PRODUCTIVITY ESTIMATES OF MOOSE POPULATIONS:
A REVIEW AND RE-EVALUATION

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Abstract: Estimates of moose population productivity in North America are often obtained from herd composition surveys done with the aid of light aircraft. Timing of the surveys may be adjusted to estimate gross productivity through neonate:cow ratios, or net productivity expressed as ratios between cows and 6-month-old calves, short yearlings or long yearlings. All of these estimates are biased by numerous variables, some of them ecological. Neonate surveys must be timed to achieve an optimum balance between the progression of parturition and early calf mortality. Calf:cow ratios in November are affected by search effort during the surveys and by the aggregation behavior of cows without calves. Pre-parturition surveys tend to overestimate the occurrence of short yearlings due to group size differences in spring between cows with calves and those without. Long yearlings are often misidentified because of their variable antler characteristics. Productivity data are often used to monitor population welfare, but such data do not necessarily forecast population trends. The long-lived nature of moose allows previous reproductive performance to determine the trajectory of a population after productivity statistics change.

Biologists throughout North America have expended much effort to measure the production and survival of moose (*Alces alces*) calves. Numerous papers and reviews document moose productivity measures and discuss trends in such data within and between various populations (Pimlott 1959, Simkin 1965, Schladweiler and Stevens 1973, Bishop and Rausch 1974). In northern areas calf:cow ratios calculated from data gathered by aerial survey have provided managers with an important index to population welfare (Mitchell et al. 1964) and similar data have recently served to measure the relative success of predator removal experiments in Alaska (Gasaway et al. 1977). Estimates of moose herd productivity obtained by aerial survey are influenced by several ecological variables in addition to the well known biases inherent in aerial census procedures (LeResche and Rausch 1974, Caughley 1974a). This paper identifies some of these variables, discusses their effects on productivity estimates, and touches on the interpretation of productivity data in relation to management of moose populations.

The various components of moose population productivity were defined by the pioneering work of Douglas Pimlott (1959). I am concerned here not with productivity estimates derived from analysis of female reproductive tracts, but rather with indices of calf production and survival expressed as ratios between calves and cows or yearlings and cows, and calculated from data obtained during aerial herd composition surveys. These indices generally fall into four basic categories including neonate:cow ratios obtained in early summer, calf:cow ratios determined in late autumn, short yearling:cow ratios derived from spring surveys prior to parturition, and long yearling:cow ratios calculated from data gathered in late autumn. The techniques used to obtain herd composition data with the aid of light aircraft have been described by Rausch and Bratlie (1965) and reiterated by Bishop and Rausch (1974). Biases inherent in using ground observations to collect similar data are not considered in this paper.

METHODS

Data on group size and seasonal movements were obtained from aerial observations of 28 adult moose marked with radio-collars and 181 moose that wore numbered, canvas collars. Study animals were residents of the eastern quarter of the Nelchina Basin in southcentral Alaska. Characteristics of the study area and a generalized history of moose populations there were provided by Bishop and Rausch (1974) and VanBallenberghe (1977). Fall herd composition surveys in the study area were routinely done prior to 1975 by the Alaska Department of Fish and Game (Unpublished data, Alaska Department of Fish and Game, Anchorage). Over 1,000 moose were typically classified during each of these annual surveys.

Birth and death dates of calves born to marked moose were determined by direct aerial observations. Flights during May and June occurred at 1 to 3 day intervals. Overwinter mortality estimates for 6- to 11-month-old moose were derived from regular monitoring of radiomarked adults and their calves and by comparing fall and spring calf:cow ratios for neckbanded females encountered during random flights.

Fall herd composition surveys in this study were done in 1975 and 1976 as part of the annual management-oriented surveys conducted by the Department of Fish and Game throughout the Nelchina Basin. Pre-parturition surveys in 1976 and 1977 to measure the relative abundance of short yearlings were designed to minimize biases due to differential habitat selection by the various components of the population. Associates of radio-collared moose in dense spruce habitats were classified in the spring surveys as were moose randomly encountered during systematic searches.

An iterative life table projection (Conley 1978) was employed to simulate the trajectory of a population subject to variable recruitment rates. The initial population used was an L_x age distribution containing 1,000 female moose between the ages of 1.5 and 19.5 years. This L_x series and the age specific mortality rates accompanying it were provided by Peterson's (1977) life table analysis of the Isle Royale moose population. A computer program was written to annually load the zero cohort with a specified number of recruits, advance the number of moose in each subsequent cohort based on fixed age specific mortality rates, and compute the total size of the adult population.

RESULTS AND DISCUSSION

Neonate Surveys

Post-parturition surveys, if they accurately measure the relative occurrence of neonates, can serve to estimate gross productivity minus in utero mortality. In the absence of reproductive tract collections their potential value increases. They have also been used in conjunction with November surveys as a benchmark to estimate mortality during the first 6 months of life (LeResche 1968). Two factors that can interact to reduce the accuracy of neonate surveys are evaluated here. These are the progression of parturition and the extent of early mortality that, acting in combination, make the timing of neonate surveys a delicate balancing act.

By frequently relocating radio-collared females, the birth and death dates of 30 calves were closely approximated during 1975, 1976 and 1977. Parturition began in the study area about 20 May each year and extended through mid-June. Calf deaths due to a variety of causes including predation began immediately after birth. By 15 June of the average year, all calves had been born (Table 1) and the calf:cow ratio then would have been 108:100 had all calves lived. In fact, 40 percent had already died by the time the last ones had been born; a neonate survey then would have considerably underestimated true gross productivity.

Table 1. Changes in Neonate:Cow Ratios in the Nelchina Basin from Late May through Late June. Ratios Were Calculated from Pooled Data, 1975-1977, Based on Known Birth and Death Dates of 30 Calves Produced by Radiocollared Cows.

Date of Theoretical Survey	Proportion of Calves Born	Proportion of Calves Dead	Calves Per 100FF if All Calves Had Lived	Actual Calves Per 100FF Based on Observed Mortality
26 May	.33	.20	36	29
1 June	.70	.14	76	65
8 June	.93	.25	100	75
15 June	1.00	.40	108	65
22 June	1.00	.53	108	51

A 1 June survey, under the parturition and mortality schedules operating during the period of this study, would have produced the best match between observed and true neonate:cow ratios (Table 1). Knowledge of the proportion of calves typically born by 1 June each year could serve to correct the observed ratios obtained by actual surveys. The progression of parturition is likely subject to less year-to-year variation than is the timing and extent of early mortality.

Although data to evaluate them are not fully adequate, movement patterns of adult cows during late spring also affect the results of neonate surveys. Cow moose are not invariably faithful to parturition sites; one of my radiocollared cows gave birth at locations 28 miles apart during consecutive years. This, combined with the observed tendency of certain cows to return long distances to their winter range following the loss of a young calf, may further bias post-parturition surveys.

Autumn Herd Composition Surveys

November surveys yielding ratios of 6-month-old calves to adult and yearling cows provide the most common means of measuring net productivity of moose through aerial reconnaissance. Moose are normally aggregated in post-rutting groups that use open habitats during this season (Peek et al. 1974); these tendencies combined with the presence of snow provide ideal conditions for aerial surveys. Several U.S. and Canadian management agencies have an impressive volume of such data spanning many years. Alaska's annual fall surveys began in the early 1950's in several areas of the state and continue at present (Bishop and Rausch 1974). Because fall surveys seldom involve replications and because year-to-year differences in several important ecological factors may occur, statistical analyses of herd composition data are complex and the relative accuracy of net productivity estimates is difficult to evaluate.

In recent years fall calf:cow ratios in the Nelchina Basin have varied widely. The values obtained in my study area have ranged from 11 to 32 calves per 100 cows during the past 8 years with some of the variation explained by changing winter severity and varying predator densities. But these variables were not known to fluctuate much from 1974 through 1976 when 26, 13 and 20 calves per 100 cows, respectively, were calculated from the survey data. The extremely low ratio of 13:100

in 1975 is particularly incredible; the strength of this cohort measured the following fall revealed the second highest long yearling:cow ratio recorded since 1966.

This discrepancy prompted a closer look at the data and an attempt to identify factors that could have produced a lower than expected calf:cow ratio in 1975. A strong correlation was found between search effort and calf:cow ratios obtained during the fall surveys of 1971 through 1978 (Fig. 1). I then hypothesized that variable calf:cow ratios resulted from greater visibility of large groups of moose. If large groups of four or more moose have a higher probability of being seen during an aerial survey than small groups, and if cows with calves tend to aggregate in small groups, it follows that random or systematic surveys of limited search effort will tend to underestimate the occurrence of calves. Increased search effort, and hence increased probability of finding smaller groups, would result in higher observed calf:cow ratios. Furthermore, if group size varied from year to year, a given search effort would further underestimate calf occurrence during those years when large groups were more common.

Tables 2 and 3 provide data to test this hypothesis by comparing the proportion of small and large groups that radiocollared female moose were part of during autumn 1975 and 1976. Large groups containing cows without calves were common in 1975 and were seen more frequently during the composition survey that year compared to the survey of 1976 despite comparable search effort (Table 2). Cows with calves were aggregated mainly in groups of three or less (Table 3) during 1976, the only year when sample sizes were adequate for this comparison.

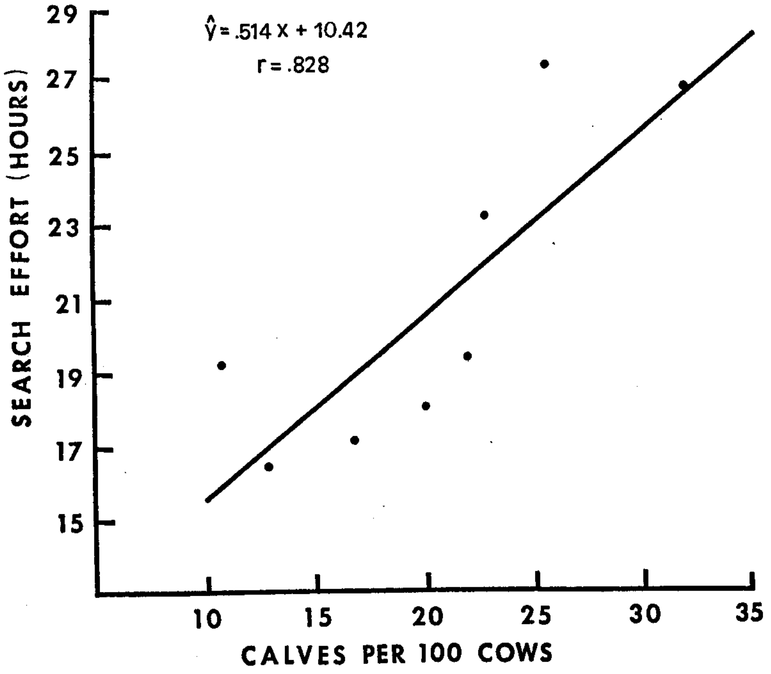

Figure 1. Relationship between search effort and calf:cow ratios of moose obtained during fall herd composition surveys in Alaska, 1971-1978.

Table 2. Aggregation Patterns of Cows Without Calves in the Nelchina Basin During Early Winter 1975 and 1976. Numbers in the Body of the Table Are the Proportion of Total Groups in Each Size Category.

	1975		1976	
Group Size	Radiocollared FF (107 Groups)	FF Seen During Herd Composition Survey (67 Groups)	Radiocollared FF (88 Groups)	FF Seen During Herd Composition Survey (174 Groups)
1-3	.71	.52	.89	.72
4+	.29	.48	.11	.28

Table 3. Aggregation Patterns of Cows With Calves in the Nelchina Basin During Early Winter 1976. Numbers in the Body of the Table Are the Proportion of Total Groups in Each Size Category.

Group Size	Radiocollared FF (47 Groups)	FF Seen During Herd Composition Survey (85 Groups)
1	0	0
2	.70	.71
3	.23	.16
4+	.07	.13

Snow depth differed markedly during these 2 years, accounted for the variation in group size and ultimately led to the tendency to underestimate the 1975 calf crop. Snow depth in fall 1975 was inadequate to trigger migration (VanBallenberghe 1977) in contrast to 1976 when radiocollared moose were known to leave survey areas by early November. Nearly 60 percent of the groups containing radiocollared females in fall 1976 consisted of only one moose indicating that post-rutting aggregations had largely dissolved that year prior to migration. This further suggests that an alternative explanation, simply that the 1975 calf crop was in fact poor, and as a result cows without calves were aggregated into large groups, is not entirely viable. Indeed, net productivity may have been lower in 1975 than in 1976 but I regard the data as inadequate to measure the relative degree of difference. Conservative estimates of net productivity were likely obtained during both years; search effort during the two surveys was in the lower range of values shown in Figure 1.

These data emphasize the need to determine an optimum search effort for each survey area and support the concept of standardizing search effort to minimize year-to-year variation in the survey data. Replicate surveys with populations of different known aggregation patterns would result in a better understanding of how variation in group size affects productivity estimates.

Short Yearling Surveys

The results of two mid-May surveys to determine short yearling:cow ratios in the study area are contained in Table 4. Observed ratios of 21 and 25 yearlings per 100 cows in 1975 and 1976, respectively, were much higher than calf:cow ratios observed in these same populations 6 months earlier.

Estimates of overwinter mortality based on the fate of calves with radiocollared females and on random sightings of up to 71 neckbanded cows per spring were applied to the fall ratios to calculate expected yearling:cow ratios. These were only 48 and 64 percent, respectively, of the observed ratios. The accuracy of the expected spring ratios depends on the accuracy of both the fall ratios and the overwinter mortality estimates, as well as the extent of mortality of adult cows between fall and spring. It is probable that the observed spring ratios overestimated the true occurrence of yearlings despite fall calf:cow ratios that may have been conservative. That these results are not unique to the study area is corroborated by the results of a March 1974 survey over a broad area of the Nelchina Basin and the spring 1975 data provided by Gasaway et al. (1977) for Game Management Unit 20A in interior Alaska. Both indicated net gains, rather than losses, of calves over winter.

Table 4. Observed and Calculated Yearling:Cow Ratios Obtained During Mid-May Surveys in the Nelchina Basin, 1976 and 1977. Calculated Ratios Resulted From Reducing the Calf:Cow Ratios Obtained Six Months Earlier to Reflect Overwinter Mortality.

Year	Date of Survey	Total Sample	Short Yearlings Per 100FF	Calves Per 100FF Previous Fall	Estimated Winter Mortality of Calves	Calculated Short Yearling Per 100FF Ratio
1976	11-14 May	219	21	13	21%	10
1977	16-18 May	258	25	20	22%	16

The hypothesis that spring herd composition surveys, like their early winter counterparts, are biased by the aggregation behavior of cows without calves was tested by comparing group size distributions for radiocollared females from mid-March to mid-May 1977. The strong tendency of radiocollared cows without calves to remain solitary during spring was indicated by the finding that single individuals comprised 71 percent of 124 observed groups containing instrumented animals. Although cows with calves were seldom with other moose, milk groups of two or three individuals were among the largest groups present during spring. If the random search pattern of spring surveys tends to overlook single moose, as I believe it does, this would explain the tendency of these surveys to overestimate the true occurrence of yearlings.

Long Yearling Surveys

None of the productivity measures involving neonates, 6-month-old calves, or short yearlings are as useful as those based on the occurrence of long yearlings, but all are far easier to accurately estimate by aerial survey. Numerous problems accompany accurate measurement of net productivity based on ratios of 18-month-old bulls to adult and yearling cows; some of these are related to accurate identification of yearlings, others stem from the variable nature of yearling moose behavior. The yearling:cow ratios calculated from surveys plagued by these problems are often poor approximations of net productivity. Efforts to improve accuracy may be unrewarding.

In hunted populations, a largely unknown and often variable fraction of the yearling males are removed prior to the fall surveys. For most populations in Alaska the proportion of yearlings shot is not measurable despite reasonably accurate harvest data and the use of check stations in some areas. The known vulnerability of yearlings to hunting, hunting of bulls only, a lack of older bulls and a harvest comprised of 30 percent yearlings (Bishop and Rausch 1974) suggest that a large proportion of yearling bulls are shot each year in accessible portions of the Nelchina Basin. Attempts to measure the strength of the yearling cohort by assuming an equal sex ratio among yearlings and doubling the number of yearling bulls seen during November surveys are therefore always conservative.

An additional source of error may result from the assumption that yearling sex ratios are equal. Moose calves, like those of other cervids, may be subject to differential mortality by sex, and an unequal sex ratio at birth may result from poor maternal nutrition or an age distribution skewed toward older females.

The ability to accurately identify yearlings based on antler characteristics (Peterson 1955) or body size (Haber 1977) is critical to the accuracy of long yearling:cow ratios. Yearling bulls display a wide range of antler types; these may vary with time in the same population. I have examined yearling bulls with velvet-free antlers less than 2 inches long, while others had palmated antlers with spreads exceeding 30 inches. In the Nelchina Basin, where moose numbers are not presently food limited, less than half of the bulls classified as yearlings in November have spikes or small, forked antlers. Furthermore, there is no general agreement among those who conduct the surveys as to what constitutes the upper size limit of yearling-type antlers.

The behavior of yearling moose is poorly understood; their social interactions and dispersal patterns have received brief attention in the literature but no published data are extensive. Yearlings are the social class most likely to disperse, but I have known some that did not. The stimulus to disperse may result from social pressure, food supply, or genetic factors, any one of which may be affected by several other factors including intense hunting pressure. If the necessary stimuli are present in a moose population and if substantial numbers of yearlings are gained or lost, the results should be evident, although probably not explainable, in the data from fall surveys. Perhaps these movements account for the occasionally observed, implausible long yearling:cow ratios that are observed during fall surveys from time to time.

Interpretation of Productivity Data

The various productivity statistics outlined above can be used to describe the rate that young moose enter a population. This rate and the factors that affect it are central to an understanding of the population dynamics of moose. But productivity indices used as the primary indicator of population welfare cannot stand alone in the absence of data on mortality and population trend (Caughley 1974b). Because moose populations have in excess of 20 cohorts, the effects of past trends in productivity and the age distributions that result determine the trajectory of a moose population long after changes in productivity trends occur.

The effects of past reproductive successes or failures on moose population performance were simulated with an iterative model based on the hypothetical age distribution of moose on Isle Royale (see Methods). Thirty-four calves per 100 cows in November were required to keep the initial population of 1,000 moose aged 1.5 to 19.5 years stationary with the age specific mortality schedule calculated from Peterson's (1977) life table. Five simulated years of 13 calves per 100 females produced the age distribution shown for the declining population in Table 5; an increasing population was similarly produced with 48 calves per 100 cows. These populations continued on their established trajectories, albeit at altered rates of increase, for 9 years after fall calf:cow ratios were restored to the approximate level required for stability. A biologist faced with managing these two populations in the absence of past data on productivity would experience the paradox of watching one population decline while the other increased when both had currently comparable productivity statistics. This emphasizes the value of continued annual surveys spanning many years.

Table 5. Simulated Changes in Age Distribution and Total Numbers for Moose Populations Subject to Different Recruitment Rates. Data Were Generated With an Iterative Life Table Projection Based on Peterson's (1977) q_x and L_x Schedules for Isle Royale Moose.

Cohort Group	Proportion of Population in Each Cohort Group		
	Stationary Population (34 Calves per 100FF)	Declining Population (13 Calves per 100FF for 5 years)	Increasing Population (48 Calves per 100FF for 5 years)
2.5-5.5	.488	.252	.593
6.5-11.5	.446	.653	.355
12.5-19.5	.066	.095	.052
Total Population Year 5	1000	637	1304
Total Population Year 14 1/	1000	524	1402
Calf:Cow Ratio Years 6 through 14	34	38	32

1/Recruitment restored to "normal" level in year 6.

The effect that a given level of productivity has on the rate of increase of a moose population obviously depends on the extent of mortality experienced by the population (Caughley 1974c). Mortality rates of adult moose have seldom been accurately measured. This deficiency, coupled with an inability to measure rate of increase and undue reliance on productivity data, has had serious management consequences for moose in several areas of North America.

Interpretation of productivity information may also be clouded by failure to refine survey data. Robinson (1962) recognized that fall calf:cow ratios were a crude expression of productivity when variable numbers of yearling cows and non-breeding 2-year-olds comprised the cow base used for ratio calculations. In increasing populations with large yearling cohorts and few yearlings that breed, ratios of calves to adult and yearling cows result in productivity indices that are deceptively low. The more restrictive ratio of calves to adult females, which takes into account the proportion of juveniles in the population, results in a productivity index of greater utility.

Finally, Pimlott's (1959) advocacy of percentage expressions of productivity, and the tendency of subsequent workers to follow his example, have produced a confusing element in the moose literature. It is occasionally convenient to express productivity as the percent of calves or yearlings in the herd, but comparisons between herds or within the same herd over time are inappropriate if they fail to recognize changes in other herd components that affect percentages. For example, 6-month-old calves comprised 19 percent of the moose population in my study area in 1959 and 18 percent in 1974. However, ratios of 44 and 27 calves per 100 cows, respectively, were recorded during these 2 years. A much lower proportion of bulls and fewer yearlings occurred in the population in 1974, but percent calves remained constant despite a significant decline in productivity.

LITERATURE CITED

Bishop, R. H. and R. A. Rausch. 1974. Moose population fluctuations in Alaska, 1950-1972. Naturaliste can. 101:559-593.

Caughley, G. 1974a. Bias in aerial survey. J. Wildl. Manage. 38(4):921-933.

_________. 1974b. Interpretation of age ratios. J. Wildl. Manage. 38(3):557-562.

_________. 1974c. Productivity, offtake and rate of increase. J. Wildl. Manage. 38(3):566-567.

Conley, W. 1978. Population modeling. Pages 305-320 *In* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America. Stackpole Books. 494pp.

Gasaway, W. C., D. Haggstrom and O. E. Burris. 1977. Preliminary observations on the timing and causes of calf mortality in an interior Alaskan moose population. Proc. N. Am. Moose Conf. and Workshop. 13:54-70.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Unpubl. Ph.D. Thesis, Univ. British Columbia, Vancouver. 786pp.

LeResche, R. E. 1968. Spring-fall calf mortality in an Alaska moose population. J. Wildl. Manage. 32(4):953-956.

_________ and R. A. Rausch. 1974. Accuracy and precision of aerial moose censusing. J. Wildl. Manage. 38(2):175-182.

Mitchell, H., R. Ritcey, K. Mundy and D. Robinson. 1964. Variations in moose populations of British Columbia. Proc. Annu. Conf. West. Assoc. State Fish Game Comm. 44:133-141.

Peek, J. M., R. E. LeResche and D. R. Stevens. 1974. Dynamics of moose aggregations in Alaska, Minnesota and Montana. J. Mammal. 55(1):126-137.

Peterson, R. L. 1955. North American moose. Univ. Toronto Press, Toronto, Ontario. 280pp.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. Natl. Park Serv. Sci. Monogr. Ser. 11. 210pp.

Pimlott, D. H. 1959. Reproduction and productivity of Newfoundland moose. J. Wildl. Manage. 23(4):381-401.

Rausch, R. A. and A. Bratlie. 1965. Annual assessment of moose-calf production and mortality in southcentral Alaska. Proc. Annu. Conf. West. Assoc. State Fish Game Comm. 45:140-146.

Robinson, D. 1962. Management of moose by population ratios. Proc. Annu. Conf. West. Assoc. State Fish Game Comm. 42:81-89.

Schladweiler, P. and D. R. Stevens. 1973. Reproduction of Shiras moose in Montana. J. Wildl. Manage. 37(4):535-544.

Simkin, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 29(4):740-750.

VanBallenberghe, V. 1977. Migratory behavior of moose in southcentral Alaska. Proc. Int. Congr. Game Biol. 13:103-109.