

## EVIDENCE OF CARRYING CAPACITY EFFECTS IN NEWFOUNDLAND MOOSE

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**ABSTRACT:** Newfoundland moose (*Alces alces americana*) increased following 1904, the year of successful introduction, to peak numbers in 1958. The population subsequently decreased to record low numbers by 1973, when an area-quota management system was instituted throughout the island (112,000 km<sup>2</sup>) in 38 moose management areas, in part, to respond to issues related to habitat and accessibility for hunting. Subsequent quota-management manipulations permitted the island-wide population to increase in accessible areas to record high numbers by 1986, after which populations again decreased, to a 1999 estimate of 125,000 animals (post-hunt). We hypothesise that, unlike most studied irruptions of cervid populations, moose populations in Newfoundland, and subsequently habitat carrying capacity ( $K$ ), decreased on inaccessible range following 1958 to very low density, from which both have never recovered. Decreases in relative numbers of young moose seen while hunting and during winter classifications are consistent with increases in the number of moose seen during increase phases during 1966–99. These observations are less obvious for less accessible management areas. We explore other recruitment and density relationships as they have been developed in association with our estimate of  $K$  in moose for Newfoundland. We illustrate that, although some decrease in moose numbers following 1958 and 1986 was the result of management, changes to population size and to  $K$  also resulted in reduction in productivity, such that density dependence explains  $\geq 10\%$  and up to 76% of hunter-observed recruitment.

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Moose (*Alces alces*) populations are often difficult to compare because of geographic differences in scale, habitat continuity, and the relative importance of various mortality factors, including hunting, which introduces issues of hunter accessibility and its effect on population dynamics (Van Ballenberghe and Ballard 1998). Fundamental questions remain about what limits or regulates moose populations as there is much geographic variation in the relative effects of predators, human hunting, and primary production (Gasaway et al. 1992, Crête and Courtois 1997, Saether 1997, Crête and Daigle 1999). Habitat carrying capacity ( $K$ ) is a concept that assists managers in area comparisons and in resolving

when density-dependent effects are predicted to occur (McCullough 1999, Person et al. 2001). Approximation of  $K$  for cervids has been discussed in theory by Caughley (1976), and as an experiment by McCullough (1979). Crête (1989: 378) described  $K$  as a bounded rather than a constant value, varying with effects of winter snowfall, annual primary productivity, and forest succession. The usefulness of McCullough's approach to calculate  $K$  in areas where habitat changes is a problem also discussed generally in the original text (McCullough 1979: 156).

In this paper, we attempt to estimate  $K$  using hunter reports of several local populations of moose. We compare areas where moose management has had more

and less success in Newfoundland over the past 4 decades. We hypothesise that, unlike most studied cervid populations (McCullough 1997), moose populations in Newfoundland, and subsequently  $K$ , decreased on inaccessible range to very low density following initial irruptions, from which both have never recovered. We also predict that with an approach of more accessible, hunted populations to our estimates of  $K$  for these areas, lower numbers of young moose would be seen during hunting trips. These predictions allow us to illustrate density dependence in Newfoundland moose based on hunter reports during 1966–99. The relative importance of density-dependent versus density-independent factors for fluctuations in ungulate populations in the absence of predation can be tested by the following specific questions: (1) are indices related to moose abundance (i.e., moose observed by hunters), or to hunting (i.e., total days of hunting and total licences issued) more important in explaining recruitment observed by hunters in autumn; (2) do all management areas experience declines following observed peaks in moose density; and (3) are observations of abundance related to observations of recruitment by hunters? Our contention that variation in density-dependent reproduction depends on variation in  $K$  in time and space (Crête 1989) is contrasted to claims that regulation of moose density is dependent on hunter functional response, and that habitat or food supply may influence only the synchronicity of population cycles in Newfoundland (Ferguson and Messier 1996). We show limitations in hunter functional response to moose density in Newfoundland, and we offer guidelines that may assist moose management in the future.

## POPULATION AND MANAGEMENT HISTORY

The island of Newfoundland (Fig. 1), which encompasses 112,000 km<sup>2</sup>, forms a test case of the question of population regulation, because of the absence of predators of adult moose other than hunters. Four adult moose (*A. a. americana*), 2 females and 2 males, were successfully introduced to Newfoundland from New Brunswick, Canada, in 1904 (Pimlott 1953, Broders et al. 1999). Rapid dispersal and low densities characterized the first 25 years of population increase (Pimlott 1953) and wolves (*Canis lupus*) were extirpated during that period (Mercer 1995). During 1953–56, an increase rate was estimated for insular Newfoundland at 0.33, based on observations of young moose in mid-winter surveys (Pimlott 1959a). Keith (1983) later calculated an average intrinsic rate of increase of  $r = 0.23$  for North America in situations of

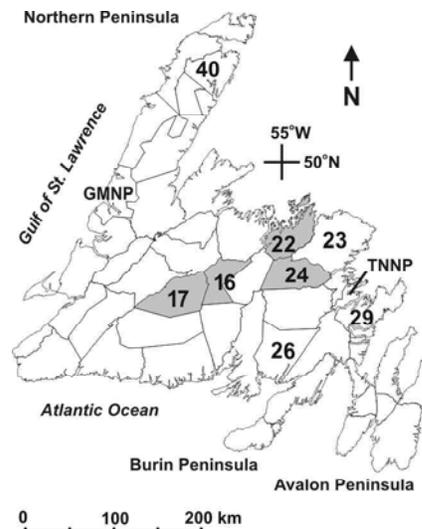


Fig. 1. Selected management areas in Newfoundland in which trends observed by either-sex, resident moose hunters are compared. Shaded region is referred to as central Newfoundland in this paper. Gros Morne National Park (GMNP), Terra Nova National Park (TNNP), and other areas referred to in the text are indicated.

unlimited food supply and minimal predation and hunting. Pimlott (1959a) underestimated late-winter mortality of young, but provided a rate that is closer to the potential rate of increase for moose. At a rate of increase since introduction between  $r = 0.23$  and  $r = 0.33$ , densities of moose would have exceeded those associated with the pre-hunt population estimate of 217,000 for insular Newfoundland during a second peak in the 1980s, for which more complete aerial survey data are available (Mercer 1995). Corresponding densities of moose of  $> 2 / \text{km}^2$ , including unforested areas, reflected minimum densities for the island excluding the Avalon and Northern Peninsulas, where populations were still expanding during the 1950s. Mercer and Manuel (1974) estimated that the first island-wide peak population occurred around 1960, and also that this peak was  $> K$ . Pimlott (1959a) similarly assessed populations in central Newfoundland during 1953–56 to have been  $> K$ ; twinning assessed elsewhere at 17% of births was as low as 3% in management areas 16 and 17 at that time. During 1958–72, the moose population decreased, likely as a result of further increased mortality and decreased productivity, particularly in

inaccessible areas (Mercer and Manuel 1974). The 1958 peak in population size was likely the largest to have occurred in Newfoundland.

Detail on the earliest efforts in moose management during 1935–58 were reported by Pimlott (1959b). Subsequently,  $< 8\%$  of the island introduced area quota management during 1964–71. In 1973, major changes were made to hunting regulations on the assumption that a combination of habitat productivity and hunter accessibility influenced density-dependent reproduction (Mercer and Manuel 1974). An island-wide area quota system was instituted in that year, whereby hunting became restricted to 36–38 management areas. With a new computerized draw, 50% fewer licences for moose were sold and approximately one-half the licences were male-only tags (Fig. 2). Low licence issue through the 1970s and 1980s was undoubtedly the main reason for a population increase during the 1980s (Mercer 1995). Major changes to the hunting season for Newfoundland moose prior to 1958 were made only in 1952, when seasons were shortened from 15 weeks island-wide to 4 weeks in accessible areas and 8 weeks in inaccessible areas; this

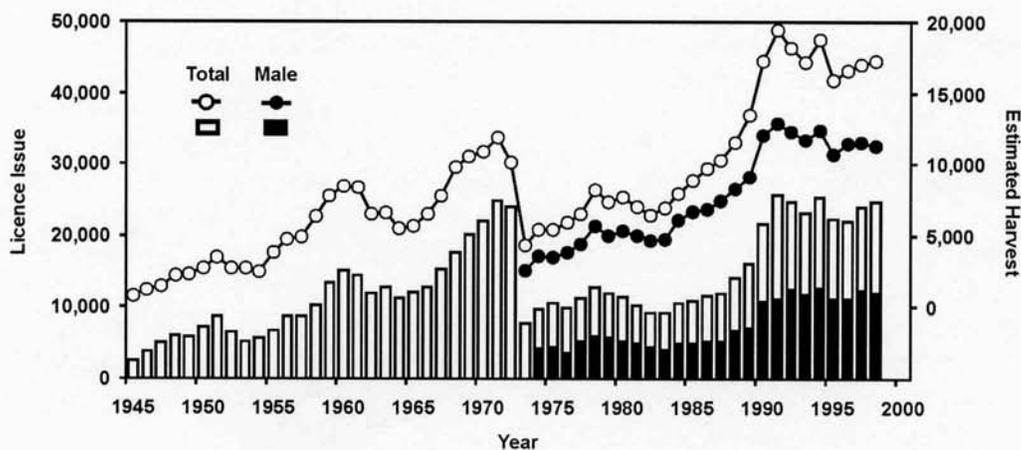


Fig. 2. Trends in moose management for insular Newfoundland, 1945–98. Bars represent annual either-sex (unfilled portions) and male-only (filled portions) moose licence issue, and circles represent total (open circles) and male (solid circles) kill estimates from hunter returns. Limited issues of “calf-only” and “female-only” licences beginning in 1987 are not included in this figure.

change may have caused the decrease in licence sales from 8,660 that year to 6,523 in 1953 (Pimlott 1959b). Later, minor changes to season length did not appear to affect licence sales (Mercer 1974). Gradually, hunting seasons have increased in length, beginning in September or October and ending between December and February; in 2002 the moose season was 15 weeks long, including a two-week, bow-hunting season. In 2002, 27,820 moose licences were available in insular Newfoundland (Mercer 1995).

### METHODS

We define  $K$  as the maximum density of moose that can be supported at equilibrium, in a stable environment and in the absence of time lags, as McCullough (1979) defined KCC. More generally, our definition agrees with Odum (1953), who defined  $K$  as the upper asymptote of the logistic or sigmoid curve describing unimpaired population growth. The inflection point of the S-shaped curve describing such growth has been used to determine maximum sustained yield (MSY), also termed inflection point carrying capacity (ICC) by McCullough (1979). MSY has been shown to occur near  $0.6 K$  for ungulates (McCullough 1984, Person et al. 2001).

Much of the information for determining changes to the issue of moose licences (“quotas”) in Newfoundland remains the same as that reported in Mercer and Manuel (1974). Annual response to a questionnaire (“return”) attached to every moose licence is usually  $> 75\%$ , but only following 1–2 reminders mailed to nonrespondents in February or March after the season closes. Initial returns, including a completed questionnaire and the lower mandible of any moose taken on a licence (individual licences have always been for 1 moose), are about 50% of licence sales to resident hunters without a reminder. The mailed remind-

ers are the extent of enforcement, although wildlife regulations stipulate returns are mandatory within 7 days of a kill or by the end of the hunting season. Data from completed questionnaires are coded digitally and archived by June of each year, and records in this form date back to the 1966 hunting season. Hunter trends are calculated annually from the resulting time series up to the hunting season of the previous year. On this timetable, the most recent hunter information can help set quotas only for the following hunting season, because draw notices (indicating successful licence applicants for the next season) are mailed by June each year.

Among those questions answered by moose hunters (including co-licence holders in a party hunt), the most reliable information has been considered for the calculation of trends by moose management area, as follows: (1) average number of animals reported killed by licence type (either-sex or male-only hunters) as a percentage of all licences sold by type (“hunter success”); (2) average number of days spent hunting by all licence holders spending at least 1 and at most 24 days hunting by licence type (“days of hunting”); and (3) average number of moose seen by the licence holder divided by the average number of days of hunting reported (“moose seen / day of hunting”). In instances where management areas were subdivided only for a portion of our study period, 1966–99, we pooled data from subareas for our trend calculations. We adjusted hunter success from the calculation using initial questionnaire respondents by assuming success of all nonrespondent hunters was represented by reports from reminder respondents. Hunter respondents given first reminders only reported no difference in success from second-, third-, or fourth-reminder respondents, although all nonrespondents reported lower success than initial respondents without reminders (Wild-

life Division, Newfoundland and Labrador, unpublished data). We did not exclude any either-sex, resident licence holders in the calculation of days of hunting and moose seen / day of hunting. We reported, in addition to hunter success, a fourth trend; kill rate; expressed as total estimated moose killed / 10 days of hunting, a factor of the division of hunter success by days of hunting. We tracked licence issue and kill estimates from 1945, the year of the first general season for all Newfoundland excluding the Avalon and Burin Peninsulas, to 1999, the last year of records available to us (Pimlott 1953, Mercer and Manuel 1974, Mercer 1995). From these figures, we calculated hunter success for either-sex licence holders.

Additional information on questionnaire returns has been collected and archived but not regularly used in management, including information regarding co-licence holders, area access, age, and sex of moose seen during days of hunting, number of moose seen by calendar day, and date and location of moose kill. Herein, we calculate a fifth trend, using age and sex classification of moose reported seen by hunters as an index of recruitment in autumn. For all hunters reporting “calves seen,” we calculate the number of young as a ratio of the number of “cows seen” (young seen / 100 adult females). We excluded, in this instance, hunters who did not report seeing “calves,” because there exists considerable bias in the sighting and identification of young moose, as discussed by Pimlott (1959a) and Mercer (1974). We show trends for the either-sex, resident moose hunter in insular Newfoundland (averages for the island portion of the province of Newfoundland and Labrador), in central Newfoundland (averages for management areas 16, 17, 22, and 24), and in management area 26 on the south coast (Fig. 1). A network of forest access roads makes areas 16, 17, 24, and 22

the more accessible hunting areas studied, with mean geographic distances to the nearest road in each of these areas 2.4, 1.1, 1.0, and 0.7 km, respectively (Mercer 1995). Area 26 is among the least accessible hunting areas in Newfoundland, with a mean distance to the nearest road of 9.6 km. Thus, area 26 offers a likely example of a moose population at  $K$  (Mercer and Manuel 1974).

To correspond our estimates of moose seen / day of hunting from hunter reports to moose density, and to calibrate hunter estimates of recruitment in autumn with mid-winter, aerial observations, we considered area 24, in which sufficient aerial surveys had been conducted to form a time series similar to hunter trends. We used 8 estimates of population size, between 1973 and 1997, obtained from helicopter counts in winter with stratified random surveys, in which we adjusted all counts by a factor of 2.7 to correct visibility bias, an average correction factor for forested areas in Newfoundland (Oosenbrug and Ferguson 1992, Gosse et al. 2002). Counts were divided over the entire survey area (including unforested regions) of area 24 to obtain average density in animals per square kilometre.

We reported all linear relationships between indices with adjusted  $r^2$ . Stepwise multiple regressions, from which we reported Mallows' statistic ( $C_p$ ), were used to determine significant predictors of recruitment observed by groups of hunters, from insular and central Newfoundland, and from management areas 16, 17, 22, 24, and 26. In each stepwise procedure, we allowed variables to enter if they were significant at  $P < 0.10$ , and to stay in the model if they were significant at  $P < 0.05$ . We included among those variables, for the corresponding hunting area, moose seen / day of hunting for the same year and for the previous year, young / 100 adult females

seen during the previous year (an auto-correlated series), total number of days of hunting, and total number of licences issued for the same year (measures of hunting). For each hunting area, including the requirement for lagged data, during 1966–99,  $n = 33$ , except in the case of area 26, where missing data allowed only  $n = 29$ . We presented the models resulting from the stepwise procedures using principal component regressions (Sokal and Rohlf 1995), and for each significant model, we reported  $F$ ,  $P$ , adjusted  $r^2$ , the corresponding eigenvalues of the covariance matrix, the sum of squares associated with the first principal component, and the error sum of squares. Principal component regressions were chosen because all hunter trends were continuously variable and subject to measurement error and multicollinearity as a result of the same hunters used as data points in all calculations, and also because the measurement units (moose seen) were often identical in our models. That is, a principal components approach corrects for multicollinearity and for Type I error (Sokal and Rohlf 1995).

## RESULTS

Moose hunter success has varied to some extent with moose licence issue (Fig. 3). The most obvious recent trends have been the steady increase in hunter success during the 1970s following the decrease in licence sales in 1973, then a gradual decline in success during the 1990s, beginning about 1987. That pattern was similar to what was observed following peak populations and peak licence sales in the 1960s. To some extent, increase in hunter success also tracked increases in moose populations, because success during the early 1980s continued to increase with modest increases in licence sales. If hunter success is the most representative gauge of moose density available for the 1950s and 1960s, then the peak population occurred in 1958 (Fig. 3). The average number of moose seen by hunters and the kill rates estimated in all licence areas have been closely correlated, when expressed relative to the number of hunters and to the average number of days spent hunting (Fig. 4). Hunter success has been more variable than moose seen or kill rate, and kill rate has had higher variation than moose seen / day of hunting. Hunting trips were shortened or lengthened based on hunter success and not directly on the

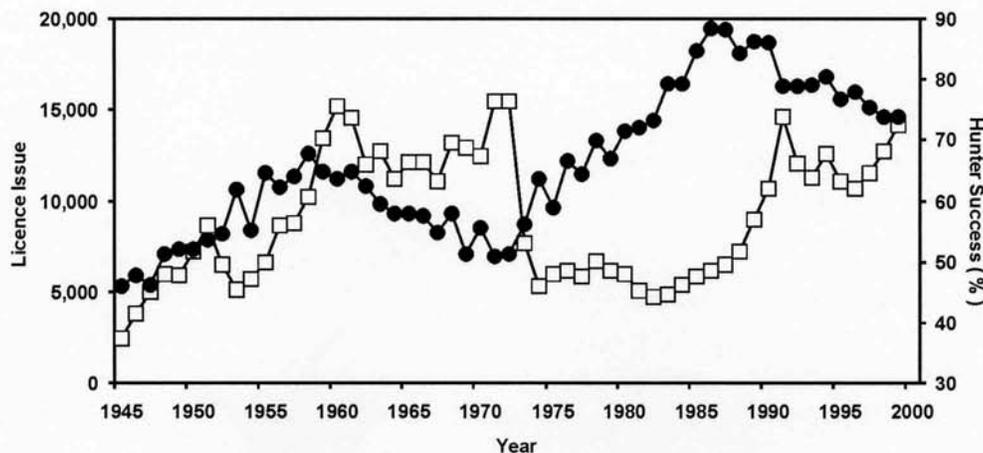


Fig. 3. Either-sex moose licences issued to resident hunters (squares) and hunter success (solid circles) for insular Newfoundland, 1945–99.

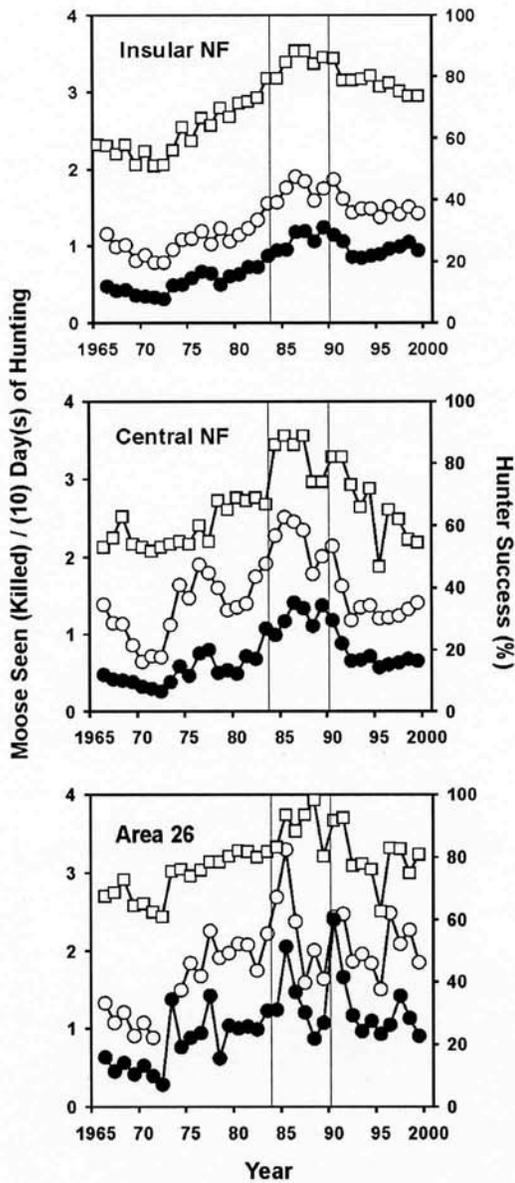


Fig. 4. Moose seen / day of hunting by either-sex, resident moose hunters (left axis, solid circles), kill rate in moose killed / 10 days of hunting (left axis, open circles), and hunter success (%), right axis, and squares), for either-sex, resident moose hunters, 1966–99. Boxed area is 1984–89, when peak moose densities occurred. Correlations between moose seen and kill rates, for insular Newfoundland,  $r^2 = 0.91$ , for central Newfoundland,  $r^2 = 0.80$ , for area 26,  $r^2 = 0.67$ ; correlations between moose seen and hunter success, as above,  $r^2 = 0.89, 0.59, \text{ and } 0.43$ , respectively.

number of moose seen; indeed, number of days spent hunting varied inversely with the number of moose reported by hunters (Fig. 5). This trend was consistent across licence areas when the number of moose seen was divided by the number of days of hunting.

All management areas experienced a decline in the number of moose reported by hunters following a peak during 1984–89, a portion of the time series we have referenced for its potential in illustrating density-dependent effects (Fig. 4). Before this time and since about 1973, number of moose seen / day of hunting increased, with a smaller peak in some areas in the late 1970s. This trend is least obvious for area 26, the area that has had the most variation in the number of moose seen by hunters among years. Variation in hunter success in area 26, unlike in the other areas, is not explained by the number of days of hunting (Fig. 5). Our population trends in moose seen indicate that current moose density in insular Newfoundland is about 25% less than the peak period of 1984–89 (Fig. 4). The recent decline in moose density was apparently greater in central Newfoundland, where our trends indicate at least a 50% decrease. Areas 16, 17, 22, and 24 decreased in the number of moose seen / day of hunting since reports during the peak period (Table 1) by about 75, 65, 55, and 50%, respectively (not shown). The peak period was characterized on average by more than double the number of moose reported seen (0.83–1.84 / day) compared with the rest of the series (0.48–1.65 / day), and hunter success reports of > 80% compared with < 80% for most of the period of investigation (Fig. 4).

Our trend measuring recruitment in autumn, the ratio of young seen / 100 adult females, was inversely related to the number of moose seen / day of hunting (Fig. 6). This prediction was strongest for area 17, weak-

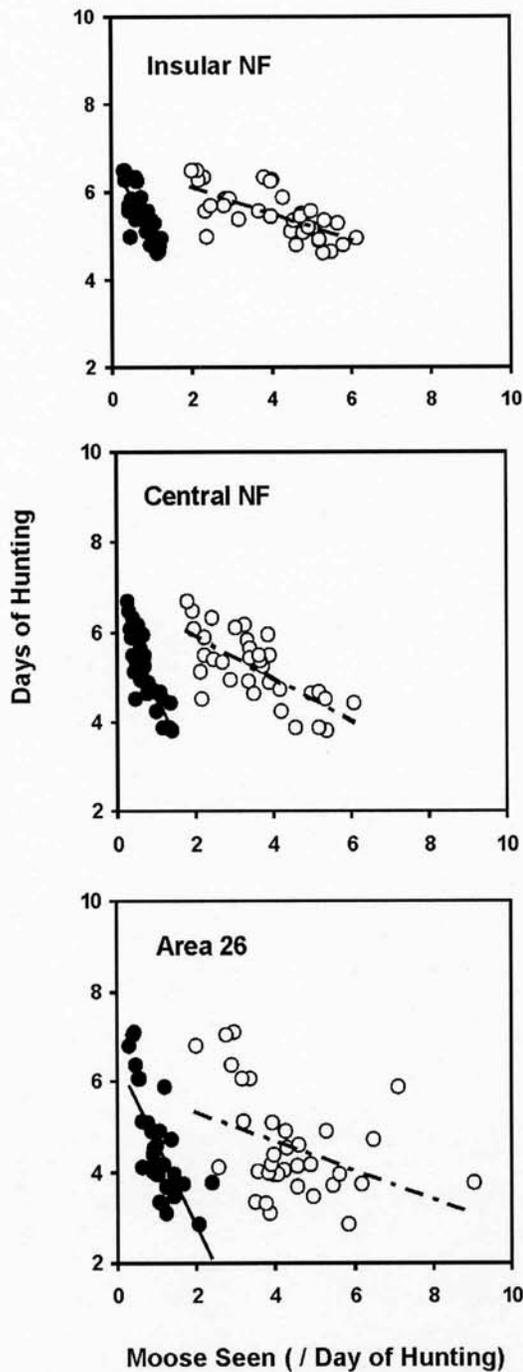


Fig. 5. Average number of days of hunting by either-sex, resident moose hunters, 1966–99, as a function of moose seen / day of hunting (solid circles, as in Fig. 4,  $r^2 = 0.65, 0.71,$  and  $0.56,$  respectively) and number of moose seen by hunters (open circles, as in Fig. 4,  $r^2 = 0.48, 0.50,$  and  $0.02,$  respectively).

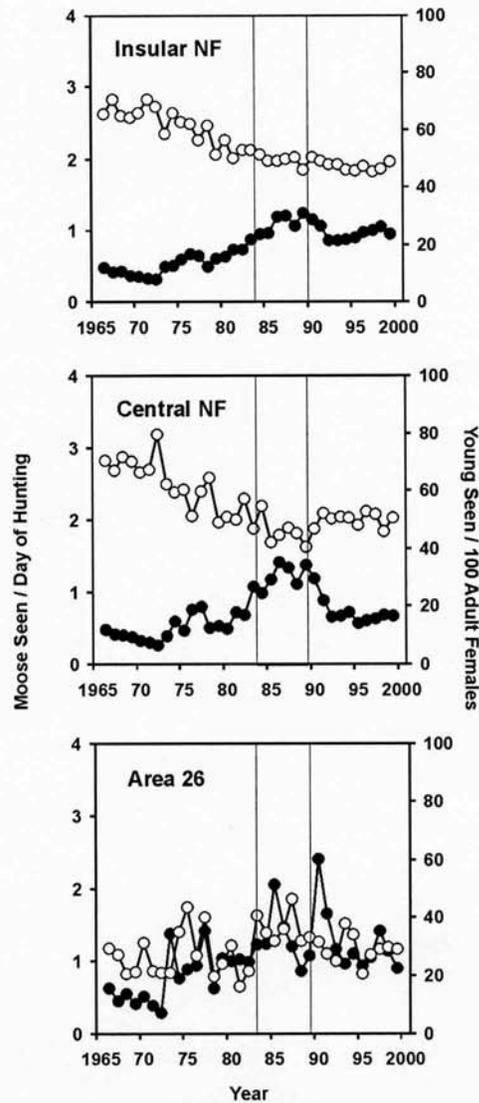


Fig. 6. Moose seen / day of hunting (solid circles) and young seen / 100 adult females (open circles) by either-sex, resident moose hunters in insular Newfoundland, central Newfoundland, and area 26, 1966–99 (boxed area is 1984–89).

est for area 22, and area 26 was an exception, having the lowest apparent recruitment throughout the time series (Table 1). Excluding this less accessible area, during the peak period in moose seen / day of hunting, average reports of young moose ranged for all areas from 43–49 seen / 100 adult females, while for the rest of the time series,

Table 1. Mean values for moose seen / day of hunting (M), hunter reports of autumn recruitment in young seen / 100 adult females (R), and hunter success (S, %), during 1984–89 and 1966–99 (excluding 1984–89). Theoretical habitat carrying capacity,  $K$ , is derived from the longer period, by extrapolating hunter reports, where possible, to an autumn recruitment rate of 20 young seen / 100 adult females using linear regression (see Fig. 7).  $K$  is reported in moose seen / day of hunting,  $\pm$  95% confidence intervals (from linear regression), and as density (/ km<sup>2</sup>) using the correspondence from Fig. 8. We also report slope and adjusted  $r^2$  for the regressions, where  $P < 0.05$ .

Hunting area	1984–89			1966–99						K	
	M	R	S	M	R	S	slope	$r^2$	$P$	Moose seen (/ km <sup>2</sup> )	
Insular NF	1.10	49.4	85.2	0.69	56.4	68.0	-30.4	0.80	0.000	1.88 $\pm$ 0.51	7.5
Central NF	1.23	45.7	83.0	0.60	57.3	61.7	-25.1	0.42	0.000	2.00 $\pm$ 0.61	8.0
Area 16	1.47	46.1	95.7	0.48	57.8	72.6	-30.9	0.17	0.016	1.60 $\pm$ 0.48	6.4
Area 17	1.85	42.6	95.2	0.76	58.1	72.1	-26.0	0.63	0.000	2.24 $\pm$ 0.64	9.0
Area 22	1.59	47.2	93.0	0.66	59.4	79.1	-39.1	0.26	0.007	1.66 $\pm$ 0.44	6.6
Area 24	0.83	49.1	91.7	0.56	57.9	73.9	-28.1	0.31	0.001	1.94 $\pm$ 0.59	7.8
Area 26	1.32	35.9	89.5	0.98	28.7	75.9	—	—	0.131	—	—

reports were 14–36% higher, ranging from 56–59 seen / 100 adult females. During 1984–89, the relationship between young seen / 100 adult females and moose seen / day of hunting formed a consistently shallower slope than the rest of the series, making the graphed relationship for the entire study period appear slightly curvilinear (Fig. 7). Hunter reports from area 26 suggest that there was a lower threshold in young moose reported in autumn of about 20 seen / 100 adult females. When we extrapolated the relationship excluding the peak period in other areas to estimate potential moose seen / day of hunting at 20 young seen / 100 adult females (i.e., at a theoretical zero population increase, or  $K$ ), based on area 26, all areas produced similar estimates of 1.6–2.2 moose seen / day of hunting (Table 1). Consistently in all areas, according to stepwise regression, moose seen / day of hunting and the autocorrelated series lagged 1 year (young seen / 100 adult

females in previous years), explained the most variance in young seen / 100 adult females. The best model fit occurred in areas 17 and 22, and in insular Newfoundland as an average (Table 2). In no areas were indices related to hunting (i.e., total days of hunting and total licences issued) significant in explaining recruitment in autumn according to stepwise regression. The principal component regressions also showed our models to be significant in all cases except in area 22, and the first principal component, explaining nearly 100% of the covariance in the 2 series, indicated that moose seen / day of hunting was negatively associated with the autocorrelated series, as in Fig. 7, and explained a similar amount of variance as the linear regressions, as in Table 1,  $r^2 = 0.11$  to 0.76.

The match resulting from comparing hunter trends to aerial surveys in area 24 appeared to be approximately 4x the number of moose seen / day of hunting to arrive at

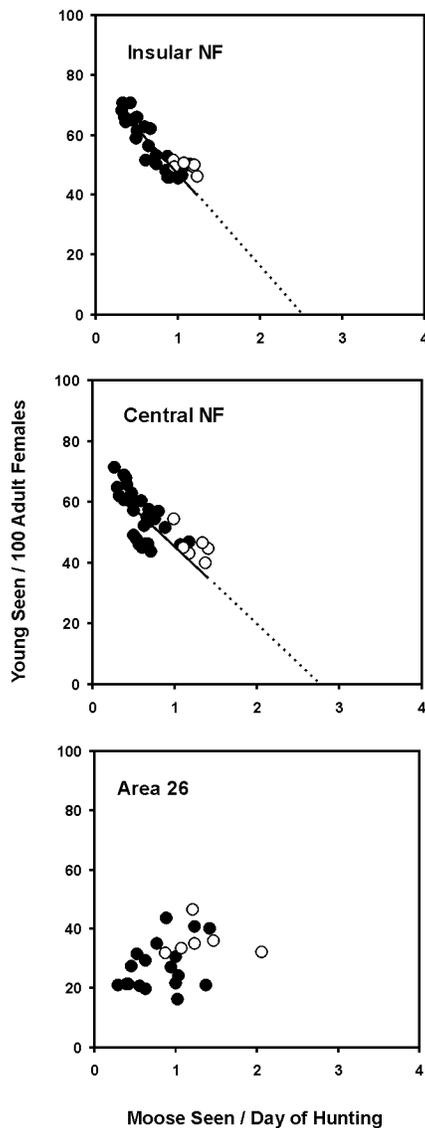


Fig. 7. Young seen / 100 adult females plotted against moose seen / day of hunting by either-sex, resident moose hunters in insular Newfoundland, central Newfoundland, and area 26, 1966–99 (solid circles). A linear regression is fit through the period, excluding observations from 1984–89 (open circles), and is extended toward the x-axis to make predictions about habitat carrying capacity, *K* (see Table 1).

density estimates in moose / km<sup>2</sup> in this area, although the relationship between the 2 indices was weak,  $r^2 = 0.08$  (Fig. 8). The 4 survey results from the 1970s and the

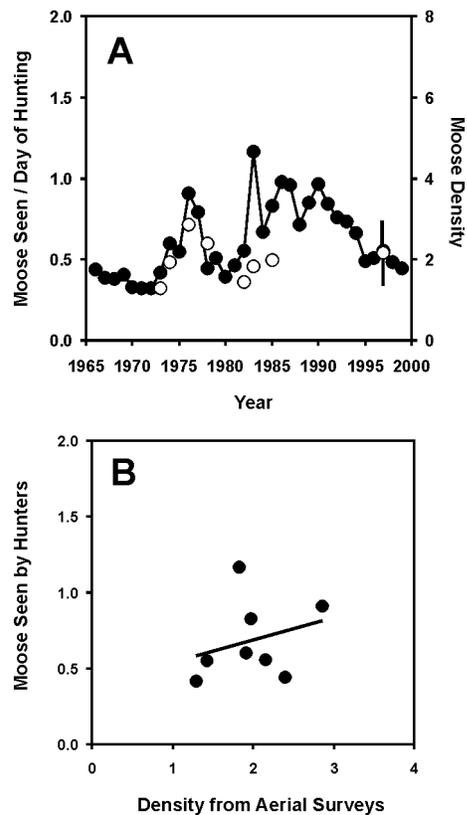


Fig. 8. Correspondence between moose seen / day of hunting by either-sex, resident moose hunters (left axis, solid circles) and moose density ( / km<sup>2</sup>) estimated from mid-winter, aerial surveys (right axis, open circles) in area 24, (A) as a time series and (B) as a regression for corresponding years. The 90% confidence interval for moose density is a vertical line over the 1997 aerial survey estimate in (A), used to calibrate the series.

survey result in 1997 weighed heavier than the estimates from the 1980s in our comparison. Expressed in both instances as young / 100 adult females, the hunter observations of recruitment in autumn and aerial surveys of mid-winter recruitment in area 24 produced a near match, although the relationship is also weak statistically,  $r^2 = 0.03$  (Fig. 9). Matching our predictions for moose seen / day of hunting at 20 young seen / 100 adult females with the correspondence to aerial survey data in area 24, we suggest that densities of 6–9 moose /

Table 2. Results of principal component regressions of autumn recruitment in young seen / 100 adult females in Newfoundland moose populations by hunting area, using either-sex, resident hunter reports of “calves” and “cows” seen during their trips, 1966–99. We report eigenvalues and factor loadings for 2 principal components, PC<sub>1</sub> and PC<sub>2</sub>, of the covariance matrix between moose seen / day of hunting (M) and the autocorrelated series of young seen / 100 adult females in the previous year (R<sub>t-1</sub>). We report from the stepwise regression procedures producing M and R<sub>t-1</sub> as the only significant predictive variables: Mallow’s statistic (*Cp*); we report from the regressions using PC<sub>1</sub> to predict autumn recruitment: *F*, *P*, adjusted *r*<sup>2</sup>, sum of squares (SS), and error sum of squares (SSE).

Hunting area	PC <sub>1</sub>			PC <sub>2</sub>			Statistics from regression models					
	Eigen-values	Factor loadings		Eigen-values	Factor loadings		<i>Cp</i>	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	SS	SSE
		M	R <sub>t-1</sub>		M	R <sub>t-1</sub>						
Insular NF	67.59	-0.03	1.00	0.02	1.00	0.03	2.9	102.5	0.000	0.76	1,600.7	484.0
Central NF	95.21	-0.02	1.00	0.05	1.00	0.02	2.1	39.6	0.000	0.55	1,587.6	40.1
Area 16	130.41	-0.02	1.00	0.13	1.00	0.02	1.1	4.8	0.036	0.11	557.5	3,612.8
Area 17	167.57	-0.02	1.00	0.10	1.00	0.02	3.5	17.3	0.000	0.34	1,815.2	3,244.9
Area 22	233.40	-0.02	1.00	0.14	1.00	0.02	2.2	3.7	0.065	0.07	785.2	6,626.7
Area 24	108.79	-0.01	1.00	0.04	1.00	0.01	1.8	16.9	0.000	0.33	1,123.9	2,058.7
Area 26	280.21	-0.02	1.00	0.19	1.00	0.02	1.0	4.2	0.052	0.11	1,027.1	6,149.2

km<sup>2</sup> approach *K* for moose in Newfoundland (Table 1).

## DISCUSSION

### Habitat Carrying Capacity for Moose

McCullough (1979) extended the linear regression of rate of recruitment on post-hunt population size to a theoretical zero population increase to obtain an estimate of *K* for white-tailed deer (*Odocoileus virginianus*) in the George Reserve, Michigan, USA. Although McCullough’s (1979) regression suggested linearity, our data indicate curvilinearity in the relationship between recruitment observed in autumn and population size (Fig. 7). Linearity appears to be a reasonable interpretation of recruitment in autumn for Newfoundland moose during the increase phase (1973–83), until peak densities were achieved. This difference from McCullough’s (1979) interpretation may be explained by the possibility that the George Reserve deer herd, which peaked at 34 deer / km<sup>2</sup> during 1952–71, before a

hunting experiment, was not allowed to reach densities high enough to show a decline to *K*. Post-hunt peak density was 19 deer / km<sup>2</sup> and mean density was much lower. In 1935, estimated density for the George Reserve deer herd reached 48 deer / km<sup>2</sup>. Deer population densities in other areas with no hunting have been higher yet. For example, in Saratoga National Park, New York, USA, without hunting, densities ranged between 37–74 deer / km<sup>2</sup> and averaged 53 deer / km<sup>2</sup> during 1985–94 (Underwood and Porter 1997). This density may be similar to densities observed in other parks where hunting is prohibited or restricted. McCullough (1997) reported very high densities in a population of black-tailed deer (*O. hemionus columbianus*) on Angel Island (2.2 km<sup>2</sup>), California, USA. There, during a period of 20 years (1965–84), 5 peak populations were recorded to average more than 100 deer / km<sup>2</sup>. These densities did not appear to be declining over time.

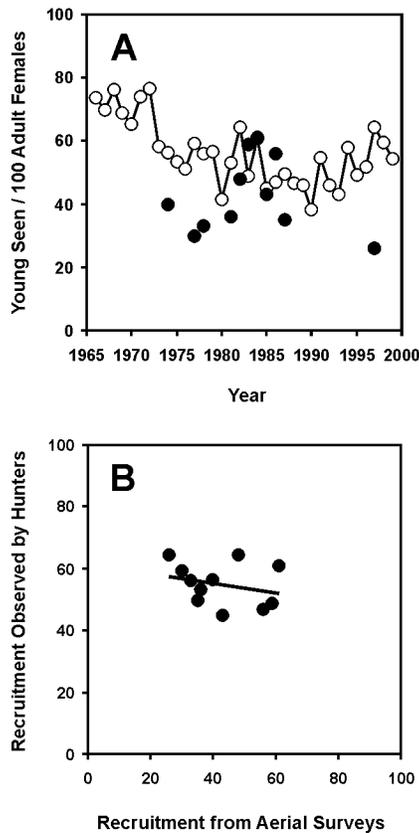


Fig. 9. Correspondence between young seen / 100 adult females by either-sex, resident hunters (open circles) and by observers during mid-winter, aerial moose surveys (solid circles) in area 24, (A) as a time series and (B) as a regression for corresponding years.

We estimate that  $K$  in Newfoundland boreal forests approximates 6–9 moose / km<sup>2</sup>, calculated from theoretical hunter reports of 1.6–2.2 moose seen / day of hunting at an extrapolated hunter-observed autumn recruitment of 20 young / 100 adult females (Table 1). This estimate depends on the assumption that changes to young seen / 100 adult females did not occur with changes to moose density for area 26 and that moose seen / day of hunting varied presumably only with annual weather or other random effects (i.e., area 26 was at  $K$  throughout our period of observation, when autumn recruitment was 20–40 young seen / 100 adults; Fig. 7). The related assumption of

zero population growth means that mean mortality between autumn and the following spring is about 30 young moose / 100 adult females. Our hunter trend involving moose seen / day of hunting produces a conservative estimate of real moose density at high values, because: (1) we used a more conservative correction factor for visibility bias than indicated specifically for area 24 (Oosenbrug and Ferguson 1992); (2) there are many kills that occur with < 1 day of hunting, but our index of hunting effort does not measure less than that period; and (3) on average hunters see more moose when days of hunting are fewer, and hunting trips are very short when hunter success is > 80%. Thus, our investigation of  $K$  from extrapolating moose seen / day of hunting is likely to be an underestimate particularly at high densities; again, this contrasts McCullough's (1979) conclusion that linear regression overestimates  $K$ . Combining observations along several hunting routes, we also generalize the effect of changing habitat on our estimate of  $K$ . However, our estimate of  $K$  for moose is higher than estimates elsewhere, especially in the presence of wolves (Gasaway et al. 1992, Van Ballenberghe and Ballard 1998).

Our estimate of  $K$  in Newfoundland should be compared to past density estimates for this unique situation. As an example of estimates during the first peak of moose densities in the boreal forest, densities in area 17 in 1960 were observed at 4.6 moose / km<sup>2</sup> (Bergerud and Manuel 1969). This figure was likely an underestimate of the real population size, because the equivalent of 5.0 moose / km<sup>2</sup> were shot along roads in 1962 (Bergerud et al. 1968). Multiplying the 1960 estimate by our visibility correction factor for forest of 2.7 would result in 12 moose / km<sup>2</sup> as a minimum density for area 17, such that this earlier peak exceeds our upper estimate of  $K$ . Estimates of moose density calculated only

for areas of forest cover, in inaccessible parts of Newfoundland (cf. area 26), were stable but highly variable since 1960 (as in Fig. 4), and were often  $> 12$  moose / km<sup>2</sup> (Mercer 1995). To further support our estimates of  $K$ , which we suggest may have been exceeded by the peak densities achieved by all dispersing and expanding populations in Newfoundland, new densities recorded in lowland forests in Gros Morne National Park, without legal hunting, were 3.4 moose / km<sup>2</sup> (uncorrected) and 7.4–10.6 moose / km<sup>2</sup> depending on the visibility correction factor (McLaren et al. 2000). In nearby area 40, where moose have recently reached their highest numbers, the post-hunt density ranged from 3–4 moose / km<sup>2</sup> (uncorrected) or 8–10 moose / km<sup>2</sup> (using the average visibility correction factor of 2.7) during 1989–99 (Mercer 1995).

Comparisons may also be made among the estimates of deer and moose densities above if food production in different vegetation types and biomass production differences of the ungulates are considered. Crête and Manseau (1996) and Crête and Daigle (1999) have performed reviews of this type, in which they suggested that variation in moose biomass depends on the presence of other deer species and on the existence of predators. Moose on the south shore of the St. Lawrence River in the absence of wolves reach 740 kg / km<sup>2</sup>, while even in the presence of wolves, they reach a biomass exceeding 1000 kg / km<sup>2</sup> on Isle Royale (Crête and Daigle 1999). In the forage-limited area these authors studied, on the Québec-Labrador Peninsula, where wolves are present, production estimates are 78 young / 100 adult females, and autumn recruitment is relatively high (90% survival to autumn) compared with our estimates for Newfoundland. Our calculation of  $K$  in moose in the forested areas of Newfoundland may be as high as the equivalent

of 3 young, 8 adult females, and 4 adult males (Table 1), which, according to Crête and Daigle's (1999) estimates, approaches 5,000 kg / km<sup>2</sup>. To compare, 100 white-tailed deer / km<sup>2</sup>, with the same sex and age ratio, approaches 5,200 kg / km<sup>2</sup>. These estimates can apparently only be achieved in the absence of additive predation (Gasaway et al. 1992, Van Ballenberghe and Ballard 1998, Person et al. 2001).

### Population Dynamics in Newfoundland Moose 1904–99

Differences in  $K$  and resulting differences in population dynamics reported in this paper can be explained by differences in hunting pressure / unit area relative to local density of moose. For example, if we compare central Newfoundland areas, then area 24, with the smallest amplitudes in moose seen / day of hunting (not shown), maintains a higher kill rate and a consequently lower density at peak, as well as a higher hunter-observed young to adult female ratio (Table 1). In area 24, licence issue also explains more of the variance in the number of young relative to adult females reported seen than in any of the other areas, suggesting a stronger influence of hunting. In contrast, an inaccessible area, such as area 26, has a much lower kill / unit area relative to its density (Fig. 4), and, as a result, a consistently low young to adult female ratio (Table 1). In general, we conclude that barren areas of Newfoundland (40% of insular Newfoundland and represented here by area 26), or other areas less accessible to hunting, following a population peak approaching  $K$  in the 1950s, moose populations decreased and remained very low thereafter (Fig. 10). In Terra Nova National Park (forested and accessible but with negligible, illegal hunting of moose), the moose population now behaves similar to inaccessible areas in that it also experienced no recovery after a decline

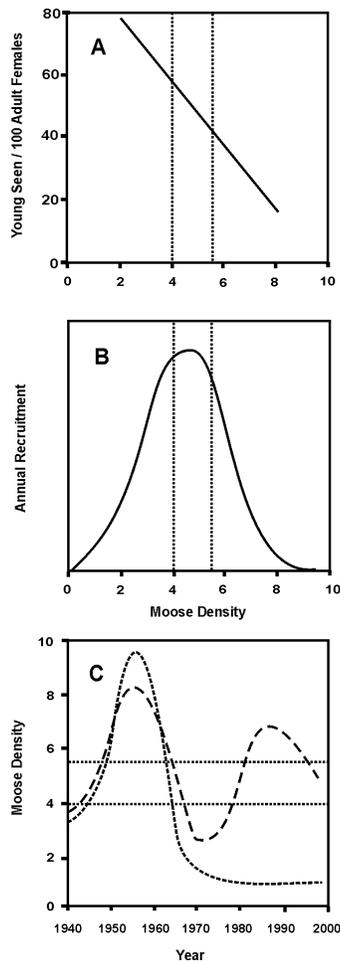


Fig. 10. Summary of observed and theoretical population dynamics for moose in insular Newfoundland: (A) young seen / 100 adult females by either-sex, resident hunters (solid line) as a function of estimated moose density ( $/\text{km}^2$ ), with our range estimate of maximum sustained yield (MSY) for forested habitat as vertical dotted lines; (B) annual recruitment (solid line) as a function of moose density (MSY, range as in (A)); and (C) a representation of population changes during 1940–2000 in forested, accessible areas (longer dashed line), which included 2 peaks above MSY (range as in A, now represented by horizontal dotted lines), in 1958 and in 1986, and in forested portions of less accessible areas (shorter dashed line), in which density-dependent effects near or beyond our estimate of  $K$  resulted in a permanent decline in moose after 1958. This figure was adapted from McCullough (1984).

following a 1958 peak in density. We predict that in this area, the population will remain low for many years; current estimates of mid-winter recruitment from the last aerial survey are 20 young / 100 adult females in the park (Gosse et al. 2002), consistent with our estimates of zero population increase. We also predict that the moose population in Gros Morne National Park under present management will decrease from its present high density and follow a similar trend. This population dynamic is also different from that of other parks (e.g., Isle Royale National Park, Michigan, USA; McLaren and Peterson 1994) and other areas with wolves.

In areas of Newfoundland more accessible to hunters, the population dynamic is much different. We describe 2 major peaks in moose density (1958 and 1986) both exceeding MSY but not necessarily  $K$  (Fig. 10). We maintain that the decline following the 1958 island-wide peak in moose resulted in part from hunting in some accessible areas, but also from a natural die-off caused by habitat destruction when populations grew  $> K$  in less accessible areas. Mercer and Manuel (1974) recorded low autumn recruitment in all areas they reviewed, where young observed as a percentage of winter-surveyed moose were 20–40% in accessible areas and 10% in inaccessible areas. Those authors hypothesized that the difference in winter recruitment was a result of destruction of winter food resources. According to a study of areas of different forest productivity in Norway, differences in spring recruitment in moose begin with a measurable change in fecundity (Saether et al. 1996). In Newfoundland, a similar change in fecundity was observed in the 1980s in area 24 – consistent with the decline in young / 100 adult females observed in mid-winter, aerial surveys (Fig. 9), there were 44% young moose observed as twins in 1983, 21% in 1984, 18% in 1985, and gener-

ally < 5% in current classifications (Mercer 1995). Nutrition-induced changes in vulnerability to predation likely result in later changes to summer recruitment, owing to the importance of mostly compensatory predation by black bear (*Ursus americanus*), estimated at 22% (area 24) to 38% (elsewhere in central Newfoundland) of young moose during summer (Mercer 1995). For central Newfoundland moose populations, we further estimate that density-dependent effects were not evident until a density of about 2 animals / km<sup>2</sup> was reached (Fig. 10), corresponding to about 0.5 moose seen / day of hunting (Fig. 7). This density is below our estimate of MSY, taken at 0.6 K, or about 3.5–5.5 moose / km<sup>2</sup>.

Using 2 methods, the moose population in insular Newfoundland was estimated in 1988 at 167,000 (post-hunt) and 217,000 (pre-hunt), and a population decline was predicted (Mercer 1995). If we use the post-hunt estimate, along with our assessment of the recent population decline by 25% of the peak density in 1986 (Fig. 4), then the current (1999) population of moose in Newfoundland is about 125,000 (post-hunt). Local moose densities range from < 0.1 to > 8 animals / km<sup>2</sup> (Mercer 1995); thus, some populations are clearly < MSY, whereas others are probably > K (Fig. 10). Our estimate of the highest peak in moose densities from the first peak in hunter success (Fig. 3) indicates that, consistent with Caughley's (1976) interpretation for ungulates, the first irruption occurred in 1958 and has never been exceeded.

### Management of Moose without Wolves

Managers were late in responding with quota increases to the increase in moose populations in accessible areas throughout Newfoundland during the 1980s and 1990s, and were thus indirectly to blame for the latest observed declines in autumn recruitment. In the 1970s, increases in licence

issue were primarily from the promotion of the male-only licence and the opening of new hunting areas; only by the late 1980s did total licence sales increase substantially as a response to increasing moose densities (Fig. 2). Since 1974, males continue to represent 65–75% of the legal (reported) kill. McCullough (1979) illustrated that a male-only harvest cannot move a population away from *K*, and that MSY cannot be achieved without harvesting females. Combined with relatively little change in density of moose (a 25% decline) during the 1990s (Fig. 4), harvest of most moose populations in Newfoundland has led to declines in sex ratio (Mercer 1995). Licence issue has not substantially changed throughout the 1990s, resulting in some new density-dependent declines in autumn recruitment in areas where moose have arrived more recently, such as the Northern Peninsula (McLaren et al. 2000). Although this generalized example of passive or precautionary management in licence issue was a response to presumed stable or declining moose populations and declining hunter success (Fig. 3), this management was inconsistent with the decline in autumn recruitment also reported by hunters, especially in central Newfoundland (Fig. 6). Moose management in areas without wolves and a lack of rigid control of hunting is a difficult enterprise.

We illustrate the use of hunter statistics to show a biological phenomenon. For management of moose, it is useful to have measures of abundance and recruitment that are more cheaply obtained than by aerial survey, and hunter indices have often been suggested as an approach (Courtois and Crête 1993, Timmermann 1993). Other measures of abundance and recruitment based on cohort analysis, through more detailed investigation of the age structure of the hunter-killed population, rely on estimates of both kill and hunter effort, result-

ing in high and sometimes misleading correlations between reconstructions and the hunter indices, on which they are based (Fryxell et al. 1988, Ferguson 1993). Attempts to calibrate these reconstructions with hunter indices result in circular arguments that have nonetheless been suggested for use in management (Fryxell et al. 1988, Ferguson and Messier 1996). For a discussion of biases in such methodology, see Caughley (1976). We apply hunter reports in an uncorrected fashion, taking advantage of their annual recurrence, to measure relative moose abundance over time. We calibrate these reports to real population dynamics by including hunter observations of young moose as a measure of autumn recruitment. Trends from areas with frequent misreporting by hunters (not shown), such as coastal areas 23 and 29 (Fig. 1), do not include correlations between moose observations as we have shown here, but we suggest that correlations between young and adult moose would not be directly misreported from areas that do show consistent trends. Our main conclusion is that, while some of the decrease in Newfoundland moose numbers following 1958 and 1986 is the result of management, changes to population size relative to  $K$ , as well as changes to  $K$  in some areas, resulted in density-dependent reproduction effects explaining  $\geq 10\%$  and up to 76% of the decrease (Table 2). Our conclusions are consistent with what Saether (1997) terms a “general hypothesis” regarding the relative importance of density-dependent versus density-independent factors for fluctuations in ungulate populations in the absence of predation.

In contrast to our interpretation of moose population dynamics in Newfoundland (Fig. 10), the assumption in an argument forwarded by Ferguson and Messier (1996) is that Newfoundland hunters (and their managers) have always kept moose  $< K$ . Un-

fortunately, we note that the basis of their argument, their measures of functional response in hunters, whether as effort (number of days spent hunting) or as kill rate (number of kills / licence / day), are not independent of their measure of moose density, which itself is based on hunter effort, measured by the number of days spent hunting (Ferguson 1993). Ferguson and Messier’s (1996) argument for cycling in moose based on cohort reconstruction of population size, prompted by the analysis conducted by Fryxell et al. (1988), is subject to non-independent validation of population estimates, against kills / day of hunting and moose seen / day of hunting. As we show (Fig. 4), these indices are highly correlated. Moreover, biases in behaviour of hunters affect kills / day of hunting, as discussed by Hatter (2001). The 2-year delay in management response to information obtained from hunters (see Methods) is the most obvious of the “time lags” referred to by Ferguson and Messier (1996) in their argument for delayed density dependence in Newfoundland moose hunting. We do not agree that this delay is responsible for cycling in moose. MSY densities have not been maintained in Newfoundland; moreover, moose populations reached either 1 or 2 peaks, during which reproduction was observably affected (Fig. 10). Such missed opportunities or mistakes have more to do with the past actions of moose managers or with the absence of predation and consequent delayed regulatory mechanisms in moose populations (Saether 1997) than with “socio-political changes [or] political events” (Ferguson and Messier 1996: 156).

Careful interpretation is required to understand population changes from indices of moose abundance, because these indices invariably represent a wide variety of populations with different dynamics in different habitats. In our most precise estimate of  $K$ , from combined data for all of

insular Newfoundland, we average the observations of hunters for moose in different habitats and in different stages of population increase. Managers should note that our estimate of  $K$  is a range, and  $K$  varies naturally both in time and space (Crête 1989). Moreover, our estimate, particularly for forested regions, is affected by expansion of forestry operations and thereby continuous supply of new habitat areas during the period of data collection; the same reason Pimlott (1953) accounted for the increase in moose during the early part of the 20<sup>th</sup> century. Also, extrapolation by linear regression does not explicitly take into account density-dependent effects in moose that may become apparent only at higher densities than those observed over our management period (we report a decline in density dependence at a threshold of 20 young seen / 100 adult females). Further, we have no indication from hunter returns whether both winter and summer habitat affect  $K$ , but we assume both are important.

The structure, succession and composition of natural forest communities have continued to be altered in inaccessible areas like area 26, so that their ability to produce moose has been marginalized (Fig. 6). Assuming as we have that area 26 represents a population at  $K$  throughout our study period, we show how weather, as well as other random effects, can create variation in moose seen, young seen, and hunter success between years (Figs. 4 and 6). Our hunting indices reflect only areas that are hunted, mostly space that is < 2 km from a road. Even in accessible areas, there is considerable moose range that is > 2 km from road, which forms refugia, in which habitat quality is reduced when density is >  $K$  from lack of hunting. Throughout such areas, regenerating fir (*Abies balsamea*), birch (*Betula papyrifera*, *B. cordifolia*, and *B. alleghaniensis*), and other hardwoods (e.g., *Cornus*, *Prunus*, *Sorbus*)

have been eliminated except for some heavily browsed, sparsely distributed saplings. On the south coast, moose depend on atypical foods, such as branches of blown down trees, lichens, and low shrub and herb communities (Albright and Keith 1987). Eventually, population condition is affected under these circumstances (Ferguson et al. 1989), as for Gros Morne National Park (McLaren et al. 2000). During periods of increasing population size observed in the 1980s, yearling harvest as a proportion of the moose hunt increases, and following these increase phases, jaw size declines (Mercer 1995). An example of a population introduction and subsequent crash following poor condition occurred when moose were experimentally transported to Brunette Island, between the Burin Peninsula and the south coast of Newfoundland (Mercer 1995). In contrast, as we considered for central Newfoundland, accessible areas of moose in Newfoundland support a population fluctuating around a “long-term equilibrium” density, unlike their erupting phase from 1904–58 (Fig. 10). We speculate, consistent with predictions by Saether (1997), that for moose in Newfoundland in the absence of hunting, a stable equilibrium between the population and food resources is not possible.

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