

The cumulative effect of consecutive winters' snow depth on moose and deer populations: a defence

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Summary

1. L. D. Mech *et al.* presented evidence that moose *Alces alces* and deer *Odocoileus virginianus* population parameters are influenced by a cumulative effect of three winters' snow depth. They postulated that snow depth affects adult ungulates cumulatively from winter to winter and results in measurable offspring effects after the third winter.

2. F. Messier challenged those findings and claimed that the population parameters studied were instead affected by ungulate density and wolf indexes.

3. This paper refutes Messier's claims by demonstrating that his results were an artifact of two methodological errors. The first was that, in his main analyses, Messier used only the first previous winter's snow depth rather than the sum of the previous three winters' snow depth, which was the primary point of Mech *et al.* Secondly, Messier smoothed the ungulate population data, which removed 22–51% of the variability from the raw data.

4. When we repeated Messier's analyses on the raw data and using the sum of the previous three winter's snow depth, his findings did not hold up.

Key-words: deer, moose, population, snow, wolf.

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Introduction

Mech *et al.* (1987) found that snow depth summed over 3 consecutive years may influence population parameters of moose *Alces alces* L. on Isle Royale, Michigan, and white-tailed deer *Odocoileus virginianus* Zimmerman in north-eastern Minnesota, USA. They found significant effects of cumulative snow depth on deer fawn:doe ratios, moose calf:cow ratios, percentage moose twinning rate and percentage annual change in deer populations. They postulated that this influence is not necessarily measurable after each winter. Rather there is a nutritional momentum in adult female ungulates that, when accumulated over enough years, influences the development and survival of offspring enough to be measurable.

Wolves *Canis lupus* L. were the primary mortality factor in the systems. However, no relationship was

found between wolf numbers and ungulate population parameters. Thus wolves were considered secondary to ungulate nutrition as a contributing factor to ungulate mortality. Further evidence of the nutritional effect of weather conditions summed over consecutive years was provided by Feldhamer *et al.* (1989).

The conclusions of Mech *et al.* (1987) were challenged by Messier (1991). Messier used three methods that differed conceptually from those of Mech *et al.* (1987). First, he smoothed the raw ungulate population data. Secondly, he added two new independent variables, ungulate density and a predation-rate index, and applied them to the smoothed data in a Pearson partial-correlation analysis. Thirdly, instead of using 3-year's snow depth as an independent variable, he used only the first previous winter's snow depth. He then asserted that the conclusions of Mech *et al.* (1987) were erroneous.

In one analysis in which Messier (1991, Table 4) used his other factors as covariables, he did try summing the snow depth from several previous winters. With two of the three dependent variables for which

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he attempted the analyses, he confirmed the Mech *et al.* (1987) findings, and with the third he used only 16 of the 23 data points. He explained the relationship he found as a food-competition phenomenon. He also concluded that wolf predation was significantly influencing ungulate population change. We demonstrate here that Messier's (1991) findings resulted from methodological errors.

Methods

We attempted to sort out the influence of each of the three new approaches Messier applied to the data. If predation index and ungulate density really do influence change in ungulate numbers, this should be demonstrable with the raw data. However, if the relationships Messier found did not hold with the raw data, then they were attributable to the smoothing. We also compared Messier's (1991) smoothed population data with the raw data.

We duplicated Messier's (1991) analyses for percentage deer population change, fawn:doe ratio, moose calf:cow ratio and percentage moose twinning rate, but with the raw data. The only exception was that we used the sum of the snow depths for the three previous winters (Mech *et al.* 1987). We based the wolf-predation index and wolves per 100 deer on our raw data (Table 1).

Results and discussion

Smoothing resulted in a 51% loss in variability of the deer population data and a 22% loss in variability of

the moose population data. The differences between raw and smoothed moose data for a given year varied from -13% to +32%, and for the deer data from -32% to +44% (Messier 1991, Tables 1 & 2). The differences were compounded when applied to the percentage change in population. For example, in one case for raw data, annual change was -44%, whereas for smoothed data it was +17% (Table 2).

When we repeated Messier's (1991) analysis using the wolf-predation rate index, moose density, and the previous three winters' snow depth regressed against the raw data, 3-year snow accumulation entered the analysis first for three of our dependent variables (Table 3). For all four dependent variables, this factor explained more variation than did Messier's new factors (Table 3). With the moose twinning rate on Isle Royale, the wolf-predation index did explain more variation ($R^2 = 0.29$) when only 16 data points were used as Messier (1991) did. (Either the predation index or moose-density data were unavailable for the remaining seven points.) However, when we used all the available data ($n = 23$), our three winters' snow accumulation explained 42% of the variation ($P < 0.01$; Table 3). Thus the strongest relationship to the raw data remains with the sum of the previous three winters' snow depth.

Messier (1991, Table 4) did confirm the relationship that Mech *et al.* (1987) found between the Isle Royale moose calf:cow ratio and the sum of the previous three winter's snow accumulation ($R^2 = 0.51$; $P < 0.01$), but he dismissed this finding.

We recognize the limitation of population estimates and the usefulness of smoothing for certain objectives.

Table 1. Wolf predation index (on moose) and wolf:deer ratios derived by Messier (1991, Table 1) based on smoothed moose and deer population data compared with same indexes derived by the present authors based on original data (Mech *et al.* 1987)

Winter	Predation rate index based on		Wolves per 100 deer based on	
	Messier-smoothed	Original	Messier-smoothed	Original
1966-67	4.16	4.16	—	—
1967-68	3.72	3.72	—	—
1968-69	7.99	7.48	—	—
1969-70	5.17	5.23	—	—
1970-71	6.12	8.08	—	—
1971-72	8.24	8.05	—	—
1972-73	8.34	7.89	—	—
1973-74	8.63	7.49	—	—
1974-75	12.14	10.51	—	—
1975-76	15.12	15.20	3.73	3.63
1976-77	14.75	18.00	3.44	3.44
1977-78	13.30	14.85	4.12	4.91
1978-79	10.73	9.52	3.66	2.93
1979-80	9.29	9.63	4.63	4.45
1980-81	7.34	7.95	4.02	4.02
1981-82	5.83	6.45	3.34	4.04
1982-83	5.17	4.60	3.19	3.70
1983-84	4.45	4.63	1.68	1.41
1984-85	3.94	3.48	1.87	2.70

Table 2. Comparison of original moose and deer population data used by Mech *et al.* (1987, Table 2) with the smoothed data used by Messier (1991, Tables 1 & 2)

Winter	% moose population change		% deer population change	
	Messier-smoothed	Original	Messier-smoothed	Original
1968-69	-10	-16	—	—
1969-70	-9	-30	—	—
1970-71	-8	24	—	—
1971-72	-7	-4	—	—
1972-73	-6	2	—	—
1973-74	-6	-5	—	—
1974-75	-5	-18	—	—
1975-76	-4	-21	-13	-16
1976-77	-3	7	-11	-26
1977-78	-1	24	-8	39
1978-79	1	-15	-5	-21
1979-80	4	-1	0	-5
1980-81	6	4	5	-12
1981-82	10	36	11	17
1982-83	13	-4	15	95
1983-84	16	37	17	-44
1984-85	18	—	19	84

but in the present situation smoothing only added to any existing inaccuracies and yielded highly misleading results. Smoothing density data and then using the smoothed data to calculate percentage density change produces a completely determined relationship between percentage density change and density.

When density is smoothed with a function, d , then density for year y is $d(y)$, density for the subsequent

year is $d(y+1)$, density change is $d(y+1) - d(y)$, and percentage density change is:

$$\Delta(y) = \frac{d(y+1) - d(y)}{d(y)} \quad \text{eqn 1}$$

As is apparent from equation 1, once the density function is determined, percentage density change is also

Table 3. Results of step-wise regression analysis of data smoothed by Messier (1991) compared with those of similar analyses of original data (Mech *et al.* 1987)

Dependent variable	Messier-smoothed data				Original data			
	Independent variable	R^2_*	R^2_{total}	P	Independent variable	R^2_*	R^2_{total}	P
Deer fawn:doe ratio ($n = 9$)	Deer density	0.33	0.34	0.01	3-year snow	0.48	0.48	0.04
	Wolf index†	0.02	0.36	0.68	Deer density	0.16	0.64	0.16
	1-year snow	0.01	0.37	0.80	Wolf index	0.07	0.71	0.32
Change in deer density ($n = 10$)	Wolf index	0.47	0.47	0.03	3-year snow	0.50	0.50	0.02
	Deer density	0.19	0.66	0.09	Deer density	0.07	0.57	0.34
	1-year snow	0.09	0.75	0.20	Wolf index	0.00	0.57	0.99
Moose cow:calf ratio ($n = 14$)	Wolf index	0.15	0.15	0.17	3-year snow	0.51	0.51	<0.00
	Moose density	0.38	0.53	0.01	Wolf index	0.06	0.58	0.24
	1-year snow	0.05	0.58	0.31	Moose density	0.01	0.59	0.62
Moose twinning rate ($n = 16-23$)	Wolf index	0.21	0.20	0.08	3-year snow	0.42‡	0.42	<0.01
	Moose density	0.01	0.21	0.65	—	—	—	—
	1-year snow	0.02	0.22	0.63	—	—	—	—
Change in moose density ($n = 19$)	Wolf index	0.42	0.42	<0.01	Moose density	0.21	0.21	0.07
	Moose density	0.38	0.80	<0.01	Wolf index	0.19	0.40	0.07
	1-year snow	0.01	0.81	0.48	3-year snow	0.01	0.41	0.72

*Summarized from Messier (1991). We were able to replicate all of these figures except that we obtained a R^2 of 0.10 ($P = 0.27$) for the regression of moose cow:calf ratio against wolf index instead of the R^2 of 0.15 ($P = 0.17$) that Messier derived.

†Wolf index for the deer variables is the wolf:deer ratio of Messier (1991) and for the moose variables is the wolf-predation-rate index of Messier (1991).

‡Our multiple regression analysis of moose twinning rate, using the original data and Messier's (1991) new variables, yielded $R^2 = 0.29$ ($P = 0.03$; $n = 16$) with wolf index. Because data for these variables were only available for 16 data points, this analysis could not be applied to the total data set of 23, which was used for the original analysis.

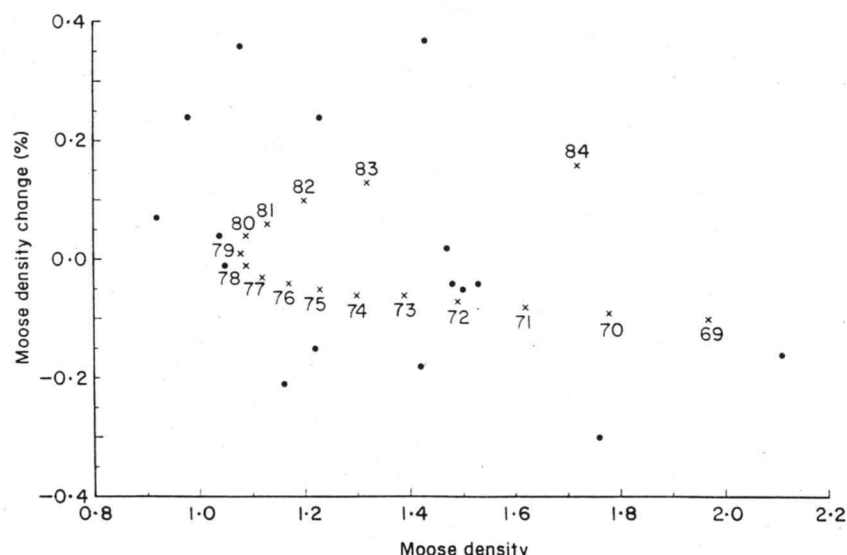


Fig. 1. Moose population data ($n \text{ km}^{-2}$) from Isle Royale smoothed ($\times$) by Messier (1991) and used in his analysis compared with raw data ($\bullet$) of Mech *et al.* (1987). Numbers by data points refer to the last two digits of the year for which the smoothed data apply, e.g. 76 refers to spring 1976.

determined. In addition, percentage density change based on the smoothing function does not always adequately represent raw percentage density change as Messier suggests, nor can it always be represented by a linear relationship, as Messier suggests by using multiple-linear regression (Fig. 1).

If smoothing is necessary to 'substantially alleviate the effect of imprecise density estimates', as Messier stated, then the sampling variability for variables based on density estimates should be significantly greater than the residual variability about the original regression models. While independent data are not available to test this hypothesis, we calculated asymptotic upper bounds for sampling variability for percentage annual change in deer and moose populations using standard variance formulae and standard statistical propagation-of-error techniques (Cameron 1982). We then compared these upper bounds to the residual mean-square errors for the regressions using standard *F*-tests ($\alpha = 0.05$). For percentage annual change in both deer and moose numbers, the upper bounds were not significantly greater ($P > 0.10$) than the residual mean-square errors. Thus we conclude that sampling variability does not obscure the short-term trends that were modelled and that smoothing is not required for these data.

A second problem was Messier's use of annual ungulate density to explain annual percentage change in ungulate density. Even with no relationship between density change and density, there is still an inverse relationship between percentage density change and density because larger densities decrease percentage density change while lower densities increase percentage density change. While Mech *et al.* (1987) used percentage density change, their analyses did not include predictors that were of mathematical necessity related to it.

Thirdly, Messier (1991) overlooked the main point of the Mech *et al.* (1987) paper, which was that their population parameters were related to the sum of the three previous winters' snow depth. Messier used only the first previous winter's snow depth when evaluating his additional independent variables.

A fourth problem appears to involve a simple misunderstanding. Messier (1991) stated that 'If a cumulative effect of winter snow is a real phenomenon, one would predict a progressive increase in r^2 within the effective integration period'. However, this is not what Mech *et al.* (1987) postulated. Rather, the cumulative effect they proposed acts on the adult nutritional condition eventually (after 3 years) affecting foetuses in ways that can be measured. That effect, while sometimes apparent after the first or second winter, was primarily manifested after three winters in the study areas. In another study, wolves did not start killing caribou calves < 1 month old until summers following two winters of above-average snowfall (Adams, Dale & Mech 1994), and the annual proportion of caribou cows killed did not increase until during the second consecutive winter of above average snowfall (Mech *et al.* 1994).

We conclude, therefore, that the Mech *et al.* (1987) original findings using raw data still stand.

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