The Seventh North American Caribou Conference,
Thunder Bay, Ontario, Canada,
19–21 August, 1996.

Needed: less counting of caribou and more ecology

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Abstract: Most aerial surveys designed to estimate numbers of caribou (*Rangifer tarandus*) lack clear objectives, are inaccurate and imprecise, lack application, and often are doubted by the public. Sources of error in surveys are bias (inaccuracy) and sampling error (imprecision) caused largely by sampling units (strips, secrions of strips, quadrats, or photographs) being inappropriate for highly variable group sizes and distributions. Many visual strip surveys of caribou on calving grounds were inaccurate by 136-374%. Photographic surveys of calving caribou are more accurate but usually have coefficients of variation (*CV*) of 20-40%, whereas a *CV* of about 15% is required to detect a 50% change in population size between surveys. Extrapolation of such counts to population size produces unacceptable accuracy and precision. Consequently, no conclusions can be made about changes in population numbers between or among surveys because even large natural fluctuations fall within confidence limits. These problems combined with difficulties of managing caribou populations in remote areas of northern Canada indicate that scarce funds may be better allocated to ecological studies.

Key words: accuracy, bias, census, precision, *Rangifer tarandus,* surveys.

Rangifer, Special Issue No. 10, 15–23

Introduction

As a member of a caribou management board, I became concerned that population estimates of two large herds of caribou (*Rangifer tarandus*) were inadequate for management. Additionally, board members did not understand the reliability of survey results or how they were obtained. An attempt at a simple explanation for the board grew into this review of caribou surveys.

There are few experimental studies that explore accuracy and precision of caribou surveys because of high costs in remote areas. Therefore, I use experimental results for moose (*Alces alces*) in forest cover and pronghorns (*Antilocapra americana*) in open and shrub habitats to most-closely simulate what may be expected from caribou surveys in those cover types.

I briefly review survey terminology, examine accuracy and precision of some current methods, recommend improvements in design, and examine alternatives to surveys. This paper is not a review of all survey methodology. Most comments refer only to strip transect and photographic surveys of the Beverly and Qamanirjuaq herds of caribou. *The focus is on problem definition and potential solutions.*

First of all we must define terms and become familiar with statistical terms and sample design. Bookhout (1994) provided a good review, using examples from wildlife studies. Consult statistical texts for further information.

Accuracy

Accuracy is closeness of a measured or computed value to its true value (Sokal & Rohlf, 1981). Accuracy can only be measured if the number of caribou in a prescribed area is known. An accurate survey method is one that will reliably estimate the actual number of caribou in an area on average when repeated many times (Eberhardt, pers. comm.).

Bias (departure from reality) in counting, sampling, and analysis results in inaccuracy (Jolly, 1969b). There are many sources of bias in visual strip surveys (Caughley, 1974; Heard, 1985; Crête *et al.*, 1991; Couturier *et al.*, 1996). High and variable bias causes density estimates to vary considerably among observers in the same aircraft (Thomas, 1969; Heard, 1985).

Precision

Precision tells us nothing about survey accuracy. The amount of variation in normally-distributed measurements is *variance* or its square root, *standard deviation* (*SD*). In surveys, it is a measure of variation in numbers of caribou in each of the sample units (areas). *Precision* is sampling error as measured by *standard error* (*SE*). The *SE* is standard deviation divided by the square root of sample size (n) or n -1 if *SD* is calculated using n and not n-1 (Bookhout, 1994). Sampling error is zero if the same number of caribou occur in each sample unit. A knowledge of how precision is derived can guide surveyors in sample design, i.e., reduce variation in caribou numbers among sampling units and increase sample size to reduce *SE*. For example, with constant variance, *SE* is reduced by half as n is increased from 16 to 64.

The *SE,* when combined with a probability (*P*) level, yields *confidence limits* (*CL*) and their interval, the *confidence interval* (*CI*). At $P = 0.90$ (alpha = 0.1), it is incorrect to state that there is a 90% chance that the actual number of caribou in a survey area is within the *CI*. Rather, assuming no bias, the *CI* is likely to contain the true population size in 90% of surveys of the same type and intensity.

Survey results should consist of an estimate, confidence limits (*CL*), probability level, and sample size. Presenting results as the sample mean ± *SE* is not meaningful to people who cannot calculate approximate *CL* from *SE* values.

Statistical texts define confidence interval (*CI*) as the interval between *CL*s (Steele & Torrie, 1960). Caribou biologists (e.g., Goudreault, 1985; Farnell & Gauthier, 1988; Crête *et al* , 1991; Couturier *et al.,* 1996) refer to estimates ± "*CI*" but the *CI* is half textbook definitions. For example, the 1976 estimate for the George River herd was 63 463 ± 30% ($P = 0.90$") (Goudreault, 1985). This example points to the need to define terms (Bookhout, 1994).

Precision is also measured by a coefficient of variation (*CV*). It is standard deviation divided by the estimate and usually expressed as a percentage. To confuse matters, *CV* is also defined as *SE* divided by the estimate and expressed as a fraction or a percentage. It should be designated as CV_{se} to distinguish it from CV_{sd}. The CV_{sd} is the preferred index of precision for comparisons among surveys because it is relative to population size and independent of probability and sample size.

Randomness

Most surveys are random or systematic. Many statistics are based on an assumption that samples are drawn randomly from a normal distribution. Systematic surveys generally are efficient and may produce suitable estimates but they can produce biased estimates of *SE* (Caughley, 1977; Cochran, 1977). All survey statistics and sampling designs are based on assumptions about distribution, variance, randomness, and independence of samples (Eberhardt, 1978a, b). Often, assumptions are ignored but rarely with reason. For example, a recommendation to sample in two directions (Cochran, 1977; Couturier *et al.*, 1996) can complicate sampling designs and inflate variance if caribou are in linear groups. Constraints of caribou movements, costs, weather, aircraft availability, and personnel means that the best theoretical sampling design may be impracticable.

Stratification

Stratification is division of a survey area into two or more parts (strata) based on density, degree of clumping, or some other attribute. Its purpose is to reduce variance and therefore *SE* and *CL.* In *optimum allocation,* sample units are proportioned to estimated variance or density in each stratum. The purpose is to get a precise count of a high proportion of a population. Survey biologists urgently need guidelines regarding thresholds of density and degree of clumping beyond which any sampling design will produce imprecise estimates. Post-survey stratification may be done in certain types of systematic surveys (Jolly, 1969a; Anganuzzi & Buckland, 1993) but with caution (Caughley, 1977). Post-survey stratification of systematic quadrats might produce the most-precise estimates and be cost effective.

Stratification can result in lower precision if it unduly partitions sample size. Surveyors should attempt to achieve a large sample size in each stratum because *SE* decreases with sample size whereas power increases. However, an estimate of required sample size is necessary to achieve a cost-efficient survey.

Stratification within systematic surveys with 50% coverage produced some erratic estimates of pronghorns (Kraft *et al.*, 1995). Confidence intervals did not contain the known population size half the time. Even some precise (CV = 13%) designs produced CIs that did not contain the known number of pronghorns.

A minimum total count may be necessary in part of a caribou distribution because aggregations of widely differing numbers are unevenly distributed. Variance is likely to increase sharply as clumping increases. It may also be necessary to change the size and shape of sampling units to reduce variance and edge bias. Stratification is difficult when sizes and shapes of indiscrete caribou groups are constantly changing in response to environmental variables and a distribution is moving over landscapes with few defining landmarks. One potential solution is for an independent observer to stratify distributions during a survey based on relative densities and degree of clumping. The boundaries would be logged using a geographical positioning system.

Coverage

Coverage (proportion of area sampled) and sample size usually are directly related and consequently the relative effect of each on reported CVs is unclear. That explains why data on the effect of coverage on accuracy and precision can be contradictory. For example, coverage of 0.23% produced relatively accurate (*vs.* July photography) but imprecise estimates of population size (Couturier *et al.*, 1996). Conversely, coverage below 33% produced accuracy below 80% in 1.6-km-wide strip surveys of caribou on tundra (Cameron *et al.*, 1985). In contrast, strips 100 m wide on each side of an aircraft and covering <4.4% of an area gave much more accurate estimates of pronghorns than strips 1.6 km wide and covering 35% of a survey area (Pojar *et al.*, 1995). However, CVs of pronghorn estimates decreased progressively with coverage of 16%, 33%, and 50% (Kraft *et al*, 1995). Acceptable average CVs (11-13%) were achieved only with stratification and 50% coverage, similar to surveys for muskox (*Ovibos moschatus*) (Graf & Case, 1989). If coverage of 50% is required for precise estimates, then perhaps a minimum total count should be considered.

A finite population correction factor is necessary where coverage is high (Eberhardt, pers. comm.). Variance is reduced by the coverage fraction, i.e., 50% if half the population is surveyed.

Survey objectives

Objectives must include survey justification and accuracy/precision components. Justification may include: (1) monitoring, (2) management, (3) population analysis, and (4) hypothesis testing (Eberhardt, 1978b). Generally, the need for greater accuracy and precision increases in the order listed.

A CV of 12-15% was considered necessary for management (Gasaway *et al*, 1986; Crête *et al.*, 1991). However, a CV of <10 is required to detect a 30% difference between two surveys at P = 0.90 (Heard, 1985). Only a 50% change would be detected with a CV of 15% (Heard, pers. comm.). Some surveyors wish to detect a 15% difference between surveys (Pojar *et al.*, 1995) necessitating a CV of <5. A CV of 13% was considered precise by Kraft *et al.* (1995), relative to a mean CV of 29% for several designs.

Much emphasis is now placed on power and calculation of required sample size. The greatest conservation concern is not detecting a significant decline in numbers, which is a Type II error. Power is 1 minus the probability of a Type II error. Heard (pers. comm.) suggested that power of detecting population change should be 90% (beta = 0.10). Surveyors should carefully define their objectives and calculate required accuracy, precision, power to detect change, and required sample size (Eberhardt, 1978b). For example, 100 radio-collared caribou are required to detect a 20% change in mortality rates with 80% power (Walsh *et al*, 1995).

Examples of accuracy and precision from surveys

Viewers tend to underestimate numbers in large groups. For example, visually estimated numbers were low by 21% for 27 groups containing 114 to 796 caribou clearly visible in large photographs (Thomas, 1969).

Failure to detect caribou can be a major source of bias but rarely is it measured. A correction of 20% (estimate x 1.25) was adopted for many surveys in Canada (Thomas, 1969; Heard, 1985) but case studies in survey literature reveal that bias often is much higher. Intensive searches for caribou within quadrats in forested habitat yielded 33% and 74% more caribou than "normal" searches (Farnell & Gauthier, 1988).

Data for moose illustrate detection problems in forest cover. For example, only about a third of moose were seen in narrow strips in conifer forest

Table 1. An example, selected because of unusually low coefficients of variation (*CV*), of results of visual strip and photographic surveys of caribou on the calving grounds of the Qamanirjuaq herd in June 1988.

Survey type	Sample size	Estimate	*CV*	90% *CL*[1]
Visual strip	20	56 000	11	45 000 - 67 000
Photo	15	160 000	13	123 000 - 197 000

[1] *CL* = confidence limits = estimate ± $SE \times t_{0.1}$. Data from Heard & Jackson (1990b).

cover (Gasaway *et al.*, 1985; Anderson & Lindzey, 1996).

Relatively precise visual strip and photographic surveys of caribou on a tundra calving ground produced concurrent estimates that differed by a factor of 2.9 (Table 1). The average factor for seven such paired comparisons was 2.34 (1.4-3.7) (Heard & Jackson, 1990a & b). Visual strip surveys produced caribou population estimates about half those obtained from quadrats (Fong *et al.*, 1985). Similarly, visual estimates of pronghorn numbers based on two strips 0.8 km-wide were half of estimates from quadrats (Pojar *et al.*, 1995).

The CV_{se}s of 13 visual strip surveys over calving grounds averaged 12.4% (Heard & Jackson, 1990a, b; Heard, pers. comm.). The *CV*s of stratified strip surveys of tundra caribou on Southampton Island were 29.1% and 34.7%; those of random quadrats 11.6% and 16.3% (Heard & Ouellet, 1994). Those differences in CVs relate in part to a larger sample size for quadrats (35 & 48 *vs.* 18 & 24). Estimated *CV*s of sightability-corrected quadrat samples of two woodland caribou herds in Yukon were 24.2% and 14.8% (Farnell & Gauthier, 1988).

Sampling errors (precision) associated with photographic surveys of caribou on calving grounds often are unacceptably large (Table 2). Wide *CL*s do not permit firm conclusions about population trends (Fig. 1). Photographic samples of caribou on calving grounds generate *CV*s of 5% to 32%, which progressively increased with each of three ratios used to estimate population size (Table 3). In NWT, long-term average ratios with estimated *CV*s of 10% are used for the second and third ratios (Heard & Jackson, 1990a). In any 1 year, those ratios may each be inaccurate by 10%, adding further uncertainty to estimates. Photographic surveys of calving grounds have produced unusable population estimates in 2 of 13 surveys (Table 2).

Discussion and recommendations

Objectives and sampling design

Survey objectives must be clearly stated and include components of management, accuracy, precision, and trend detection. Surveyors must either learn about the complexities of survey design or consult a biometrician with experience in aerial surveys.

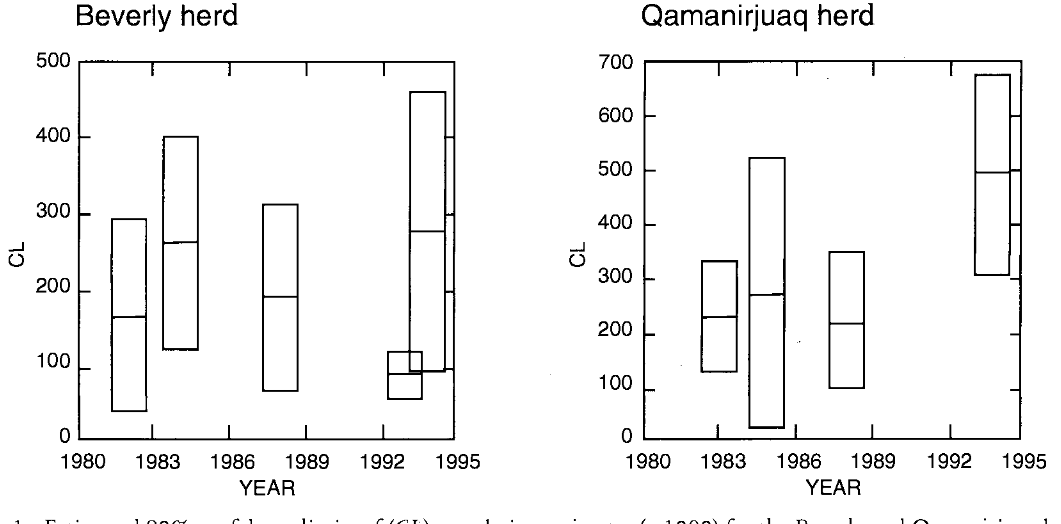

Fig. 1. Estimated 90% confidence limits of (*CL*) population estimates (x 1000) for the Beverly and Qamanirjuaq herds derived from 1982-1994 photographic surveys of calving grounds. Data from Heard & Jackson (1990a, b) and Gunn (this issue).

Table 2. Precision of herd estimates (X 1000) obtained by photographic surveys of the calving grounds of the Beverly and Qamanirjuaq herds from 1982 through 1994.

Year	Estimate[1]	*SE*[2]	90%*CL*[3]	Source[4]
Beverly herd				
1982	164	72	38 - 290	1
1984	264	81	123 - 404	1
1988	190	71	66 - 313	1
1993	87	18	56 - 118	2
1994	277	107	91 - 462	3
Qamanirjuaq herd				
1983	230	59	126 - 334	4
1985	272	142	22 - 522	4
1988	221	72	94 - 349	4
1994	496	105	310 - 682	3
George R. herd[5]				
1984	644	97	483 - 805	5
1986	283	66	173 - 394	5
1988	682	147	437 - 928	5
1993 (adult method)	982	135	759 -1204	6
1993 (calf method)	749	151	501 - 998	6

[1] Population estimate = caribou on calving grounds x proporrion of parturient cows x (1/pregnancy rate) x (1/proporrion of cows in adult population) (Heard, 1985).

[2] SE = standard error. It is the *SE* of caribou on the calving grounds and the *SE*s associated with 3 ratios used to extrapolate to a population estimate (Heard & Jackson, 1990a, b).

[3] Confidence limits (*CL*) as mean estimate ± *CL* at P = 0.90 (alpha = 0.10).

[4] Sources: 1: Heard & Jackson, 1990a; 2: Williams, 1995; 3: Gunn, this issue; 4: Heard & Jackson, 1990b; 5: Crête *et al.*, 1991; 6: Couturier *et al.*, 1996.

[5] Values are for all caribou in October.

Surveyors must design surveys that are expected to produce acceptable accuracy and precision. If costs do not justify benefits, then a survey should be canceled.

Perhaps surveys of caribou should be designed only by survey specialists because the field biologist is unlikely to become competent in this complex methodology. Sampling design is highly technical, complex, and controversial. For example, there are many methods of analyzing trend data (Hatfield *et al.,* 1996).

Detection of a 10% or 20% difference in population size between surveys is not possible with common survey sampling methods. In fact, only a change of 50% between surveys is detected by most photographic samples of all caribou on calving grounds (Heard, pers. comm). Frequent surveys are too costly and long survey intervals are insensitive to shott-term fluctuations in numbers. Detection of a significant change in population size may be delayed many years if several surveys are required to detect a trend. Variation is a critical component of nature and we must recognize limitations in attempting to compartmentalize it statistically.

Counts of forest-tundra caribou

I favor attempts at total counts of aggregations during July (Valkenburg *et al* , 1985; Parker, 1972; Heard & Jackson, 1990b; McLean & Russell, 1988; Couturier *et al.*, 1996). Photography of July aggre-

Table 3. Coefficient of variation (*CV* = 100 *SE*/estimate) for photographic surveys of adult caribou on calving grounds, for parturient females on calving grounds, and extrapolated total population size of the Beverly, Qamanirjuaq, and George River herds of caribou.

	Coefficient of variation (%)		
Population/ year of survey	Calving grounds	Parturient females	Total population
Beverly herd[1]			
1982	19.5	41.7	44.0
1984	25.5	27.1	30.6
1988	25.9	34.7	37.4
1993	11.6	15.1	20.6
1994	32.3	35.9	38.6
Qamanirjuaq herd[1]			
1983	17.5	21.6	25.8
1985	12.3	50.3	52.3
1988	13.0	29.6	32.8
1994	NA	15.9	21.3
George River herd[2]			
1984	4.8	7.2	15.0
1986	17.9	21.0	23.4
1988	13.7	16.8	21.6
1993 A[3]	11.8	12.0	13.7
1993 C[3]	NA	19.0	20.1

[1] Data from Heard & Jackson, 1990a, b; Williams, 1995; Gunn, this issue.

[2] Column 3 is adult cows (not parturient females) and total population includes calves of the year. Data from Crête *et al.* (1991) and Couturier *et al.* (1996).

[3] A and C are esrimates based on numbers of adult females and calves, respectively.

Table 4. Generalized and subjective rating of the accuracy and precision of some surveys used to enumerate large forest-tundra herds of caribou.

No.	Survey type	Accuracy	Precision	Relative cost
1	Systematic visual strip (transect)	Often poor	Fair-good	Low
2	Random quadrat	Good	Poor-fair	Moderate
3	Photo: caribou on calving ground	Good	Good	High
4	Photo: adjust #3 results to ad. females	Good	Fair-good	Very high
5	Photo: adjust #3 to parturient females	Fair	Poor	Very high
6	Photo: adjust #5 to total population	Poor-fair	Poor	Very high
7	Photo: total count & intensive search	Excellent	Excellent	Moderate
8	Photo: partial count + radio ratios	Excellent	Good	Extreme
9	Photo: partial count + strip surveys	Good	Good	High
10	Total visual count	Variable	Variable	Wide range

gations that contain all sex and age classes usually produces estimates of adequate accuracy and precision, unlike most other types of surveys (Table 4). Use of a minimum real population size is a conservative approach to management. Accuracy is high and variation is almost nil if a near-total count is achieved. It is low if an adjustment must be made for a small proportion of "missing" caribou, as the variation may only apply to 5-10% of the population. Caribou outside photographed aggregations can be surveyed or estimated by ratios of radio-collared caribou (McLean & Russell, 1988; Couturier *et al* , 1996). Radio-collared caribou in post-calving aggregations led biologists in Alaska to 87-90% of all caribou found through extensive searching (Valkenburg *et al* , 1985). A photographic count of July aggregations is less costly than calving grounds surveys and associated sampling, which can cost up to $200 000 (Crête *et al* , 1991). That technique is improved with radio-collared caribou but I agree with Valkenburg *et al.* (1985) that they are not essential.

If a *CV* of 10% is considered adequate for photographic samples on calving grounds, then only 1 of 12 surveys have achieved that precision for estimates of all caribou on calving grounds and for parturient females (Table 3). If a *CV* of 15% is deemed adequate, then 6 of 12 surveys achieved that objective for all caribou on calving grounds and 2 of 12 for parturient females. However, *CV*s of 10% and 15% still only permit detection of population changes of 30% and 50%, respectively (Heard, pers. comm.). Furthermore, a significant proportion of adult cows in the George River herd were not on the designated calving ground in 1 year (Couturier *et al.*, 1996). It would be necessary to put more than 100 radio-collars on cows to accurately adjust for those absent (Couturier *et al.*, 1996). In contrast, <4% of radio-collared females were outside the "core" calving grounds of the Qamanirjuaq herd from 1985 through 1988 (Heard & Stenhouse, 1992).

Extrapolation of population size from photographic estimates of caribou on calving grounds is not justified. There is unknown or poor accuracy and precision of three ratios used in such calculations. Further, there is no agreement on what sampling units or scale should be used for photo surveys (Heard, 1985; Crête *et al* , 1991; Couturier *et al* , 1996). Only Crête *et al.* (1991) adjusted photo counts for sightability bias.

Precision of calving ground surveys and others can be increased with attention to caribou distribution followed by adjustment of sampling units and stratification. A sampling objective is to stratify optimally and to construct sampling units within strata that will have the least variation. In reality, stratification is difficult and no unit size or shape will avoid sampling error. Kraft *et al.* (1995) warn potential surveyors of the danger of estimating abundance of aggregated populations.

Improved visual surveys

The accuracy of visual strip surveys can be improved. All caribou must be readily detected within viewing strips or sightability bias must be measured. One method of correcting for visibility bias is to compare caribou density in strips (belts) at several distances from an aircraft. Distance of caribou groups can be calculated from aircraft altitude and angle to the horizon, preferably measured by a second observer on each side of an aircraft. Adjustments for sightability vary among many factors, consequently correction factors should be developed for average conditions encountered in each survey.

Fewer caribou are missed by people experienced in scanning for animals under survey conditions. Observers should be trained to count aggregated caribou in photographs before a survey. Larger groups must be photographed. Counts of observers with low sightability should be adjusted to those with high sightability. Surveys should be conducted when caribou are in open habitats and contrast between caribou and background is high. Radar altimeters improve estimation of altitude and coverage. Sample size required to achieve a specified CV should be calculated as a survey progresses. In reality, the goal may not be achievable if the variance is large.

The multiplier effect of biases results in some gross underestimates of population size. Surveyors will readily admit that they may miss 20% of caribou and they may undercount numbers in groups by 20% but they are reluctant to increase their estimate by 1.56 to account for both biases. Every surveyor should attempt to measure accuracy in several sampling units in their survey area.

Credibility

The 1980 visual strip survey of the Qamanirjuaq herd produced an estimate of 38 000 ± 26 000 (90% *CL*) caribou. Such surveys subsequently were found to underestimate populations by an average of 234%. The estimate evoked a crisis herd situation when none existed and credibility of biologists was lowered.

Low estimates for caribou populations also led biologists to speculate without evidence that emigration and calving ground infidelity was the cause (Gates, 1985; Heard & Calef, 1986; Williams, 1995). Most female caribou in forest-tundra populations return to the same calving grounds annually and there is little emigration or immigration (Parker, 1974; Heard, 1983; Goudreault, 1985; Heard & Stenhouse, 1992; Valkenburg, this issue). Even when bias is reduced, as in sharp photographs of adequate scale, surveyors should first suspect that the real population size may be outside the confidence interval of anomalous survey results.

Another problem arises when improved or more-intense sampling produces higher population estimates when a decline may be occurring. Past estimates are subject to veneration with repeated uncritical use over time. Most historic estimates of forest-tundra caribou based on visual strip surveys were biased, probably by factors of 2-3. The consequences of inaccurate and imprecise estimates, and weak attempts to explain them, is that a growing number of resource users simply reject survey results.

In remote areas of northern Canada, management of caribou is not possible unless hunters agree that a problem exists. Data from herd monitoring was not used by the caribou board I sit on except to recommend slight changes to resident and commercial quotas.

Because surveys are inaccurate and imprecise, it is misleading to announce a population estimate as say 4312. Rounding is required to the nearest 1 or 2%.

A need for ecological studies

Even if caribou numbers could be estimated accurately and precisely, the data are not useful unless ecological studies indicate causes of population fluctuations or there is an ability to reduce harvest or natural mortality. The relative importance of limiting factors is not known for most populations because comprehensive ecological studies are expensive and mortality statistics are unreliable. Ecological studies generally are piecemeal responses to proposed developments in parts of caribou ranges. The best approach is to identify important habitats and attempt to protect them from activities that would be unacceptably detrimental. Without adequate safeguards on habitat, caribou populations will dwindle. An understanding of survey inaccuracy and imprecision may cause biologists to direct resources to other forms of population analysis, such as estimates of fat reserves, pregnancy rates, and recruitment, and to habitat use and requirements.

Conclusions

1. Main sources of error in caribou surveys based on sampling methods are bias (inaccuracy) and sampling error (imprecision) caused by highly variable group sizes and distributions relative to sampling units.
2. Visual strip surveys of caribou on calving grounds were inaccurate by an average factor of 2.3 relative to photo based estimates, however, most surveys of caribou are of unknown accuracy.
3. Most visual and photographic survey estimates are imprecise, having coefficients of variation (*CV*) of 10-50%, whereas 5-10% is required to detect changes in population size of 15-30% required for management.

4. Limitations of surveys must be explained to the public and estimates always expressed with lower and upper confidence limits along with any additional uncertainty. Variability in nature limits our ability to precisely quantify it.
5. Only minimum total counts, particularly photography of aggregations in July, produce results acceptable for conservative management of caribou.
6. Other indices of caribou population "performance" such as pregnancy rates, calf survival, and body condition and growth indices may be preferable to inaccurate and imprecise estimates of population numbers.
7. Many surveys for population size should be replaced by ecological studies that focus on habitat requirements in relation to limiting factors that affect reproduction and survival.

Acknowledgements

Reviews by Lee Eberhardt, Sam Barry, Frank Miller, Anne Gunn, Harry Armbruster, and two others were most helpful. I thank managers of Canadian Wildlife Service and Environment Canada for their support.

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