

EFFECTS OF MATERNAL AND GRANDMATERNAL NUTRITION ON DEER MASS AND VULNERABILITY TO WOLF PREDATION

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ABSTRACT.—In a Minnesota ecosystem, mass of female white-tailed deer (*Odocoileus virginianus*) fawns and adults, and survival of adult females in the face of wolf (*Canis lupus*) predation, were directly related to maternal nutrition during gestation. Mass of single male fawns produced by 2-year-old females, and survival of yearlings to 2 years of age were related directly to the nutrition of their grandmothers.

Nutritional deprivation in female laboratory rats has resulted in the following characteristics of first and second-generation offspring: stunting; impaired antibody formation; delayed emergence of motor activities and response to auditory stimulation; reduced neonatal cerebral mass, cerebral DNA, and cerebral protein content; and in marked learning deficits at maturity (Bresler et al., 1975; Chandra, 1975; Cowley and Griesel, 1963; Zamenhof and Van Marthens, 1977, 1978; Zamenhof et al., 1971, 1972). In domestic livestock, protein deprivation of gravid females reduced birth mass, weaning mass, rate of gain, and survival of first-generation offspring (Corah et al., 1975; Gunn, 1977; Hight, 1966; Pond, 1973). Although first-generation birth mass or size effects are known for a few wild species (Clutton-Brock et al., 1982; Peterson, 1977; Verme, 1962, 1963, 1965), and increased predation on prenatally deprived first-generation moose (*Alces alces*) has been found (Peterson, 1977), naturally occurring second-generation effects have not been reported.

Deer carry fetuses throughout winter when adults routinely undergo a negative energy balance, the severity of which depends on snow depth and temperature (Gerstell, 1937; Maynard, et al., 1935; Moen and Severinghaus, 1981; Severinghaus, 1981). Because it restricts food availability and affects the ability of deer to reach food, snow depth is a standard predictor of nutritional condition of adult females, and it strongly influences prenatal nutrition of their fawns born in May and June (Arnold and Verme, 1963; Murphy and Coates, 1966; Thompson and Thompson, 1949; Verme, 1962, 1963, 1965). Thus, snow depth can be used as an independent variable in analyses of effects of nutrition of adult deer on various characteristics of their offspring.

STUDY AREA

This study was conducted in a 2,500-km² area in the eastcentral Superior National Forest of northeastern Minnesota (48°N, 92°W). The area is near the northeastern limit of deer range and is cool temperate, with annual snowfall averaging >1.0 m from mid November through mid-April. Forests of the region are mixed coniferous-deciduous (Nelson and Mech, 1981). The deer population ranged from 0.2 to 0.4 deer/km² during the study (Floyd et al., 1979; Nelson and Mech, 1986a). Wolf predation is the major source of natural mortality for deer in the area (Hoskinson and Mech, 1976; Nelson and Mech, 1981).

METHODS

We live-captured adult female deer and their 8–10-month-old fawns by use of rocket nets from 1974 through 1985. Mother-offspring groups were determined by association during capture and after radiocollaring. Because legal hunting by firearms was restricted to antlered deer, the chances of orphaning of fawns were low. We weighed the deer on spring scales, radiocollared them, and monitored their survival in the presence of wolf (*Canis lupus*) predation (Nelson and Mech, 1981, 1986b, 1986c).

By tooth-sectioning and counting annuli (Gilbert, 1966), we determined the year of birth of each adult female. Then, we examined weather records for snow depths (U.S. Department of Commerce, Climatological Data, Minnesota, 1965–1985) during the winter preceding their birth. We created a snow-depth index for each winter by summing the weekly snow depths (m) over the winter. The snow-depth index for the winters preceding births of adult females provided an inverse estimate of the nutrition of mothers of adult females while the adult females had been in utero. Mothers of adult females were grandmothers of fawns, so we then also had an estimate of the nutrition of the grandmothers.

Relationships between fawn mass and the snow-depth (nutritional) indices of their mothers and grandmothers were estimated by multiple-linear regression. Because mass was expected to be related to month of capture, and adult mass was expected to be related to age (Mech and McRoberts, 1990), these relationships were considered first. Thus, reported relationships were significant after first accounting for the relationships with month of capture and age.

Mortality of radiocollared deer was determined by monitoring of signals and direct ground observation for signs of wolf predation, usually in snow (Nelson and Mech, 1981, 1986b). Survival rates of radiotagged adult females and fawns were estimated by standard methods comparing the number of deaths from wolf predation as ratios with the total duration of the monitoring periods for various cohorts (Heisey and Fuller, 1985; Nelson and Mech, 1986c). Data were pooled for cohorts born after winters of low accumulation of snow (good nutrition) and compared with pooled data from cohorts born after winters with deep snow (poor nutrition). With fawns, samples were only large enough to compute survival rates through 2 years of age. Survival differences were compared by using *z*-tests, with differences considered significant at $P \leq 0.05$.

RESULTS

Our data base included the snow-depth (inverse nutritional) index for the grandparent generations during pregnancy, weights of 105 first-generation fawns and 99 first-generation adult females (148 weights including recaptures), estimates of survival for 84 first-generation adult females, weights of 57 second-generation fawns, and estimates of the survival of 51 second-generation fawns through 2 years of age. The values (m) of the snow-depth index over winter follow (year indicates the beginning of the winter for which the index applies): 1965, 13.41; 1966, 8.23; 1967, 4.57; 1968, 14.02; 1969, 8.84; 1970, 11.89; 1971, 10.98; 1972, 5.79; 1973, 8.54; 1974, 10.98; 1975, 10.37; 1976, 4.27; 1977, 10.06; 1978, 11.59; 1979, 7.62; 1980, 5.49; 1981, 9.76; 1982, 6.40; 1983, 9.76; 1984, 4.27; 1985, 9.76. Because our first-generation, adult-female sample was captured during a 12-year period, and their ages at capture were 2–15 years, the number of annual cohorts for which we have first-generation mass and survival data, thus the number of grandmother cohorts for which we have nutritional indices, is 18 (1966–1983). The 57 first-generation fawns included 14 single males, 11 single females, 7 sets of twin males, 3 sets of twin females, and 6 sets of mixed twins.

Weights of 42 first-generation female fawns for January-through-April and of 41 first-generation females 6–15-years old were related directly to the nutrition of their mothers while the first-generation were in utero (Fig. 1). Neither the male fawns nor the 1–5-year-old adult females showed significant relationships. Survival of first-generation fawns (both sexes) from birth (late May and June) to 5–10-months old was related directly to the nutritional condition of their mothers during the winter the fawns were in utero and to the condition of the mothers during the 2 previous winters, based on autumn and winter ratios of fawns to adult females (Mech et al., 1987). For first-generation fawns of both sexes, the survival data through the remainder of their first year (after 5–10 months of age) suggested a similar relationship, but were not significant. From 8–10 months of age through their first 2 years (the longest the analysis could be conducted because of sample size), there were no apparent differences in survival.

However, survival was significantly greater for first-generation adult females ≤ 1.8 -years old with well-nourished mothers than for those whose mothers were poorly nourished. The mean survival of 44 female deer ≥ 1.8 -years old, whose mothers were relatively well nourished during pregnancy, based on the snow index was 0.88 (30,123 deer days monitored, 11 deer killed by wolves) compared with 0.74 ($P = 0.04$) for 40 comparable deer whose mothers were poorly nourished (19,071 deer days, 16 deer killed by wolves). There was a suggestion that this difference might have been more extreme for older deer. The mean survival of 22 female deer 1.8–2.8-

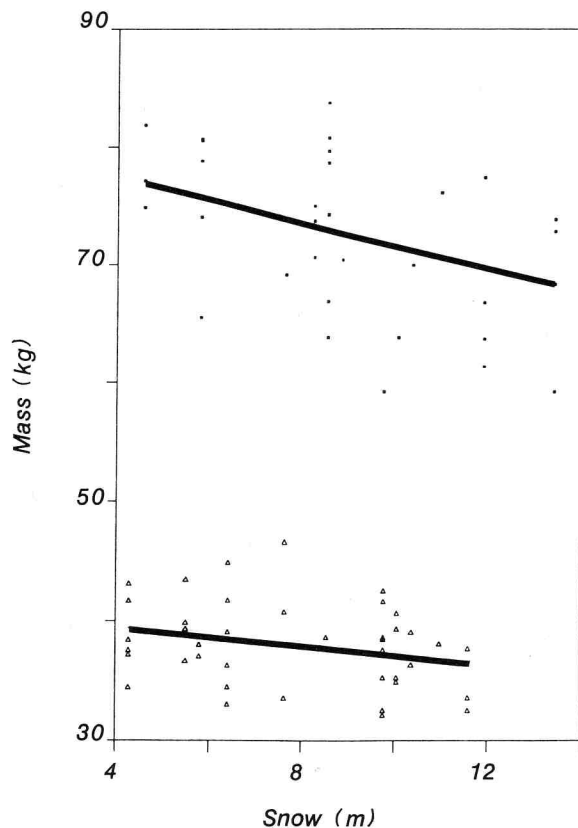


FIG. 1.—Relationship between deer mass, adjusted to January values, and cumulative snow depth, an inverse index of maternal nutritional condition, during the winter before the birth of the deer. The upper line represents mass of adult females, with estimated mass = $83.69 - 2.37 \text{ month} - 0.98 \text{ snow}$ ($R^2 = 0.32$; P overall < 0.01 ; P snow < 0.01). The lower line represents mass of female fawns (8–10-months old), with estimated mass = $42.76 - 1.74 \text{ month} - 0.38 \text{ snow}$ ($R^2 = 0.22$; P overall < 0.01 ; P snow < 0.10).

years old whose mothers were poorly nourished during pregnancy based on the snow index was 0.83 (9,411 deer days, five deer killed by wolves) compared with 0.66 ($P = 0.13$) for 19 females 3.8–8.8-years old (9,660 deer days, 11 deer killed by wolves).

Second-generation single male fawns (but not four single females) born of 2-year-old females showed a strong direct relationship between mass and grandmaternal nutrition (Fig. 2). This relationship was not evident in second-generation fawns born of older females; instead, their masses were directly related to the ages of their mothers.

Second-generation deer whose grandmothers were well nourished survived significantly better from 0.8–2.0-years of age than those whose grandmothers were poorly nourished. The mean survival through 2 years of age of 32 second-generation deer whose grandmothers were well nourished during pregnancy, based on the snow index, was 0.98 (15,604 deer-days, one deer killed by wolves) compared with 0.78 ($P = 0.04$) for 19 comparable deer (5,670 deer-days, four deer killed by wolves). This effect could not have been a coincidental influence of first-generation, rather than grandmother, nutrition because the mean snow index during the year previous to birth for our low-survival, second-generation group (22.6 m) was less than that for our high-survival group (26.5 m).

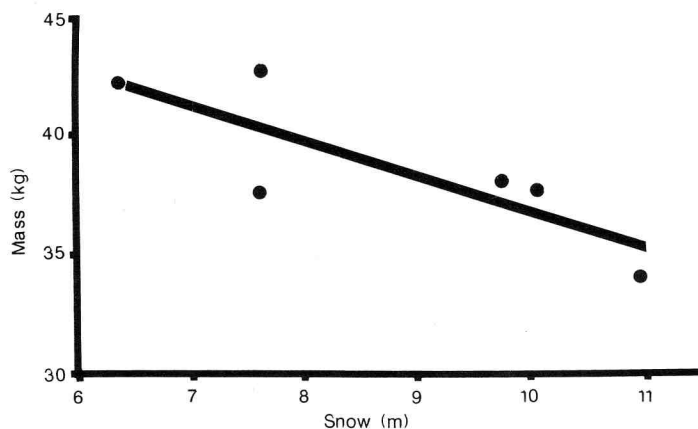


FIG. 2.—Relationship between mass of single male fawns (8–10-months old) born to 2-year-old females and the cumulative snow depth during the winter before the births of their mothers (thus an inverse index to grandmaternal nutrition). Estimated mass = $51.94 - 1.51 \text{ snow}$ ($R^2 = 0.69$; $P < 0.05$).

DISCUSSION

Our data confirm first-generation nutritional effects on mass and survival of white-tailed deer in the presence of wolf predation. More significantly, however, they also document grandmother effects on mass and survival of second-generation deer. Demonstration of second-generation mass effects was limited to fawns born to 2-year-old first-generation females only, suggesting that whatever the influence on mass transmitted from the grandparent generation, it was compensated for as the first generation matured.

We documented the effect on survival of grandmaternal nutrition on the second generation only through 2 years of age because our second-generation sample was radiotagged as 8–10-month-old fawns, and insufficient time had elapsed for enough animals to live long enough beyond 2 years for us to compare survival rates beyond.

The question of why either first or second-generation offspring with poorly nourished ancestors should be more vulnerable to wolves cannot be answered directly from our data. Although the only physical maternal and grandmaternal effect we documented is on mass, we have not investigated such other possible effects as cerebral-mass reduction, learning deficits, impaired antibody formation, or such other physical or behavioral traits that reportedly affect captive or domestic animals whose mothers or grandmothers were nutritionally deprived (Bresler et al., 1975; Chandra, 1975; Cowley and Griesel, 1963; Zamenhof and Van Marthens, 1977, 1978; Zamenhof et al., 1971, 1972). Nevertheless, it is reasonable to postulate that such effects or similar ones also characterize our study animals and that these effects explain the differences in vulnerability of our subjects to wolf predation. The tendency of wolves to kill primarily debilitated prey is well documented (Ballard et al., 1987; Carbyn, 1983; Haber, 1977; Mech, 1966; Mech and Frenzel, 1971; Murie, 1944).

Determining the mechanisms through which effects of nutritional conditions are transferred from one generation to the next two are beyond the scope of this study, although much progress has been made in this area (Lee and Chow, 1968; Stephan et al., 1971; Zeman, 1967, 1968). We emphasize, however, the implications of these findings to the field of predator–prey relations and population biology. In the first discipline, prey remains traditionally are examined for sign of debility, and if no such sign is found, the prey animal is often declared “healthy” (Mech and DelGiudice, 1985). Our study indicates that without information about the nutritional state of the mother or grandmother of the prey animal, such conclusions should be qualified. In the field of population biology, the intergenerational effects reported here may help explain lags among

trends in weather or vegetational condition and population trends of prey and their predators (Keith, 1963; Peterson et al., 1984; Mech, 1986; Nelson and Mech, 1986a). These findings also support the need for long-term investigations when dealing with large, long-lived mammals.

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