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RELATIONSHIP OF DEER AND MOOSE POPULATIONS TO PREVIOUS WINTERS' SNOW

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SUMMARY

(1) Linear regression was used to relate snow accumulation during single and consecutive winters with white-tailed deer (*Odocoileus virginianus*) fawn:doe ratios, moose (*Alces alces*) twinning rates and calf:cow ratios, and annual changes in deer and moose populations. Significant relationships were found between snow accumulation during individual winters and these dependent variables during the following year. However, the strongest relationships were between the dependent variables and the sums of the snow accumulations over the previous three winters. The percentage of the variability explained was 36 to 51.

(2) Significant relationships were also found between winter vulnerability of moose calves and the sum of the snow accumulations in the current, and up to seven previous, winters, with about 49% of the variability explained.

(3) No relationship was found between wolf numbers and the above dependent variables.

(4) These relationships imply that winter influences on maternal nutrition can accumulate for several years and that this cumulative effect strongly determines fecundity and/or calf and fawn survivability. Although wolf (*Canis lupus* L.) predation is the main direct mortality agent on fawns and calves, wolf density itself appears to be secondary to winter weather in influencing the deer and moose populations.

INTRODUCTION

Understanding population productivity and change is a major objective of population biologists, yet most ecosystems are so complex that long-term, primary predictors of these variables remain elusive. Nevertheless, long-term studies hold promise for progress (Peterson, Page & Dodge 1984). Thus, we have used long-term investigations of white-tailed deer (*Odocoileus virginianus* Zimmerman) and moose (*Alces alces* L.) to find such a predictor.

Deer and moose undergo an annual weight cycle during which they gain weight in spring, summer and autumn and lose it throughout winter (Maynard *et al.* 1935; Gerstell 1937; Gasaway & Coady 1974; Franzmann & LeResche 1978; Moen & Severinghaus 1981; Severinghaus 1981). The length and severity of winter, including snow accumulation which restricts mobility and thus food intake, are factors that determine the extent

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of the annual weight loss and the ability of the animals to recover during the rest of the year.

Deer and moose fecundity depends considerably on the degree of winter malnutrition and warm season recovery (Morton & Cheatum 1946; Cheatum & Severinghaus 1950; Robinette *et al.* 1955; Julander, Robinette & Jones 1961; Verme 1965, 1967; Ransom 1967; Mansell 1974). Furthermore, because ungulates are gravid during winter and spring, winter and spring weather potentially has a great effect on fetal development and weight and survivability of offspring (Thomson & Thompson 1948; Moustgaard 1959; Verme 1962, 1963, 1965; Arnold & Verme 1963; Murphy & Coates 1966; Alexander 1969; Willis & Wilson 1974; Robinson 1977; Berger 1979; Picton 1979, 1984; Rolley & Keith 1980; Albon, Guinness & Clutton-Brock 1983), and thus on population change (Markgren 1969; Ling 1970; Crete 1976; Mech & Karns 1977; Peterson 1977; Verme 1977; Thompson 1980).

In this article we confirm the above adverse effects of winter weather on productivity and population changes in white-tailed deer in Minnesota and moose on Isle Royale. However, more importantly we significantly extend the concept of winter influences on future populations by demonstrating a cumulative effect of snow accumulation for three to seven consecutive winters.

STUDY AREAS

Data from two study areas are used in this analysis, Isle Royale National Park in Lake Superior, and the central Superior National Forest in north-eastern Minnesota, 180 km south-west of Isle Royale (48° N, 92° W).

Isle Royale

Isle Royale is a roadless island of 544 km^2, 24–29 km from the Minnesota/Ontario shore of Lake Superior. Some 72 km long and up to 14 km wide, it is composed of a series of basaltic and conglomerate ridges covered with several stages of conifer and hardwood forests, much of which have been logged and/or burned in historic times. Deer are absent from the island, but moose and wolves have been present for more than 30 years; the only other important wolf prey there is beaver (*Castor canadensis* Kuhl), which are usually only available from April through November. Wolves constitute the main mortality factor on the moose herd, and from 1959 to 1985 winter wolf numbers have varied from 14 to 50 and moose numbers from about 500 to 1150 (Peterson, Page & Dodge 1984 and unpublished data).

Central Superior National Forest

The Central Superior National Forest study area covers about 2300 km^2 near the north-eastern limit of white-tailed deer distribution. The forests in the region are mixed coniferous–deciduous (Nelson & Mech 1981). Deer are the primary prey of the wolf in the study area, and wolves are the deer's main natural mortality factor (Nelson & Mech 1986c). Beaver and moose are alternative prey. Deer density varied from about 0·3 to 0·7 per km^2 during the study (Nelson & Mech 1986a), after having declined drastically (Mech & Karns 1977) from perhaps 3·5 per km^2 (Stenlund 1955).

Table 1. Illustration of terminology used and times population data were collected relative to snow accumulation data. The example is for population data collected during summer and autumn 1978, winter 1978–79, and spring 1979

Terminology:		Third-previous winter		Second-previous winter		First-previous winter		Current winter	
Winter:		1975–76		1976–77		1977–78		1978–79	
Period data collected:							1	2	3
Year:	1975:		1976		1977		1978		1979

1, Moose twinning rate and calf:cow ratio figures collected in summer.
2, Fawn:doe ratio data for 1958–73 collected in autumn.
3, Fawn:doe ratio 1974–85, moose survival, % change in moose and deer populations measured in winter and spring.

METHODS

Although the investigations conducted in the two study areas were underway concurrently and used some of the same methods, there were also substantial differences in some of them.

Isle Royale

This study was conducted by a series of investigators from 1958 through 1985 (Mech 1966; Jordan, Shelton & Allen 1967; Peterson 1977; Allen 1979; Peterson, Page & Dodge 1984). The overall approach has been to census wolves and moose aerially from late January through March each year and to determine the age, sex, and condition of each wolf-killed moose from the bones which are almost always available. When possible, kill remains are examined when found. However, those too inaccessible from the nearest frozen lake where the ski-plane can land are marked and inspected in May or June. Moose twinning rates and calf:cow ratios are based on summer observations from the ground (Table 1). Twinning rates are based on the number of cows with twins divided by the number of cows with twins or singletons. To determine the calf:cow ratio, both barren cows and those with calves were counted. This ratio was not obtained in some years.

Central Superior National Forest

The data used from the central Superior National Forest study (Mech & Frenzel 1971; Mech 1979, 1986) were collected primarily from 1974 through 1985 (Hoskinson & Mech 1976; Nelson & Mech 1981, 1986a), although fawn:doe ratios from 1958 through 1973 based on hunter-kill statistics were also used (Mech & Karns 1977). Deer were live-trapped by clover-trap, rocket-net, and darting. They were aged from tooth sections (Gilbert 1966), given radio-collars and were aerially radio-tracked. From November through April each doe was located one to five times per week and observed several times over the winter. Any fawns with them were noted. In late winter 1975 through 1985, deer were aerially censused, and their numbers were estimated after correction for observability bias (Floyd, Mech & Nelson 1979; Nelson & Mech 1986a) (Table 1).

During the same study, radio-tagged wolves in the area were aerially radio-tracked and counted, and the deer they killed were aerially located. Attempts were made to examine the kill remains whenever possible. However, much of the time no bones remained that could provide an indication of age; because fawns are smaller, their remains are most likely to be missing. Therefore, unlike the situation on Isle Royale, young–adult ratios in any winter's kill were of questionable accuracy.

TABLE 2. Annual snow accumulation and dependent variables used in regression analyses. Snow figures in parentheses include periods in which snow accumulation data were unavailable from Isabella, so data from other interior north-eastern Minnesota stations were substituted

Winter	Snow accumulation (m) 1-Year*	3-Year	Fawn:doe ratio next autumn/winter	% change deer nos. next winter	% moose twinning next summer	Moose calf:cow ratio next summer	% change moose nos. next winter	Proportion of calves in wolf-killed moose next winter
1957–58	343	—	128	—	—	—	—	31
–59	277	—	91	—	38	—	—	53
–60	384	10·04	81	—	15	—	—	20
–61	236	8·97	98	—	39	—	—	12
–62	249	8·69	91	—	25	—	—	21
–63	188	6·73	107	—	40	—	—	36
–64	300	7·37	85	—	48	—	—	13
–65	432	9·20	71	—	23	—	—	18
–66	528	12·60	72	—	5	—	—	8
–67	333	12·93	90	—	17	—	—	15
–68	226	10·87	66	—	19	—	—	50
–69	597	11·56	65	—	11	—	–16	53
–70	348	11·71	71	—	17	35	–30	56
–71	467	14·12	—	—	6	18	+24	48
–72	391	12·06	51	—	10	31	–4	34
–73	191	10·49	85	—	12	41	+2	46
–74	(259)	8·41	77	—	24	38	–5	24
–75	(490)	9·40	—	—	6	35	–18	28
–76	(424)	11·73	50	–16	0	24	–21	23
–77	(206)	11·20	83	–26	0	19	+7	10
–78	(358)	9·88	91	+39	20	37	+24	40
–79	(488)	10·52	88	–21	12	58	–15	18
–80	(264)	11·10	56	–5	0	29	–1	19
–81	(188)	9·40	93	–12	9	47	+4	32
–82	(353)	8·05	100	+17	7	58	+36	16
–83	269	8·10	87	+95	—	48	–4	21
–84	401	10·23	55	–44	—	—	+37	—
–85	201	8·71	—	+84	—	—	—	—

* Annual sum of maximum monthly snow depths in centimeters, November through May at Isabella, Minnesota. No previous Isabella data available. Isabella is in the deer study area 180 km south-west of Isle Royale, and is 30 km inland. Isabella figures are used because data are unavailable for Isle Royale, and the nearest other station, Grand Marais, Minnesota lies along the shore of Lake Superior, so is too influenced by the lake.

Snow accumulation

Data on snow-accumulation for each winter were the sums of the monthly maximum snow depths recorded by the National Oceanic and Atmospheric Administration at Isabella, Minnesota from winter 1957–58 through winter 1983–84 (U.S. Department of Commerce 1958–84). Isabella, which is 30 km inland, lies in the Superior National Forest deer study area 180 km south-west of Isle Royale. The Isabella figures are used with the Isle Royale data because monthly data on snow-accumulation are not available for Isle Royale; the nearest weather station to Isle Royale, Grand Marais, Minnesota lies along the shore of Lake Superior, so it is too influenced by the lake to represent the Isle Royale interior. Peterson (1977) found that February and March snow accumulations on Isle Royale ranged from 55 to 62% higher than the Grand Marais accumulations for the same period. Although data from any weather station only precisely apply to the station itself, in general they must also reflect general weather conditions for the region, especially where topography is as homogeneous as it is in this region.

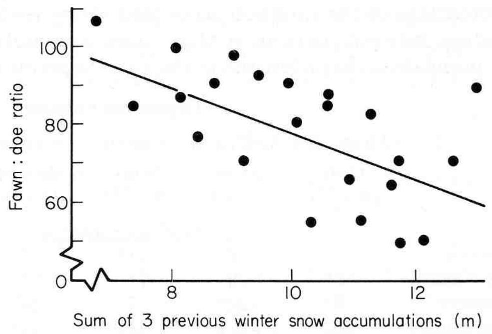

FIG. 1. Relationship between the sum of the previous three winter monthly snow accumulations (m) and the deer fawn : doe ratio during autumn and winter in north-eastern Minnesota. $R^2 = 0{\cdot}36$; $P < 0{\cdot}01$; $\hat{Y} = 134{\cdot}00 - 5{\cdot}41x$.

Statistical analyses

The following data were used: (i) the deer fawn : doe ratio in north-eastern Minneosta from autumn 1958 through 1973 based on hunter kills and from winter 1974 through 1984 based on trapping ratios; (ii) the moose twinning rate; (iii) calf : cow ratio of moose observed in summer on Isle Royale from 1958 through 1984; (iv) the annual percentage change in deer numbers in north-eastern Minnesota from late winter 1975 to 1985; (v) annual percentage change of the Isle Royale moose population from winter 1958 to 1985; (vi) snow accumulation each winter (Table 2).

We hypothesized that snow accumulations in consecutive winters would have an inverse, cumulative effect on future moose and deer productivity and population changes. For each dependent variable (items i–v above) we performed a series of regressions. Snow accumulations in individual previous winters and in sums of from two to five previous winters (Fig. 1) were used as single independent variables for first- and second-degree polynomial regressions (Table 3). The strengths of relationships are reported as R^2 values (percentage variation explained).

Use of the sum of snow accumulations in previous winters as a single independent variable assumes that the relative contributions of all winters in the sum are equal. To test this assumption, multiple linear regressions were performed for each dependent variable with snow accumulations in previous winters entering as multiple separate independent variables. The coefficients for significant relationships were always negative when snow accumulations in previous winters were used as single independent variables and when used as a sum. Thus, the coefficients for snow accumulations in previous winters in the multiple linear regressions were constrained to be zero or negative. The assumption of equal relative contributions would be rejected if the quality of the fit with multiple linear regression was significantly better than with simple linear regression.

After the above analyses were completed, we hypothesized that moose calf survival during late winter would also be influenced by snow accumulations in preceding winters. We also assumed that the percentage of calves in wolf-killed moose on Isle Royale during late winter would be a measure of winter calf survivability. (This percentage had no relationship to calf : cow ratios the preceding summer.) Thus, we used that percentage as a dependent variable in first- and second-degree polynomial regressions (Table 2). For dependent variables, we tested for a significant relationship with both the individual

TABLE 3. The percentage of the variation accounted for by regressions (% R^2) for inverse relationships between previous winters' snow accumulation and various deer and moose population characteristics in the Lake Superior region of the U.S.

Independent variable	Fawn:doe ratio ($n=23$)	Calf:cow ratio ($n=14$)	% moose twins ($n=23$)	% change in deer pop. ($n=9$)	% change in moose pop. ($n=16$)
	% R^2 accounted for				
First-previous winter	19†	0	13*	4	5
Second-previous winter	16†	20	14	5	25†
Third-previous winter	0	22*	7	14	24
Sum of 3 previous winters	36‡	51‡	42‡	45†	2

Column headings grouped under: Dependent variable.

* $\alpha=0{\cdot}10$; †$\alpha=0{\cdot}05$; ‡$\alpha=0{\cdot}01$.

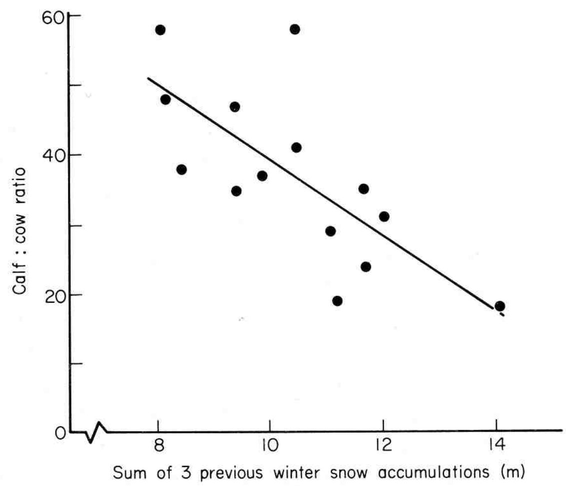

FIG. 2. Relationship between the sum of the previous three winter monthly snow accumulations in (m) and the summer moose calf:cow ratio on Isle Royale. $R^2=0{\cdot}51$; $P<0{\cdot}01$; $\hat{Y}=92{\cdot}22-5{\cdot}29x$.

preceding year's snow accumulation and the sum of snow accumulations in consecutive previous winters. However, because current winter influences would also be important (Mech & Frenzel 1971; Peterson 1977; Nelson & Mech 1986b), we added the current winter (Table 1) snow data to the previous winters' in each regression.

RESULTS AND DISCUSSION

Significant ($P<0{\cdot}10$) inverse relationships were found between each dependent variable and several of the independent variables including snow accumulations during the first-previous winter, the second-previous winter, and the third-previous winter (Table 3). However, the strongest relationships occurred between most variables and the 3-year sum of snow accumulations. The goodness-of-fits were not significantly better with a second degree polynomial than with a first degree polynomial for any combination of dependent and independent variables.

Snow accumulation during the first winter previous to birth could hardly affect current fecundity because prenatal mortality is generally low (Verme & Ullrey 1984). However, snow accumulation in the first winter previous to birth has been related to viability and weight or size of fawns up to 4 weeks of age (Verme 1963), and 9-month-old moose calves (Peterson, Scheidler & Stephens 1982), autumn fawn:doe ratios (Verme 1977), and autumn and winter moose calf:cow ratios (Thompson 1980; Rolley & Keith 1980). Our data tend to confirm this relationship, with significant relationships for fawn:doe ratios ($R^2=0{\cdot}19$) and for moose twinning rate ($R^2=0{\cdot}13$) (Table 3).

We also found significant inverse relationships between snow accumulation in the second-previous winter and fawn:doe ratios ($R^2=0{\cdot}16$), moose twinning rate ($R^2=0{\cdot}14$), and the percentage change in the moose population ($R^2=0{\cdot}25$). Such relationships with second-previous winter condition have not been reported before. The best explanation is that a strong direct nutritional influence carries over through the next winter and affects later fecundity and/or survivability then.

The third-previous winter's influence on current population characteristics could be twofold. Like the second winter's, the third's could act through nutritional momentum carrying over 2 years and directly affecting fecundity and/or prenatal nutrition. Or the third-previous winter could act through having influenced the *in utero* development of current 2-year-olds. For example, if the third-previous winter were mild, a 2-year-old cohort would be both vigorous and numerous so it might contribute greatly to the population. The individual influence of the third-previous winter itself in our study was weak with all dependent variables except the calf:cow ratio ($R^2=0{\cdot}22$) (Table 3).

Because the above findings indicate that individual winters as far back as 3 years can influence current population characteristics, it is not surprising that the individual winters' influences could combine to provide an even stronger, inverse cumulative effect on fecundity and/or survivability. For example, regarding survivability, offspring of a 2-year-old cohort would benefit from three consecutive winters of low snow preceding their birth in that: (i) their first-previous winter would have affected their own prenatal development; (ii) their second-previous winter would have favoured excellent post-natal growth of their mothers; and (iii) their third-previous winter would have promoted excellent prenatal growth and development of their mothers. Offspring of older cohorts

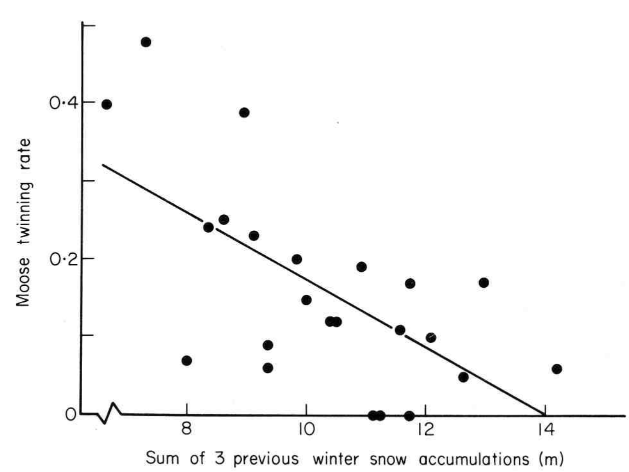

FIG. 3. Relationship between the sum of the previous three winter monthly snow accumulations in (m) and the summer moose twinning rate on Isle Royale. $R^2=0{\cdot}42$; $P<0{\cdot}01$; $\hat{Y}=0{\cdot}6265-0{\cdot}0454x$.

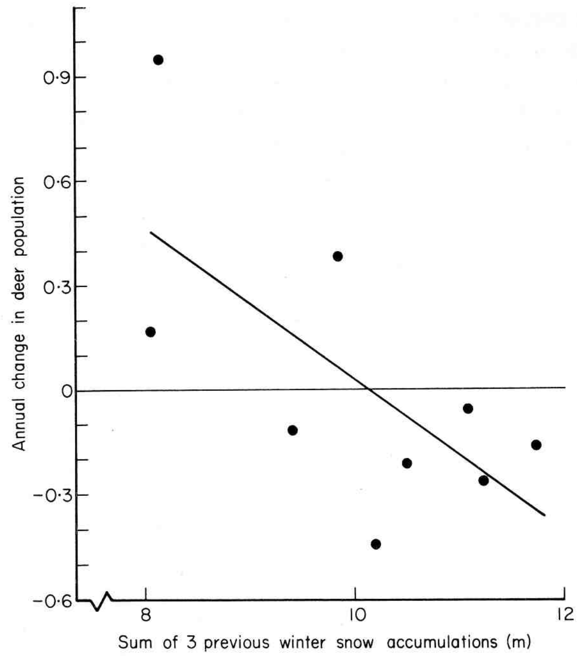

FIG. 4. Relationship between the sum of previous three winter monthly snow accumulations (m) and the percentage annual change in next winter's deer population in north-eastern Minnesota. $R^2=0{\cdot}45$; $P<0{\cdot}05$; $\hat{Y}=2{\cdot}20–0{\cdot}22x$.

TABLE 4. The percentage of the variation explained by regressions (R^2) for direct relationships between various winter's snow depths and proportion of moose calves in the wolf kill on Isle Royale from January to March, winters 1958–85. (Significance in the first-degree column indicates a significant relationship exists. Significance in the second-degree column indicates the second-degree relationship is significantly better than the first-degree relationship.)

	R^2				
	Single years		Cumulative Years		
Independent variables[a]	First degree	Second degree	First degree	Second degree	*n*
Current winter snow depth	11	11			27
First previous winter snow depth	00	00	6	7	27
Second previous winter snow depth	00	4	7	7	26
Third previous winter snow depth	11	16	19†	27	25
Fourth previous winter snow depth	17*	17	35†	53†[b]	24
Fifth previous winter snow depth	10	11	47‡	76‡[b]	23
Sixth previous winter snow depth	00	1	42‡	50*[b]	22
Seventh previous winter snow depth	00	1	49‡	50	21
Eighth previous winter snow depth	4	11	36‡	36	20
Ninth previous winter snow depth	16*	17	15	19	19
Tenth previous winter snow depth	00	00	8	9	18

* $\alpha=0{\cdot}10$; †$\alpha=0{\cdot}05$; ‡$\alpha=0{\cdot}01$.

[a] Current winter is the winter during which the percentage calves in the wolf kill was measured; previous winters are those preceding the current winter.

[b] Although the second-degree relationship is significantly better than the first-degree relationship we attribute it to a single anomalous data point.

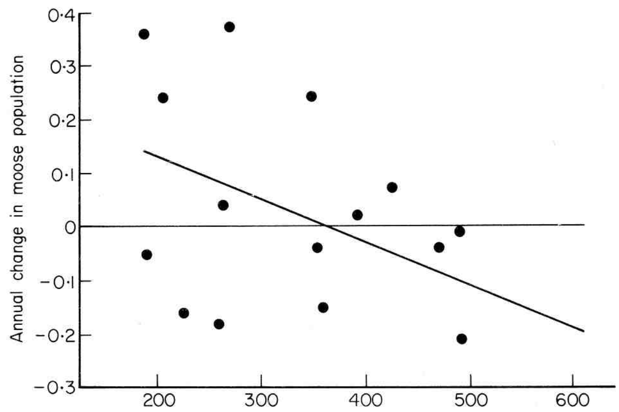

FIG. 5. Relationship between the second previous winter's monthly snow accumulation in (cm) and the percentage annual change in winter moose population on Isle Royale. $R^2 = 0{\cdot}25$; $P \leq 0{\cdot}05$; $\hat{Y} = 0{\cdot}2919 - 0{\cdot}0008x$.

would benefit from the favourable prenatal development fostered by their mothers' nutritional momentum, from the three previous winters.

Our results indicate that such a cumulative influence is strong: there is a significant relationship between the sum of the snow accumulations in the previous three winters and the fawn:doe ratio ($R^2 = 0{\cdot}36$) (Fig. 1), the calf:cow ratio ($R^2 = 0{\cdot}51$) (Fig. 2), the moose twinning rate ($R^2 = 0{\cdot}42$) (Fig. 3), and the percentage change in the deer population ($R^2 = 0{\cdot}45$) (Table 3, Fig. 4).

The assumption of equal relative contributions of snow accumulations in all winters in a sum could be rejected only for the percentage change in the moose population. However, because the relationship between this dependent variable and the snow accumulation in the third previous winter was positive rather than inverse we consider the result spurious.

Significant positive relationships were found between winter vulnerability of 8- to 10-month-old moose calves (as indicated by the proportion of calves in the wolf kill) and the sum of snow accumulations in the current, plus three to eight previous winters. Maximum R^2 values (0·47–0·49) occurred with the sum of snow accumulations in the current, plus five to seven previous, winters (Table 4, Fig. 6).

Why did five to seven previous winters affect the proportion of 8- to 10-month-old moose calves in the kill while only three previous winters influenced the other variables we studied? Our only explanation is that young cows produce offspring more likely to die early, so the winter calf population is composed mostly of calves born to older mothers, which have experienced more winters. Unfortunately, the ages of the moose cows whose calves were killed by wolves in our study could not be determined. However, survival of red deer (*Cervus elaphus* L.) calves on the Isle of Rhum (Clutton-Brock 1984) and captive white-tailed deer (Ozoga, Verme & Benz 1982) appear to be directly related to the ages of their mothers.

The inverse effect of the previous winter's snow on offspring viability the following summer is an accepted tenet of ungulate ecology. Furthermore, Verme (1969) and Picton (1979, 1984) provided evidence that deer integrate weather effects over an 18-month period. However, the cumulative effect of up to seven previous winters on survivability of 8- to 10-month-old animals has not been suggested before.

Although our explanation for the cumulative winter effect on winter survivability of moose calves invokes survivability as being a major factor accounting for some of our results, it does not rule out the possible role of fecundity in other of our results. For example, the relationships with the summer moose calf:cow ratios and twinning rates could result from annual differences either in fecundity or survivability, or a combination.

While several explanations for the cumulative winter effect are conceivable, the simplest would be that of a winter-to-winter carryover of nutritional influences. This explanation seems to be contradicted by Julander, Robinette & Jones (1961), Ransom (1967), Verme (1967) and Mansell (1974) who concluded that as long as deer have access to good quality and quantity of food in summer and autumn, they exhibit high productivity. Nevertheless, precise comparisons of fecundity or offspring survivability comparisons between mild and severe second or third previous winters have not been made. Our findings indicate that the assumption of full nutritional recovery during each summer should be re-examined.

Another implication of our findings is that the threshold of population stability for deer should fall at about 10·3 m of snow accumulation over a 3-year period (Fig. 4), and for moose, 361 cm during one year (Fig. 5). Because moose and deer populations have persisted in the study areas for long periods, these findings imply that the average winter snow accumulation and the average sum of three winters' snow accumulations should fall near the stability thresholds. From 1957–58 through 1984–85, the average snow accumulation over three winters was 10·2 m, and the average single year accumulation was 340 cm (Table 2), which are close to the predicted levels.

These results help explain Isle Royale moose population trends over the past 30 years (Peterson, Page & Dodge 1984), and the north-eastern Minnesota deer population trends for about 20 years (Nelson & Mech 1986a). Single-year snow accumulations of less than 361 cm characterized the study period through winter 1963–64 (Table 2), and the Isle Royale moose population peaked shortly thereafter. During most of the winter from

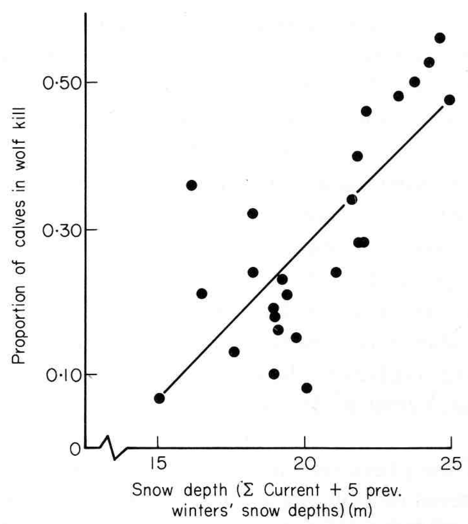

FIG. 6. Relationship between 8–10-month old moose calf survival on Isle Royale, 1958–84 and the sum of the current winter's monthly snow accumulation plus the sum of the five previous winters' monthly snow accumulation. $R^2=0{\cdot}47$; $P\leq 0{\cdot}01$; $\hat{Y}=-0{\cdot}55+0{\cdot}04x$.

1965–66 through 1975–76, the snow accumulations substantially exceeded both the deer and moose stability thresholds, and both populations hit their lows about 1977. From winter 1976–77 through 1983–84, most of the single-winter snow accumulations were less than the moose-stability threshold; the Isle Royale moose population is approaching its second peak. During the same period, three of the 3-year accumulations have exceeded the 10·3 m deer-stability threshold, and five were lower; the deer population has remained relatively stable for most of this period and has recently begun to increase.

Peterson, Page & Dodge (1984) asserted that density-dependent moose-vegetation interactions affected moose population growth on IR. The cumulative winter effects we now report for this high density moose population are probably both density-dependent, as moose density and forage abundance will influence the impact of snow of a given depth, and density-independent, for snow depth is a singular determinant of calf vulnerability to wolves in winter (Peterson 1977). In the late 1960s and early 1970s, moose density peaked simultaneously with winter snow depths, making it difficult to separate density and weather influences on the basis of available data.

As indicated above, the annual productivity differences we measured could have resulted from differences in fecundity, survivability of young, or both. However, we presented evidence that survivability must have been involved in some of the relationships. The main mortality factor in this study was wolf predation (Mech & Frenzel 1971; Mech & Karns 1977; Nelson & Mech 1986c). Nevertheless, we found no significant relationships between numbers of wolves one year as the independent variable and the percentage change in the moose population ($R^2=0{\cdot}09$; $P>0{\cdot}15$); percentage change in the deer population ($R^2=0{\cdot}05$; $P>0{\cdot}15$); calf:cow ratio ($R^2=0{\cdot}05$; $P>0{\cdot}15$), fawn:doe ratio ($R^2=0{\cdot}56$; $P>0{\cdot}15$) or moose twinning rate ($R^2=0{\cdot}22$, $P>0{\cdot}15$) the next year using up to third-degree polynomial regressions. Furthermore, the relationship between proportion of calves in the wolf kill and accumulated snow was not the product of an increase in the wolf population after runs of severe winters ($R^2=0{\cdot}11$, $P>0{\cdot}10$). Therefore, because of the strength of cumulative winter effect demonstrated in this study, it, rather than wolf density, must be considered the main determinant of changes in deer and moose numbers in our study areas.

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REFERENCES

Albon, S. D., Guinness, F. E. & Clutton-Brock, T. H. (1983). The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *Journal of Zoology (London)*, **200,** 295–298.

Alexander, B. G. (1969). Movements of deer in northeast Texas. *Journal of Wildlife Management*, **32,** 618–620.

Allen, D. L. (1979) *Wolves of Minong*. Houghton-Mifflin, Boston.

Arnold, D. A. & Verme, L. J. (1963). Ten year's observation of an enclosed deer herd in northern Michigan. *Transactions of North American Wildlife and Natural Resources Conference*, **28,** 422–430.

Berger, J. (1979). Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): an ecological interpretation. *Zeitschrift für Tierpsychologie*, **50,** 188–200.

Cheatum, E. L. & Severinghaus, C. W. (1950). Variations in fertility of white-tailed deer related to range conditions. *Transactions of North American Wildlife and Natural Resources Conference*, **15,** 170–190.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123,** 212–229.

Crete, M. (1976). Importance of winter climate in the decline of deer harvest in Quebec. *Canadian Field Naturalist*, **90,** 404–409.

Floyd, T. J., Mech, L. D. & Nelson, M. E. (1979). An improved method of censusing deer in deciduous–coniferous forests. *Journal of Wildlife Management*, **43,** 258–261.

Franzmann, A. W. & LeResche, R. E. (1978). Alaska moose blood studies with emphasis on condition evaluation. *Journal of Wildlife Management*, **42,** 334–351.

Gasaway, W. C. & Coady, J. W. (1974). Review of energy requirements and rumen fermentation in moose and other ruminants. *Naturaliste canadien*, **101,** 227–262.

Gerstell, R. (1937). Winter deer losses. *Pennsylvania Game News*, **8 (7),** 18–21, 29.

Gilbert, F. F. (1966). Aging white-tailed deer by annuli in the cementum of the first incisor. *Journal of Wildlife Management*, **30,** 200–202.

Hoskinson, R. L. & Mech, L. D. (1976). White-tailed deer migration and its role in wolf predation. *Journal of Wildlife Management*, **40,** 429–441.

Jordan, P. A., Shelton, P. C. & Allen, D. L. (1967). Numbers, turnover, and social structure of the Isle Royale wolf population. *American Zoologist*, **7,** 233–252.

Julander, O., Robinette, W. L. & Jones, D. A. (1961). Relation of summer range condition to mule deer herd productivity. *Journal of Wildlife Management*, **25,** 54–60.

Ling, H. (1970). On the composition and productivity of the moose (*Alces alces*) population in the Estonian SSR. English abstract. *Suomen Riista*, 1970, 14–23.

Mansell, W. D. (1974). Productivity of white-tailed deer on Bruce Peninsula, Ontario. *Journal of Wildlife Management*, **38,** 808–814.

Markgren, G. (1969). Reproduction of moose in Sweden. *Viltrevy*, **6,** 129–299.

Maynard, L. A., Bump, G., Darrow, R. & Woodward, J. C. (1935). *Food preferences and requirements of the white-tailed deer in New York State*. Joint Bulletin 1: New York State Conservation Department and New York State College of Agriculture.

Mech, L. D. (1966). *The wolves of Isle Royale*. National Parks Fauna Series, No. 7. Washington, D.C., Government Printing Office.

Mech, L. D. (1979). Making the most of radio tracking: a summary of wolf studies in northeastern Minnesota. *A Handbook on Biotelemetry and Radio Tracking* (Ed. by C. J. Amlander & D. W. MacDonald), pp. 85–95. Pergamon Press, Oxford.

Mech, L. D. (1986). *Wolf population in the central Superior National Forest, 1967–1985*. Research Paper NC-270. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Mech, L. D. & Frenzel, L. D., Jr. (Eds) **(1971).** *Ecological studies of the eastern timber wolf in northeastern Minnesota*. Research Paper NC-51. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Mech, L. D. & Karns, P. D. (1977). *Role of the wolf in a deer decline in the Superior National Forest*. Research Paper NC-148. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Moen, A. N. & Severinghaus, C. W. (1981). The annual weight cycle and survival of white-tailed deer in New York. *New York Fish and Game Journal*, **28,** 162–177.

Morton, G. H. & Cheatum, E. L. (1946). Regional differences in breeding potential of white-tailed deer in New York. *Journal of Wildlife Management*, **10,** 242–248.

Moustgaard, J. (1959). Nutritive influences upon reproduction. *Reproduction in domestic animals* (Ed. by H. H. Cole & P. T. Cupps), pp. 489–516. Academic Press, New York.

Murphy, D. A. & Coates, J. A. (1966). Effects of dietary protein on deer. *Transactions of North American Wildlife and Natural Resources Conference*, **31,** 129–239.

Nelson, M. E. & Mech, L. D. (1981). Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs*, **77.**

Nelson, M. E. & Mech, L. D. (1986a). *Deer population in the Central Superior National Forest, 1967–1985*. Research Paper NC-271. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Nelson, M. E. & Mech, L. D. (1986b). Relationship between snow depth and wolf predation on deer. *Journal of Wildlife Management*, **50,** 471–474.

Nelson, M. E. & Mech, L. D. (1986c). Mortality of white-tailed deer in northeastern Minnesota. *Journal of Wildlife Management*, **50,** 691–698.

Ozoga, J. J., Verme, L. J. & Benz, C. S. (1982). Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. *Journal of Wildlife Management*, **46,** 1–11.

Peterson, R. O. (1977). *Wolf ecology and prey relationships on Isle Royale.* National Park Service. Scientific Monograph, 11.

Peterson, R. O., Page, R. E. & Dodge, K. M. (1984). Wolves, moose, and the allometry of population cycles. *Science*, **224,** 1350–1352.

Peterson, R. O., Scheidler, J. M. & Stephens, P. W. (1982). Selected skeletal morphology and pathology of moose from the Kenai Peninsula, Alaska, and Isle Royale, Michigan. *Canadian Journal of Zoology*, **60,** 2812–2817.

Picton, H. D. (1979). A climate index and mule deer fawn survival in Montana. *International Journal Biometeorology*, **23,** 115–122.

Picton, H. D. (1984). Climate and the prediction of reproduction of three ungulate species. *Journal of Applied Ecology*, **21,** 869–879.

Ransom, A. B. (1967). Reproductive biology of white-tailed deer in Manitoba. *Journal of Wildlife Management*, **31,** 114–123.

Robinette, W. L., Gashwiler, J. S., Jones, D. A. & Crane, H. S. (1955). Fertility of mule deer in Utah. *Journal of Wildlife Management*, **19,** 115–136.

Robinson, J. J. (1977). The influence of maternal nutrition on ovine foetal growth. *Proceedings of the Nutrition Society*, **36,** 9–16.

Rolley, R. E. & Keith, L. B. (1980). Moose population dynamics and winter habitat use at Rochester, Alberta, 1965–1979. *Canadian Field Naturalist*, **94,** 9–18.

Severinghaus, C. W. (1981). Overwinter weight loss in white-tailed deer in New York. *New York Fish and Game Journal*, **28,** 61–67.

Stenlund, M. H. (1955). *A field study of the timber wolf* (Canis lupus) *on the Superior National Forest, Minnesota.* Tech. Bull 4. St. Paul: Minnesota Department of Conservation.

Thompson, I. D. (1980). Effects of weather on productivity and survival of moose in northeastern Ontario. *Proceedings North American Moose Conference and Workshop*, **16,** 463–481.

Thomson, A. N. & Thomson, W. (1948). Lambing in relation to the diet of the pregnant ewe. *British Journal of Nutrition*, **2,** 290–305.

Verme, L. J. (1962). Mortality of white-tailed deer fawns in relation to nutrition. *Proceedings of the National White-tailed Deer Disease Symposium*, **1,** 15–38.

Verme, L. J. (1963). Effect of nutrition on growth of white-tailed deer fawns. *Transactions of North American Wildlife and Natural Resource Conference*, **28,** 431–443.

Verme, L. J. (1965). Reproduction studies on penned white-tailed deer. *Journal of Wildlife Management*, **29,** 74–79.

Verme, L. J. (1967). Influence of experimental diets on white-tailed deer reproduction. *Transactions of North American Wildlife and Natural Resources Conference*, **32,** 405–420.

Verme, L. J. (1969). Reproductive patterns of white-tailed deer related to nutritional plane. *Journal of Wildlife Management*, **33,** 881–887.

Verme, L. J. (1977). Assessment of natal mortality in Upper Michigan. *Journal of Wildlife Management*, **41,** 700–708.

Verme, L. J. & Ullrey, D. E. (1984). Physiology and nutrition. *White-tailed deer ecology and management* (Ed. by L. K. Halls), pp. 91–118. Stackpole, Harrisburg, Pennsylvania.

Willis, M. B. & Wilson, A. (1974). Factors affecting birth weight of Santa Gertrudis calves. *Animal Productivity*, **18,** 231–236.

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