COMPARISON OF PELLET COUNTS AND AERIAL COUNTS FOR ESTIMATING DENSITY OF MOOSE AT ISLE ROYALE: A PROGRESS REPORT

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ABSTRACT: The insular population of moose at Isle Royale offers a unique opportunity to compare the effectiveness of pellet counts vs. aerial counts for estimating moose numbers. In mid-winter, moose were counted every year from the air within small sample plots distributed according to an optimum-allocation stratification. For 8 of the winters during 1980-1993, pellet groups were counted in early spring on clusters of sample plots laid out as a relatively uniform grid. A correlation between estimates from aerial and pellet surveys for all separately analyzed sectors of the island with minimal data showed a significant but very low coefficient of determination, r^2, of 0.24. This increased to 0.44 when one highly influential, aerial-stratum outlier was removed. Based on 6 of the winters for which pellet data were adequate, there was relatively close parallel between the methods of an increasing trend, culminating in the highest density of moose on the island since systematic studies began in 1959. No significant differences were found in regression-line slopes between the two methods when regressed on year, for either the whole island or the East and West sectors analyzed separately. For unexplained reasons, pellet estimates for the East sector were consistently lower than aerial estimates, while for the West they were consistently higher. The defecation rate employed in converting pellet groups to moose density, 20.9 groups/day, had been derived from aerial results in an earlier study; findings in this study do not suggest that a different rate would give a better match. Use of aerial results to calibrate the pellet results renders the two sets of results interdependent. At the same time it is argued that the best means for estimating the defecation rate in a population is from an accurate aerial census. It is concluded that the pellet method provided a reliability similar to that from aerial counts for tracking trends in the Isle Royale moose. Utility of the two methods is compared, and benefits from employing the two in parallel are suggested. Need for improvements in the sampling design and analytical procedures for both methods is indicated.

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It is commonly assumed that aerial counting is now the best means available for estimating moose populations. Pellet counts, on the other hand, are widely judged as not dependable for this purpose (e.g., Franzmann and Schwartz 1982). The relative utility of these two techniques can be examined from data collected at Isle Royale over many years, where not only pellets, but also moose observed from the air, have been estimated through counts on sample plots. Because this is an insular setting, where movement in or out essentially never occurs, the two methods have been directed at exactly the same group of animals. In contrast, in mainland settings, seasonal movements usually lead to uncertainty about whether the set of animals defined for mid-winter aerial survey is the same as that that accounted for all the pellets being counted in spring.

Two main issues are considered in this preliminary report: 1) how do trend estimates from pellet and aerial samplings compare for the same population over a series of years, and 2) are reliable estimates of moose density ever possible from pellet counts in view of the great uncertainty about defecation rates? Because all density estimates from pellet counts in this report and a previous one (Jordan and Wolfe 1980) were based on a defecation rate derived in the earlier study from aerial results, the moose-density estimates from pellets are not truly independent. Only the trend patterns are. The use of aerial results for calibrating pellet data is discussed.

BACKGROUND

Numbers of moose on Isle Royale, Michigan, a national park in Lake Superior, have been estimated for over 60 yrs (Murie 1934, Mech 1966, Peterson 1977, Allen 1979, Jordan and Wolfe 1980). Mech (1966) reviewed earlier aerial surveys, and reported his own island-wide counts in 1960 and 1961. Jordan and Wolfe (1980) developed a stratified plot sampling system for aerial counting in 1965. With modifications, this approach has been used every year since (Peterson 1977, Peterson unpubl. ann. rpts., Peterson and Page 1993). Pellet counts were made in the 1950's and 1960's on non-fixed plots by Krefting (1974). Starting in 1964, clusters of fixed plots have been gradually established over the island (Jordan and Wolfe 1980). Until 1980, distribution of these clusters was not in a systematic design, but since then an island-wide grid has been used. Pellet-count results for 1964-1979 were reported by Jordan and Wolfe (1980), and results since then are given here.

STUDY AREA

Ecological descriptions of Isle Royale relative to its moose population are given in Murie (1934), Mech (1966), Krefting (1974), Peterson (1976), and Allen (1979). The 544-km^2, 73-km-long archipelago lies in northwestern Lake Superior. It is vegetated with a relatively fine-grained mosaic of early-to-late-succession boreal, northern-hardwood, and lowland-conifer forests, interspersed with open-growth ridge tops, savannas, and herbaceous and shrubby wetlands. The last widespread disturbance was a fire in 1936 that covered about one-fifth of the island (approximately the "1936 Burn" Fig. 1).

Topography is varied, with much of the island in small but sharp ridges that mostly parallel the island's long axis; between these lie frequent wetlands and beaver impoundments. Climate is north-temperate. High and low temperatures are less extreme than on the adjacent mainland due to moderation by Lake Superior in both summer and winter.

Moose apparently dispersed out to Isle

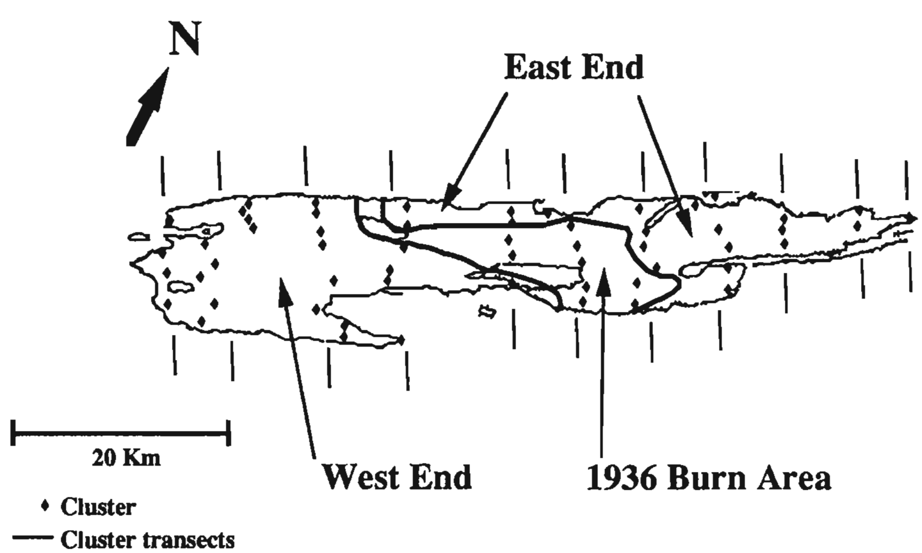

Fig. 1. The pellet-count clusters of plots, spaced along 11 cross-island transects, at Isle Royale, and the sectors used in calculating moose numbers from aerial counts.

Royale around 1900. They rapidly reached unusually high levels, estimated by Murie (1934) at 3,000 to 5,000 in the 1920's. While never that high since, moose density has averaged far higher than elsewhere in the Lake Superior region. The herd has never been legally hunted. In the late 1940s wolves, absent in historic times, appeared on the island, and have since exerted a major impact on moose, which comprise their only large-mammal prey on the island (Mech 1966, Peterson 1977). In general, wolves have not suppressed moose below the capacity of the forage to support them, and the forests are strongly shaped by moose browsing. Rather, predation has prevented moose from suppressing woody growth as severely as they did before the wolves arrived (Murie 1934), thus preventing catastrophic die-offs, as occurred in the 1930's. The wolf population has been at an unusually low level during the last 6 years of this study. The cause, while still unknown, does not appear related to a shortage of prey (Peterson unpubl. ann. repts.).

METHODS

Basic procedures for both pellet and aerial counts were described by Jordan and Wolfe (1980), and are briefly re-described here, including recent modifications. Each winter (or dormant season) is referred to by the calendar year that begins during that season.

Aerial Counts

Surveys were flown at Isle Royale with a ski-equipped Super Cub from mid or late January to early March, the period when ice on inland lakes and harbors is suitable for such aircraft. Moose were counted using an intensive, circling pattern within relatively small plots of 0.6-1.7 km^2. Plot counts were adjusted for loss of sightability relative to extent of conifer overstory (Peterson and Page 1993). Plot boundaries were defined by topographic and vegetational features that were easily and precisely indentifiable, both from the air and on maps or aerial photos, hence plots were not of equal size.

Sample design was a stratified, optimum-allocation scheme. At the start of each winter, 3 or 4 moose-density strata were mapped from an aerial survey of relative snow-track density, and each stratum was assigned an approximate level of moose density. A proportional allocation of total plots among the strata was calculated, based on an estimated density variance and the area of each stratum. From the pool of allocated plots, the sequence in which they were counted was scheduled so as to maintain a running balance among strata and among sectors of the island. This accommodated for the operational condition that, in a given winter, neither the total number of plots counted nor the length of the counting period could be reliably predicted.

Estimated moose density for a stratum was the average of densities from plots counted within that stratum. This was converted to total moose based on the area of the stratum. During the early years of this study, strata and density calculations extended island wide, so a population estimate was derived by totaling numbers across all strata. More recently, due to apparent inconsistencies among parts of the island, subtotals were first calculated for each of three sectors— West, 1936 Burn, and East (Fig. 1)— within which stratified sampling had been used. Because earlier data have now been re-analyzed based on the separate sectors, island-wide figures in this report differ in some instances from those reported earlier by Peterson (unpubl. ann. rpts.) and quoted by Timmermann and Whitlaw (1992).

Pellet Counts

Moose density during the dormant season was estimated from spring counts of pellet groups on 4.57-m radius, circular plots of 65.74 m^2. The circle is believed to be the optimal plot shape for pellet counting: a) being defined by a single point, questions of near-boundary groups are quickly and precisely resolved by stretching a tape from that point; b) it is easy to do a systematic search by continuous reference to the single center marker; and c) having the minimum of edge per unit area, borderline cases are minimized. Plot size, established at the onset of sampling in 1964 (Jordan and Wolfe 1980), has for the most part served the untested assumption of being a) small enough to minimize missing pellets and to preclude excessive time for doing one plot where pellets are abundant, but b) large enough to avoid numerous null readings. The latter became a problem during years of relatively low moose numbers in some parts of the island. When, occasionally some portion of a plot was snow-covered or water-washed, that portion was deducted from the total area used in calculating pellet density. Most plots (fixed) were marked with a metal stake for relocation. For those not yet fixed, the locale of sampling was still in the same vicinity each year, and data from these plots were analyzed the same as for all other plots.

Counting was started as soon after snow melt as possible and completed before ground vegetation was dense enough to mask easy visibility of pellets, and before standing water became too cloudy for seeing pellets at <0.5m depth. We obliterated pellets on fixed plots to preclude recounting them the following year. Otherwise, non-current, winter pellets were distinguished by presence of moss, insect holes, decomposition, or by being leaf-covered. The transitional feces of spring and fall, ("pellet-pies") were not included in the count on the assumption that feces dropped during the designated accumulation period, 20 September to 25 May, are primarily in pellet form. This is based on observation notes. Timing of the fall and spring transitions, however, varies by 1-3 weeks among years, hence creates a source of error in the data analysis. Plots were arranged in clusters, a cluster being 10 or more plots, 61-m apart along a line. In the earlier study, some 40 clusters were distributed in an irregular pattern that was neither a random nor uniform design. To adjust for the lack of representativeness in that study, plot data were stratified in several schemes, the preferred one being based on strata drawn up for the winter aerial counts (Jordan and Wolfe 1980).

For this study, a uniform grid was created: 11 transects were spaced somewhat evenly along and perpendicular to the island's long axis. Clusters were spaced an average of 1.5km (sd=0.30) apart along the transects (Fig. 1). Each cluster represented an average of 9.7 km^2 land area. The grid, however, was not rigidly uniform. Some 27 fixed-plot clusters established in the earlier study were incorporated into the new scheme in order to continue long-term data records. This accounts for the irregularities in the grid pattern (Fig. 1).

For converting pellet density to moose days, we used a defecation rate of 20.9 groups/day. This had been derived in the earlier study (Jordan and Wolfe 1980) by a) selecting the population estimate from the winter in which aerial results were believed to be most accurate among the seven winters of counting, b) multiplying that total by the estimated days of pellet accumulation, (247), to calculate total moose days that winter (1969), and c) dividing the total moose-days into the total of pellet groups estimated from the pellet survey that year. The assumption that one season's aerial count was better than the others remains untested— as do most conclusions about aerial counts.

Use of the 20.9/day rate from the previous study gave density estimates that were similar enough to the aerial estimates that there was no basis for changing this rate. Furthermore, if we assumed that the aerial results in both studies were completely reliable, then this is the best rate available. Thus, while the rate is not independently derived, as discussed below, it does have a real basis.

The sampling unit for computing local density of pellet groups was the plot cluster; that density was the sum of pellet-groups on all plots divided by the sum of plot areas. Variances were calculated among clusters, but not among plots. Since plots within clusters were spatially associated, among-plot variance is not relevant to results reported here.

The 20.9/day rate was then used to calculate moose-days/km^2, which in turn was transformed to moose density, based on the assumed pellet-accumulation period of 20 Sept to the date of counting or to 25 May (247 days), whichever was earlier.

"Moose days" from pellet density represents the sum of moose presence over the pellet-accumulation period. Hence a moose-density estimate calculated from moose days represents some sort of average over the deposition period. During that period, the population would be declining from mortality with no recruitment (pellets dropped by new-borns in May would not be included). As in Jordan and Wolfe (1980), a straight-line decline of 14.4% was assumed. Accordingly, the population represented by pellets is equivalent to the number present at the period's midpoint, 20 January. For direct comparison to the time of aerial-counts, centered some 4 wks later, pellet results were reduced by 1.8% in accordance with the assumed mortality rate.

For the whole island and for each aerial-count sector, moose-density estimates were separately derived by averaging densities from all clusters lying within the area of interest. Pellet counts were not made every year, and in no one year were all 56 clusters counted. Minimum number of clusters used for estimating density within one of the three sectors was 9, and for the entire island was 26, with a reasonably representative distribution (Table 1). Calculation of island density for two of the winters included adding in a few clusters that were not counted that year but were counted either the year before or the year after. In these adjacent years the sample had been inadequate for a separate estimate. In one case, the augmentation from an adjacent year comprised 4 (9%) of the clusters used, and in the other it was 5 (20%). In one of these cases— augmenting the 1993 island estimate with clusters from 1992, while there had not been enough 1992 clusters counted to make a whole-island estimate, there had been enough for estimating the West End (Table 1).

Comparisons Between Methods

Results in this study are expressed as moose density rather than total number. However, the density figures from pellet counts do not have the same independent standing as those from aerial counts, since the defecation rate was derived from aerial results, albeit in an earlier study and with no certainty about reliability of the aerial results. The density estimates from pellet counts are used in this report primarily as a means for comparing trends between the two methods, - a procedure that does not require certainty about the defecation rate. A discrepancy in the land area to which each of the methods applied was discovered too late for recalculating all the estimates. Pellet estimates were designed to reflect the entire archipelago, while the aerial data reflect only the main island, omitting some 25 km^2 of off-shore islands, 5% of the total land area. The effect of this discrepancy appears minor, particularly in terms of comparing trends.

Although aerial counts were made every year, comparisons were made only for years in which pellet data were adequate. For direct comparison, each pellet-plot cluster was assigned to its corresponding aerial-count stratum or sector. Correlation analyses were used for comparing the two methods, and regressions were used for analyzing trend relationships in both sets. Pairs of slopes were tested for similarity by the z-test. None of the tests incorporated variances for each year's density estimates, but 95% confidence intervals

Table 1. Moose pellet-plot clusters counted on Isle Royale. For the whole-island estimates for 1989 and 1993, a few clusters were added from an adjacent year in which the sample was inadequate.

Year (Winter)	Total Plots Counted	Used for Estimates		
		Whole Island	West End	East End
1980	50	50	23	18
1981	54	54	23	21
1983	49	49	21	19
1987	47	47	25	13
1989	40	44	20	16
1990	7	0	0	0
1992	12	0	11	0
1993	26	31	14	9

are shown graphically, based on variation among clusters. Since trends were based on an intermittent, not continuous, time series, the curves in Figs. 2-4 should be interpreted accordingly.

RESULTS

Between 1980 and 1993 pellet data from 6 winters were adequate for estimating moose density for the whole island and for the East End sector, and from 7 winters for estimating the West End sector (Table 1). As a first test of how well the estimates from the two methods matched, an all-inclusive correlation was run using each annual aerial estimate from one stratum, sector, or the whole island, for which adequate pellet counts existed. While the least-squares slope was significantly different from zero ($P = 0.0011$), the coefficient of determination, r^2 was only 0.24, indicating that most of the variation remained unexplained. When one very influential outlier, a pairing in 1980 of 14.7 (aerial) and 2.7 (pellet) moose/km^2 from one aerial stratum in the East End sector, was removed, as is appropriate (Weisberg 1985), the r^2 rose to 0.44. Such an outlier is not surprising. The area involved was 2-3% of the island area and was sampled lightly by both aerial and pellet plots. This outlier does not appear in the figures below, because they represent larger units -- sectors or the whole island. The outlier did not appear to influence measurably the pellet-aerial match either for the sector or the whole island that year (Figs. 2 and 4).

Trends in island-wide moose density, based on 6 years of pellet data within the 14-year span, show a reasonably close parallel between the two methods (Fig. 2). The largest discrepancy was in 1983 when pellet results were 43% lower than aerial, and the next was in 1993 when pellet results were 14% higher. The 95% confidence intervals (Fig. 2) suggest that only the 1983 difference was significant. Both of the island-wide estimates for total moose in 1993 -- 1900 from aerial and 2350 from pellet counts -- were higher than any other estimates since systematic surveys were initiated in 1959. Density estimates from aerial counts shown here differ from those shown in Timmermann and Whitlaw (1992) for 1983 and 1987 for reasons explained in the "Methods" section.

Regression analysis of density estimates against year indicate that the least-squares lines for both methods were significantly dif-

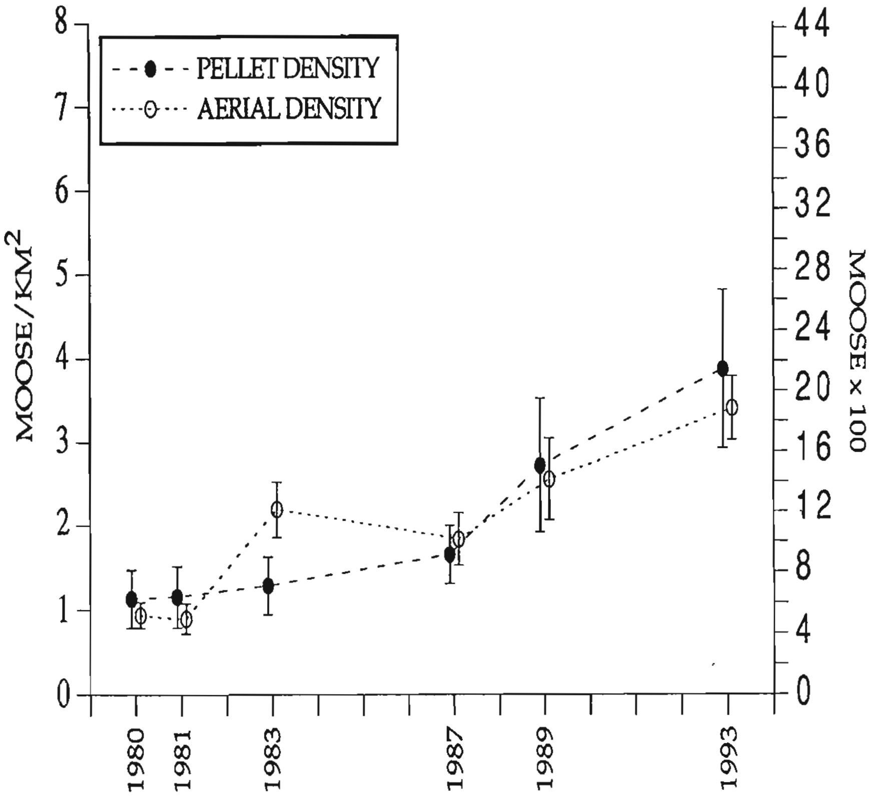

Fig. 2. Estimates and 95% confidence intervals for moose density of Isle Royale based on independent pellet and aerial sampling approaches. The connecting lines do not reflect actual year-to-year changes, because points for pellet estimates from many years are missing.

ferent from a slope of zero (Table 2). On the other hand, if the estimates from every year's of aerial counts, 1980 through 1993, are similarly analyzed, i.e. including the years in which pellets were not sampled, the coefficient of determination drops from 0.85 to 0.62 due to greater inter-year variation than appears in Figure 2. Thus the relative smoothness of the aerial curve (Fig. 2) is partly an artifact of the set of years in which pellets were counted. Whether pellet results from all years would show similar fluctuations cannot, of course, be known.

A z-test for similarity between the two slopes suggests that the null hypothesis of no difference cannot be rejected (Table 2). Had the statistical analysis incorporated variances, i.e. a weighted regression, there would be even less chance of detecting a difference between the two slopes, as can be judged (Fig. 2) from the overlap, year-by-year, in the confidence bars, except for 1983.

To test for similarity of results within two of the three aerial-count sectors, the same procedures were used as above (Figs. 3 and 4, Table 2). No results are shown for the 1936 Burn sector due to inadequate pellet data. Again, there is no basis for suspecting significant differences within either pair of slopes. It should be noted, however, that estimates of density from pellet counts were consistently higher than from aerial in the West End sector and consistently lower in the East End sector.

DISCUSSION

In an analysis of the comparative validity of pellet and aerial approaches to moose census, an island setting provides the strong ad-

Table 2. Coefficients of determination, r^2, and significance values for regressions of density estimates on years for matching pairs from pellet and from aerial surveys. To test for similarity of least-squares lines between members of each pair, Z-tests were run; the p(z) is that p-value. The time sequence was not continuous because pellets were not surveyed every year.

Survey Method	Whole Island			West End			East End		
	r^2	p=	p(z)	r^2	p=	p(z)	r^2	p=	p(z)
Pellets	0.89	0.004	>0.99	0.81	0.005	0.92	0.86	0.007	0.92
Aerial	0.85	0.009		0.65	0.029		0.91	0.003	

vantage that both surveys address exactly the same set of animals, unlike the typical case in mainland settings. Thus, while within-season movements at Isle Royale can potentially account for real differences between the two methods for a given sector, this problem does not exist for the archipelago as a whole. Disparities in results can then be attributed to one or more of the following: a) improper and/or inadequate sampling in one or both of the techniques; b) uncertainty over what portion of moose are not being seen from the air; and c) use of a defecation rate that is erroneous for that population over the dormant season. Validity of aerial estimates is not treated here, but the observability aspect was addressed recently by Peterson and Page (1993). The fact that the defecation rate used here comes from an earlier linkage to aerial results negates complete independence between these two methods. However, as pointed out below, we doubt that there is any better way to determine this rate for a non-captive population in the field.

The catch-all correlation involving all possible pairings of estimates where pellet data were adequate from each stratum, sector, or whole- island estimate, by year, showed a low degree of relatedness, even when one highly influential outlier was removed. We suspect that one source of error was that many of the points represented relatively small areas, where low numbers of aerial and pellet plots lead to high variability. Also, the smaller the area, the more likely that within-season movements of moose were underlying the non-matching data.

Inconsistencies in results from the two methods between the East and the West end sectors might suggest there was a mid-winter (aerial-count time) build-up in the East End and a corresponding out-movement from the West End. However, during 3 decades of winter aerial observations, albeit without extensive telemetry studies, there had been no indication that such movements occur. At the same time, uncertainties about the adequacy of the two sampling designs indicate a need for re-examining both. For example, confidence intervals were generally greater for pellet estimates than for aerial estimates (Figs. 2-4). This might be expected since, within a highly variable moose-density landscape, aerial sampling was analyzed according to a stratified design, while the pellet analysis was based on a single, island-wide grid. On the other hand, while confidence intervals around pellet estimates for the West End sector were also generally higher, for the East End sector they were roughly the same. Finally, it appears that the closeness of agreement in levels of density for the whole island may in part be due to an averaging of differences between the two ends; however, this is not attributed to an actual seasonal shift in moose.

Possible shortcomings of the pellet method due human error in sample counting, as suggested by Neff (1968), is far more applicable to deer than to moose in northern settings. Moose pellets, some 3-6 x larger in diameter, should be far easier to see than deer pellets. Also, counts made soon after snow melt-off are subject to little error due to decomposition or to confusion with those of previous winters; and in this study no previous pellets were left on fixed plots that had been counted the previous spring. Having done both aerial and pellet counting, one of us (PAJ) believes that the frequency of not seeing moose in a mixed conifer-hardwood forest from the air would be considerably greater than not seeing pellets on our plots.

Concerning the adequacy of the pellet sampling design, it remains to be determined whether the set of 56 clusters will provide a representative coverage of Isle Royale. For the two regions analyzed, the one with larger confidence intervals had estimates based on smaller samples, but an overall comparison between sample size and interval size shows no clear relationship.

The conversion from pellets to moose days is subject to uncertainty: as reviewed by Timmermann (1974), published estimates of the winter defecation rate of moose vary by 2-3 fold. The approach of Jordan and Wolfe

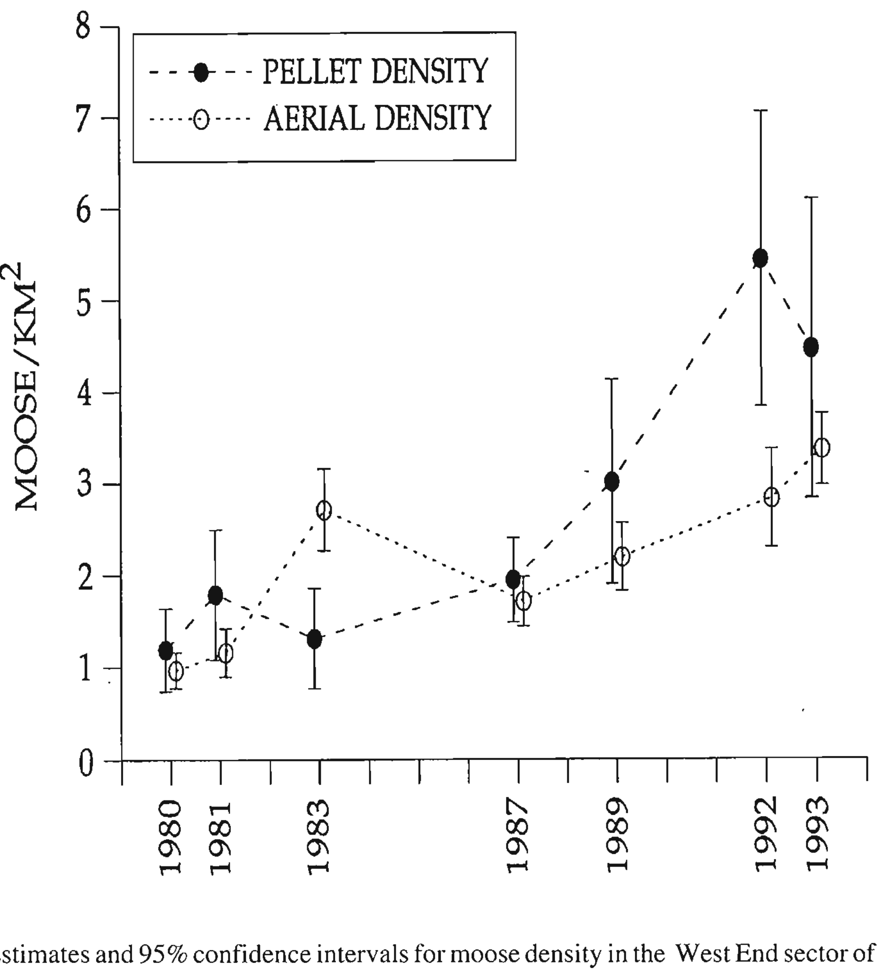

Fig. 3. Estimates and 95% confidence intervals for moose density in the West End sector of Isle Royale based on independent pellet and aerial sampling approaches. The connecting lines do not reflect actual year-to- year changes, because points for pellet estimates from many years are missing.

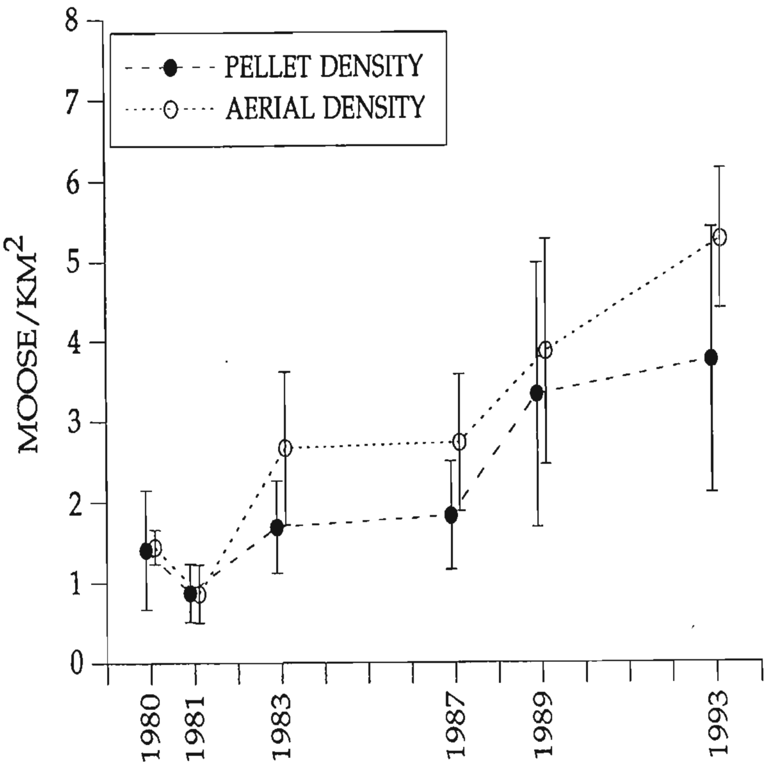

Fig. 4. Estimates and 95% confidence intervals for moose density in the East End sector of Isle Royale based on independent pellet and aerial sampling approaches. The connecting lines do not reflect actual year-to-year changes, because points for pellet estimates from many years are missing.

(1980) and in this study for defining a defecation rate differs from most others'. Instead of assuming, one must know the daily fecal output by age, sex, time of winter, forage quality, and locale. We believe that only one rate is needed-- that which reflects a population's collective production over the entire deposition season. This rate is the only one that relates directly to the data - a season-long accumulation. It is best determined by linking total deposition with an independent measure of the population, e.g., from aerial counts. Furthermore, as far as practical, each local population should be calibrated separately.

While the present study has possible short-comings in the sampling design of both methods, we argue that the population-calibration procedure is the correct approach for using pellet counts. Theoretically, if all other aspects are correct, the pellet method should be no less reliable than those aerial estimates upon which it is calibrated. And thus it even has the potential of being more dependable when conditions arise that preclude reliable aerial surveys.

When it is not feasible to test the reliability of a given method against a verified standard, the next best approach is to compare results from two or more completely independent techniques, even when each is of unknown reliability. If results do not agree, then at least one of the methods is suspect; but if they do agree, there is a reasonable chance that both are reliable. While the interdependent procedure for deriving the defecation rate violates complete independence between aerial and pellet results, this applies only for density levels, and not for comparing trends. Consequently, the dual finding that moose have increased by some 3.4 fold over the 14 years appears well verified. This conclusion is qualitatively supported by other data, such as browsing intensity, as measured on the pellet plots (Jordan unpubl.), and it parallels Peterson's conclusion (unpubl. data) that low wolf numbers during 1987-93 have underlain a major increase in moose.

Pellet counting at Isle Royale is probably less efficient than in many other moose ranges where reasonable road access exists, because the island is managed as a wilderness. On the other hand Isle Royale does have a good trail network for foot access, and there are extensive inland lakes well accessed by portage trails, along with the island's shore, all of which provide good canoe access.

Where moose density is much lower than at Isle Royale, sampling approaches would have to be adjusted, just as aerial counting. An increased plot size might be appropriate. However, for circular plots, particularly in terrain and vegetation as rough as in many Isle Royale plots, searching could become too time-consuming, and counting errors would increase sharply. Long, narrow plots (strip) might be preferable. These can be established far more easily and accurately today with the new sonar range-finders than with just tape and compass as in the past. As with designing aerial surveys, a flexible stratification scheme may be the key to effectiveness.

The following are cost estimates based on visiting all 56 clusters at Isle Royale in spring. Besides counting moose pellets, we also counted snowshoe-hare pellets and browse twigs within a small subplot, increasing time at each plot some 2-3 fold. However, this probably adds less than 15% to the total time, because the biggest time cost is for travel among clusters and between plots. The survey can be done in 25-30 days by a party of two, traveling by canoe and on foot. Time uncertainty is mainly due to bad weather interrupting canoe travel. A better plan would be to have two, 2-person parties each working 15 or so days in different sectors, because in some years suitable conditions for pellet counts do not extend up to 30 or even 25 days.

Our sampling cost is approximately 10-12 person-days/100 km^2. Surveys of both pellet and aerial counting on the same sites offer several values for research and management. Defecation rates can be calibrated by comparison with aerial counts. If in some years one method is not possible, the other can fill in. Or, because pellet counting is less expensive, it can be used as a cost-saving substitute in some years. More importantly, different types of ancillary data can be collected during the two surveys to fill in key aspects of moose ecology: from the air in winter— sex and age data, predation dynamics, and micro-habitat choices relative to snow conditions; and from the ground in spring— availability and use of winter browse by habitat type, and examination of moose carcasses.

In summary, the agreement found between density trends of moose from the two sampling methods over 14 years at Isle Royale suggests that the results, though not closely matching, are near enough to indicate that either of the methods tracks moose trends reasonably well. This comparative approach should be continued with efforts to improve both of these methods for estimating the density of moose.

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