0.001
	Lactation status*population	2, 1456	0.00	0.996
	Harvest date	1, 1456	21.01	<0.001

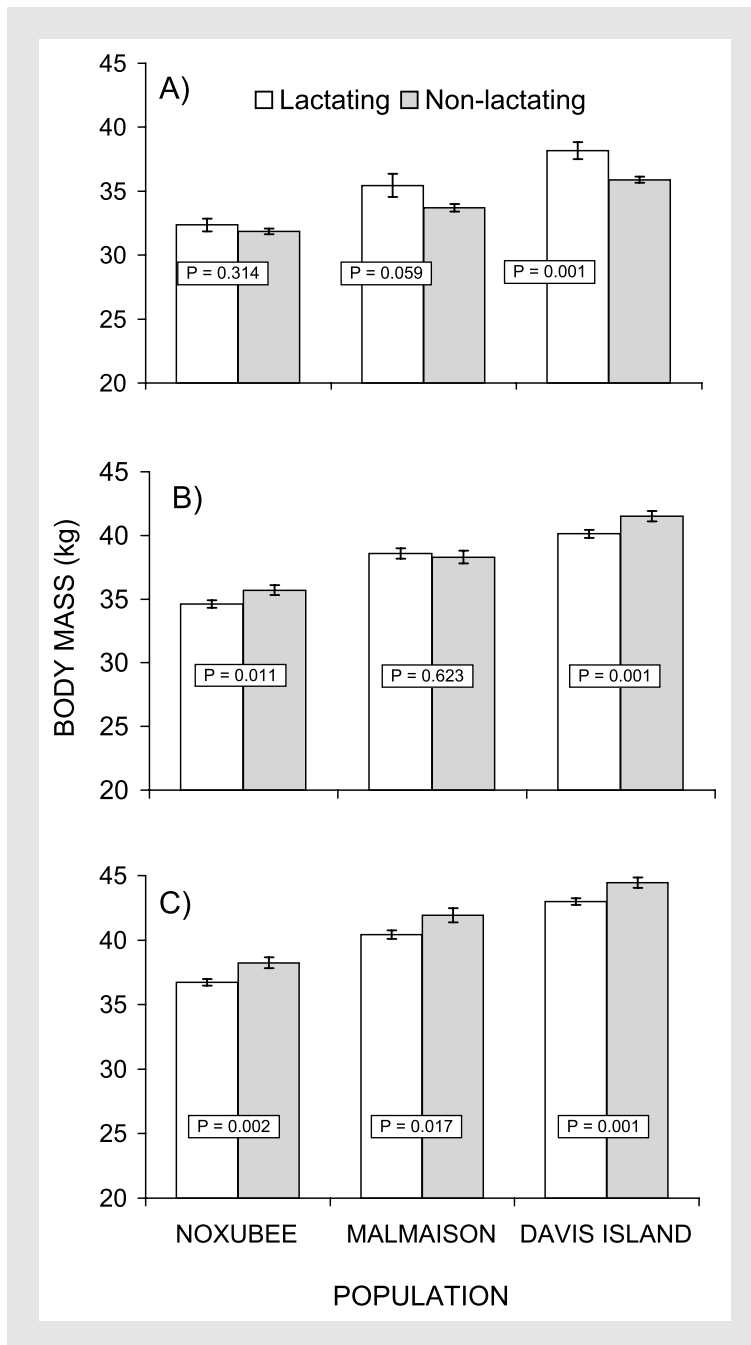


Figure 2. Adjusted least-squares means (\pm SE) of eviscerated body mass (in kg) from lactating and non-lactating 1.5 (A), 2.5 (B), and \geq 3.5-year-old (C) female white-tailed deer harvested from the Noxubee National Wildlife Refuge, Malmaison Wildlife Management Area, and Davis Island, Mississippi, USA, during 1986-2003. P-values are from t-tests comparing the difference between body mass of lactating and non-lactating females within age class and population.

to quantify the effect that reproduction may have on individuals, we compared body mass of individuals recorded as lactating versus those not lactating

whereas, in older age classes, lactating females were generally lighter than non-lactating females (see Fig. 2).

using a mixed ANCOVA linear model (Littell et al. 1996). We developed an ANCOVA model for each age class, with lactation status, population and the interaction lactation status*population as fixed effects, harvest year as random effect and harvest date as covariate. All date-adjusted means are reported using an average harvest date of 1 December.

Results

Body mass was more variable for fawn cohorts than for 1.5, 2.5 and \geq 3.5-year cohorts ($P \leq 0.05$). Mass of 1.5-year cohorts was more variable than mass of 2.5-year and \geq 3.5-year cohorts ($P \leq 0.05$). Body mass of 2.5-year and \geq 3.5-year cohorts exhibited similar variability (Table 1).

Body mass of cohorts was not correlated among years ($P > 0.05$; Table 2). Mass and % lactation of 1.5-year cohorts were positively correlated within year ($r = 0.413$, $P = 0.009$; $N = 41$; Table 3), but no other correlations existed within or among years between mass and % lactation. Percent lactation of cohorts was not correlated among years ($P > 0.05$; Table 4), nor was % lactation correlated to body mass of cohorts in subsequent years ($P > 0.05$; Table 5).

For individual deer, the effects of lactation status and population were significant in all age classes ($P \leq 0.05$; Table 6) and the interaction lactation status*population was important in the 1.5 ($P = 0.093$) and 2.5-year age classes ($P = 0.060$; see Table 6). In the 1.5-year age class, lactating females were generally heavier than non-lactating females (Fig. 2),

Discussion

Our findings revealed patterns of variation in cohorts of white-tailed deer consistent with other large herbivores (Gaillard et al. 2000) in that body mass and % lactation of younger cohorts are more variable than those of adult cohorts. These results support the conclusions of Andersen & Linnell (2000) that adult female roe deer can maintain body condition despite significant increases in deer density. In their study population, body mass and litter size of adults were not related to density, but litter size of 2-year-old mothers decreased with increasing density; reinforcing the concept of younger females being more sensitive to density and environmental stochasticity than older 'prime-aged' females.

Mech et al. (1991) determined that variation in white-tailed deer cohorts in Minnesota, USA, may be related to the environmental conditions experienced by their mothers and grandmothers. The lack of correlation between average body mass of cohorts in year t and in subsequent years (see Table 2) suggests that deer can compensate for depressed growth in previous years in the environments we studied. Although we did not test for generational relationships among cohorts, we would not expect such a relationship given that cohorts appear to compensate within one year. The environmental conditions experienced by deer in our study areas may have not been severe enough to cause extreme changes in body condition. Had annual changes been more extreme, we might have documented more cohort effects. Furthermore, density may have been so low that deer had sufficient food to increase intake in years following depressed somatic development. Deer populations with greater densities, or in areas with lower food quality, may exhibit much more cohort correlation than we documented.

The positive within-year correlation between average body mass and % lactation of 1.5-year cohorts and the greater mass of lactating vs non-lactating individuals (see Table 6 and Fig. 2) support the concept of a critical mass for ovulation of 0.5-year-old females. Verme & Ullrey (1984) reported a minimum live mass of 36 kg for puberty of 0.5-year-old captive females in Michigan. Average live mass of 0.5-year-old females in our study was about 28 kg, which may explain the low incidence of puberty for this age class (see Table 1). Thus, annual variation in forage quantity or quality should influence the incidence of puberty in 0.5-year-old females as mass and condition of a few individuals exceed a critical

physiological threshold (Dusek et al. 1989, Verme & Ozoga 1987).

Verme (1969) described a negative feedback scenario for areas of suboptimal habitat and moderate deer densities where the physiological costs of reproduction negatively affect maternal body condition until weaning, just prior to the breeding season. Poor body condition then negatively affects ovulation or implantation and lessens fecundity. Decreased fecundity may then increase the mother's body condition the following year, potentially leading to a cyclic pattern of reproductive success. Based on this potential relationship, we hypothesized a negative correlation between average body mass and % lactation of a cohort in year t . Although non-lactating individuals were heavier than lactating individuals in all populations of ≥ 3.5 -year-old females, and in two populations of 2.5-year-old females (see Table 6), no relationship between mass and % lactation was documented at the cohort level for these age classes.

In fluctuating environments, changes in food quantity and quality may have a greater influence on annual changes in mass than previous year's reproductive status. Thus, the negative feedback proposed by Verme (1969) may only operate in marginal, but stable, environments. Alternatively, the pattern may be difficult to detect because reproductive rate can remain the same annually at the population level despite a cyclic pattern at the individual level.

Conclusions

Younger white-tailed deer exhibit greater annual variability than older cohorts, suggesting they are more sensitive to changes in density and environmental events that influence carrying capacity. Stochastic events (e.g. drought and winter severity) may negatively affect cohort body mass and reproduction of younger cohorts, that may recover in subsequent years given sufficient forage. However, if annual mass measurements of younger cohorts are correlated among years, then forage resources may be limiting their compensatory response.

Unlike other cervids and white-tailed deer in northern latitudes, reproduction does not appear to negatively influence body condition of female cohorts the following year in the environments we studied. Although individual ≥ 2.5 -year-old lactating females typically weigh less than non-lactating

females, females appear able to recover from the physiological costs of reproduction through increased forage intake.

Variation in morphometrics of younger-aged cohorts may index herd condition more reliably than older-aged cohorts. Older-aged deer appear to be more resilient to changes in density and environment, because they show relatively less annual variation in body mass and % lactation. Deer managers should monitor the morphometrics of younger cohorts for inference concerning herd status relative to carrying capacity and to assess the potential influence of environmental factors.

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