EVALUATION OF A MARK–RESIGHTING TECHNIQUE FOR WOODLAND CARIBOU IN NEWFOUNDLAND

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Abstract: We evaluated properties of the Petersen mark–resight technique for estimating the population size of 6 woodland caribou (*Rangifer tarandus*) herds in Newfoundland. Our objective was to determine the robustness and efficiency of a novel marking technique for estimating population size of caribou where sightability bias is marginal. We marked caribou with pressurized oil-alkyde paint applied from a helicopter. Resighting surveys were conducted 2–3 weeks later. Data from 15 radiocollared animals indicated populations were closed and marks were not lost. The probability of resighting a marked individual was independent of group size, which indicated heterogeneity in sighting probabilities had a marginal effect on the reliability of population estimates. Thus, most of the fundamental assumptions of the Petersen estimate were supported. Although we could not assess accuracy of this method, the degree of precision was dependent primarily on the number of marked animals resighted. Increasing the initial number of marked individuals did not significantly reduce the width of confidence intervals unless the total number of animals resighted also was increased. However, due to the efficiency of marking many animals in a short period, more effort can be allocated to resighting surveys without increasing costs. We believe this technique should provide a cost-effective method for obtaining precise population estimates of woodland caribou and other large mammals where sightability bias is low.

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Determining accurate and precise estimates of population abundance is fundamental for the management of big game species and furthering our understanding of conservation and population dynamics. As a consequence, different aerial census techniques have been developed to estimate population size of ungulates. Such methods include total counts of the population or counts of individuals seen within randomly selected quadrats or strip transects (Caughley 1977, Seber 1982). However, rugged terrain, poor optical conditions, variability in observer experience, and sex- and age-specific differences in the spatial and temporal distribution of animals may generate visibility biases that cause inaccurate estimates of abundance (Siniff and Skoog 1964, Caughley 1974, Samuel et al. 1992, McCullough et al. 1994). Models that incorporate population and landscape structure have been developed to correct for visibility bias (Steinhorst and Samuel 1989, Samuel et al. 1992), but financial or logistical constraints may prohibit application of such methods.

Mark–resighting techniques, such as the Petersen estimate, provide an alternative to direct counting methods and do not depend on the total number of animals observed in each sample area. Instead, estimates are a function of the ratio of marked to unmarked individuals within a sample. The Petersen method has been used to estimate population size of free-ranging white-tailed deer (*Odocoileus virginianus*; DeYoung 1985), elk (*Cervus elaphus*; Bear et al. 1989), caribou (Gauthier and Theberge 1985), and mountain sheep (*Ovis canadensis*; Neal et al. 1993). If the number of animals marked and resighted is relatively large, and certain assumptions are not violated, mark–resight methods can produce accurate and precise population estimates (Seber 1982, Krebs 1989).

Assumptions of the Petersen estimate include (1) the population is closed (i.e., no additions or losses between census periods), (2) all individuals have an equal probability of being sighted during each sampling period, and (3) marks are not lost or overlooked (Pollock et al. 1990). Although Assumptions (1) and (3) are quite robust, particularly if the interval between sampling periods is short, overestimation has been

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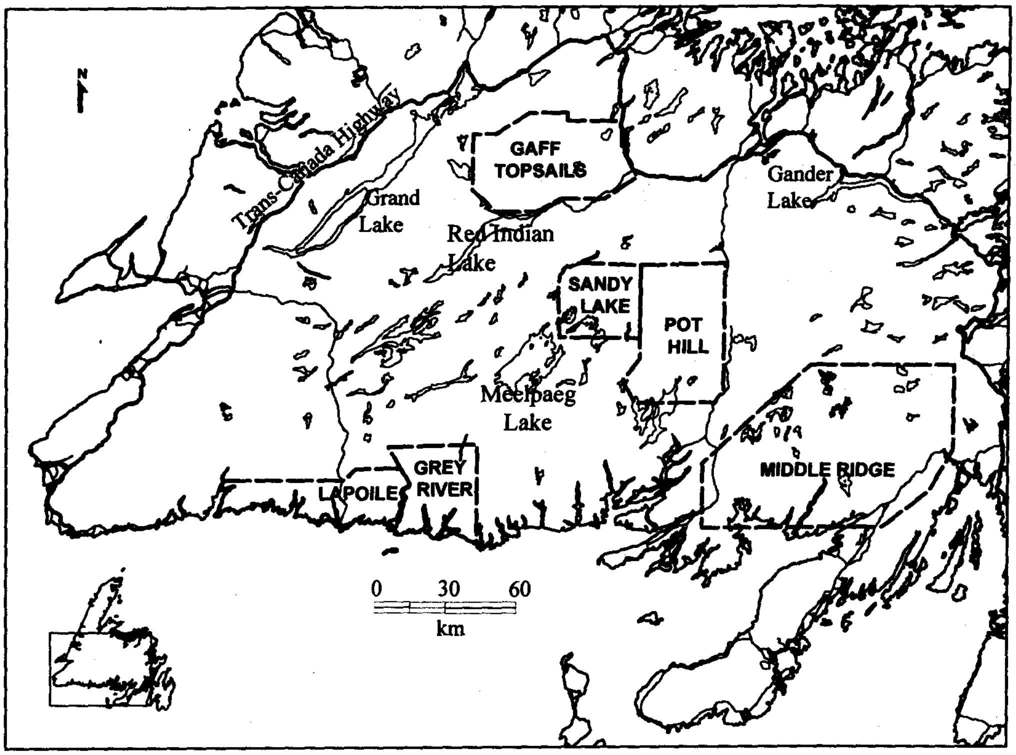

Fig. 1. Study areas of the 6 woodland caribou herds from Newfoundland, Canada.

reported due to misclassifying marked animals as unmarked (Bear et al. 1989).

Highly variable and biased estimates are due primarily to violation of Assumption (2), which has 2 components. First, heterogeneity in sighting probabilities can result from group-size effects and age- and sex-specific differences in spatial distribution (Neal et al. 1993, Vincent et al. 1996). Second, capturing and handling animals to deploy collars or ear tags can cause individuals to behave differently (analogous to "trap shyness or happiness") during subsequent surveys (McCullough and Hirth 1988). Increasing the number of animals marked and resighted will minimize the adverse effects of these 2 components on accuracy and precision. However, marking large numbers of individuals with conventional collars or ear tags may increase costs and mortality among captured animals.

A less invasive and more efficient short-term marking method might enable biologists to reduce behavior bias, obtain larger sample sizes, and reduce costs. Herein, we evaluated the application of a spray-painting technique to estimate size of 6 woodland caribou populations in Newfoundland. We determined how strongly the degree of precision was influenced by the initial number of individuals marked, total number resighted, and number resighted with marks. We also monitored radiocollared animals and analyzed the relation between group size and frequency of marked animals resighted to test assumptions of the Petersen estimate.

STUDY AREA

The study was conducted on the winter range of 6 woodland caribou herds spanning the interior to the south coast of Newfoundland and encompassing 3 distinct ecoregions (Fig. 1). The Middle Ridge Herd is located in the Central Newfoundland Ecoregion (Daaman 1983). The area is approximately 5,750 km^2 and is characterized by gentle relief with an average elevation of 250 m (Roberts 1983). Numerous lakes, ponds, and streams are interspersed with extensive shrub heaths and bogs. Vegetation is composed primarily of stunted black spruce (*Picea mariana*), larch (*Larix laricina*), sheep

Table 1. Petersen population estimates ($\hat{N}$) and mark–resighting statistics for 6 woodland caribou herds in Newfoundland, 1985–95. NT = number of line transects flown, CV = coefficient of variation, n_1 = number marked, n_2 = number resighted, m_2 = number resighted with marks.

Herd[a]	Year	Resight method[b]	NT	$\hat{N}$	95% CI[c]	CV	n_1	n_2	m_2
MR	1985	G		10,830	9,187–13,190	17.4	537	1,972	97
MR	1985	H		10,932	10,167–11,821	7.4	537	6,075	298
MR	1985	H		10,238	8,904–12,042	14.6	537	2,454	128
MR	1995	H	51	19,690	17,809–22,014	10.4	929	5,271	248
MR	1995	F	41	22,226	18,749–27,285	18.0	929	2,389	99
LP	1986	H	40	8,569	8,105–9,089	5.6	781	5,018	457
LP	1988	H	15	11,176	10,478–12,001	6.6	1,277	4,197	479
LP	1992	H	20	8,861	7,817–10,342	13.5	1,000	1,389	156
GR	1987	H		9,973	8,089–13,001	22.4	350	1,704	59
PH	1987	H	32	3,296	2,555–4,451	23.2	212	773	49
SL	1987	H	21	4,569	3,701–5,967	22.5	325	798	56
GT	1989	H	13	4,664	3,894–5,813	19.1	366	965	75

[a] MR = Middle Ridge, LP = LaPoile, GR = Grey River, PH = Pot Hill, SL = Sandy Lake, GT = Gaff Topsails.
[b] G = ground with snowmobile, H = helicopter, F = fixed-wing plane.
[c] Confidence intervals were based on the probability distribution of m_2 (see METHODS).

laurel (*Kalmia angustifolia*), and Labrador tea (*Ledum groenlandicum*). Winter snow cover is intermittent, with an annual snowfall of 300 cm from November through April. Temperatures average 16°C in July and −7°C in February (Banfield 1983).

The Gaff Topsails Herd is located in the northern interior, a part of the Long Range Barrens Ecoregion (Daaman 1983). The area consists of rolling topography with an average elevation of 400 m and covers about 2,500 km^2. Sheltered valleys are covered with forests of balsam fir (*Abies balsamea*), while the plateau is composed of dwarf shrub heaths and extensive peat bogs. Dense patches of stunted balsam fir are common near edges of bogs where soil depth supports tree growth, but wind and snow damage prevent normal development (Daaman 1983). Annual snowfall reaches 500 cm, and temperatures range from −8°C in February to 16°C in July (Banfield 1983).

The Grey River, Sandy Lake, and Pot Hill herds stretch from the south coast to the interior (Fig. 1). The area is part of the Maritime Barrens Ecoregion, with an average elevation of 230 m (Daaman 1983). Areas range from 1,630 to 6,000 km^2 and are characterized by extensive dwarf shrub heaths dominated by sheep laurel in the interior and crowberry (*Empetrum* spp.) along the coast. In areas with poor drainage, shallow fens and bogs occur and are primarily composed of tufted bulrush (*Scirpus caespitosis*). Forests are common in the Pot Hill area but are restricted to sheltered valleys in the Sandy Lake region. Plateaus are covered with patches of stunted balsam fir. Annual snowfall in the 3 areas varies from 300 to 400 cm, and temperatures fluctuate from −8°C in February to 16°C in July.

The LaPoile Herd winters farther west along the south coast in a region with similar terrain and vegetation. The area is approximately 5,730 km^2, with an average elevation of 180 m. Barrens consist of dwarf shrub heaths dominated by sheep laurel and Labrador tea. Forested valleys are covered with patches of stunted balsam fir and black spruce. Annual snowfall varies from 200 to 250 cm, and temperatures range from −5°C in February to 14°C in July.

METHODS

Mark–Resight Procedure

We conducted aerial surveys from January to March 1985–95, when sightability of caribou on snow-covered barrens was optimal. All animals were marked from a Bell 206L helicopter. For all areas, except the Grey River Herd, line transects spaced 3 km apart were flown in a north–south direction. The number of transects flown over each area ranged from 13 to 51 (Table 1). We recorded transect location with Global Positioning System (GPS) units and marked locations on a 1:250,000-scale topographic map. Marking of animals in the Grey River Herd was conducted by dividing the area into 15 blocks (100 km^2 each) and searching 4 random sample units (4 km^2) within each block. The GPS locations were also recorded for the corners of each block, and the locations were marked on a 1:50,000-scale topographic map. Flight crews consisted of a pilot, navigator, and 2 observers.

Line transects and blocks were flown at an altitude of 150 m above ground level (AGL) while an observer surveyed an area 0.5 km wide on each side of the aircraft. Altitude was maintained via the on-board altimeter, which limited deviations in transect width. In addition, scanning distance was initialized via the measured topographic distance between conspicuous landscape features. To be conservative, we excluded from population estimates those animals near boundaries and for which the location was dubious. Sighted caribou were then approached, and approximately 25% of the individuals in a group were marked with pressurized oil-alkyde paint (constant pressure of 1,551 kiloPascals). The paint was contained in paired 2.27-m^3 U.S. scuba tanks fitted with a flexible rubber delivery hose (see Mercer et al. 1990 for details on painting apparatus). We marked animals from a height of about 3 m AGL. Individuals were considered marked only if paint was applied to the midline of the back. This protocol ensured that the number initially marked, and subsequently resighted, was not biased by animals inadvertently marked by overspray.

For all caribou herds, except the Middle Ridge Herd, we conducted 1 resighting survey within 2–3 weeks of the marking period. The original transect lines, or blocks in the Grey River area, were reflown with a helicopter at an altitude of 100 m AGL. Upon sighting caribou, the aircraft descended to 10–20 m AGL, and the number of marked and unmarked animals was counted.

In 1985, the Middle Ridge Herd was censused twice by helicopter (following the above procedure), and once on the ground with snowmobile. Four 2-man crews surveyed the area using a randomized block design. In addition, the Middle Ridge Herd was censused twice in 1995, once by helicopter and once by a Cessna 185 fixed-wing aircraft.

In 1985, 15 radiocollared animals from the Middle Ridge Herd were also painted and relocated during the final resighting survey of that year. This procedure enabled us to check if the population was closed and if marks were lost.

One estimate of population size ($\hat{N}$) was calculated for each survey via Chapman's (1951) bias-corrected hypergeometric estimator:

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

and variance ($\widehat{\text{var}}$) or $\hat{N}$ as

$$\widehat{\text{var}}(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)},$$

where n_1 is the number of animals initially marked, n_2 is the total number of animals resighted, and m_2 is the number of resighted animals with marks. We calculated 95% confidence intervals based on the probability distribution of m_2 and the recommendations given by Seber (1982). In 1988 and 1992, the fraction of animals resighted with marks from the LaPoile Herd was relatively large, and confidence intervals were based on the normal approximation of the binomial distribution. For the remaining herds and years, we calculated confidence intervals as a function of the Poisson distribution (Seber 1982, Krebs 1989).

For the Middle Ridge Herd, mean population size and 95% confidence intervals were calculated, independently, for 1985 and 1995, after first testing for differences between aerial survey estimates (see Statistical Analysis). Approximate 95% confidence intervals were constructed as $\hat{N} \pm 2 \times$ standard error (SE), following the equation of Rice and Harder (1977):

$$\text{SE} = \sqrt{\frac{1}{K(K-1)} \sum_{i=1}^{K} (N_i - \bar{N})^2},$$

where K is the number of population estimates. As a relative measure of precision for $\hat{N}$, we also calculated the coefficient of variation (CV) as $\text{CV} = 1.96 \times \text{SE}/\hat{N}$.

Statistical Analysis

We used the chi-square goodness-of-fit test to determine if the frequency of animals resighted with marks was independent of group size (Siegel and Castellan 1988). Essentially, the procedure tested for a difference between the expected and observed distribution of marked animals among different group sizes. Data used in this analysis were extracted from resighting surveys of the Sandy Lake (1987), Pot Hill (1987), Gaff Topsails (1989), LaPoile (1988, 1992), and Middle Ridge (1995) herds. A total of 10,216 animals (of which 2,342 were marked) was distributed among groups ranging in size from 1 to 130 caribou. However, 95% of the animals we observed were in groups of <25 individuals and contained 75% of the number of marked individuals. Therefore, we determined the observed and expected frequencies for the number of marked individuals in group sizes of 1, 2, 3, . . . 24, and ≥25. We calculated the expected frequency of marked individuals for each group size by multiplying the proportion of marked animals in the population (2,342/10,216) by the total number of caribou observed in each group-size category.

Population estimates determined from the 2 aerial resighting surveys in the Middle Ridge areas during 1985 were compared via the goodness-of-fit method (Seber 1982:121). We also tested if the estimate determined from the ground resighting census was different than the aerial survey estimates. To reduce the Type I error rate, we only compared 1 aerial survey estimate with the ground estimate. We selected the estimate that would produce the largest effect size, and consequently maximize statistical power (Toft and Shea 1983). Finally, for the estimates obtained in 1995, we tested the effect on population estimates of using different aircraft (i.e., fixed-wing vs. helicopter) during resighting surveys.

We performed partial correlation analysis to determine the independent effect of n_1, n_2, and m_2 on the CV for population estimates (i.e., precision). Using this procedure, we were able to statistically control for the effect of 2 variables while examining how much the third variable contributed to the degree of precision.

RESULTS

Test of Assumptions

Results from the 15 radiocollared animals indicated there were no losses (mortality or emigration) from the Middle Ridge Herd during the 8-week study in 1985. All radiocollared animals were alive at the end of the resighting survey, and no individuals had moved out of the area. In addition, marks did not disappear from these animals during the 8-week period. These results suggest Assumptions (1) and (3) were not violated, at least for the Middle Ridge Herd (i.e., that populations were closed, and marks were not lost). However, with an increasing number of marked animals, the probability of losses (due to mortality or emigration) would likely increase and negatively affect population estimates. Further study with an increasing fraction of marked animals in population(s) of known size is necessary to determine how robust population estimates are to violations of Assumptions (1) and (3).

The observed and expected distribution of marked animals among different group sizes did not differ (χ^2_{42} = 36.42, $P > 0.30$), which suggests the frequency of resighted individuals with marks was independent of group size. Thus, we were able to provide partial support for the second assumption (i.e., no heterogeneity in sighting probability associated with group size).

Population Estimates and Assessment of the Technique

Caribou reacted strongly to low-level pursuit, but groups usually were spaced sufficiently so that driving animals across transect or block boundaries was restricted to the group being marked. Only animals initially sighted within survey boundaries were approached for marking. Furthermore, for instances in which simultaneous sightings of several groups were obtained, the location of each group was recorded prior to initiating marking procedures. Thus, the potential for inducing a negative bias in population estimates from the marking program was limited.

In 1985, there was no difference between the 2 population estimates determined from aerial resighting surveys for the Middle Ridge Herd ($Z = 0.80$, $P = 0.42$). Estimates obtained from aerial and ground resighting surveys also were similar ($Z = 1.01$, $P = 0.32$). The mean population size for the 3 estimates was 10,667 animals (95% CI = 432), which generated greater precision (CV = 4.1%) than each independent estimate (Table 1).

In 1995, we determined separate population estimates for the Middle Ridge Herd, using either fixed- or rotary-wing aircraft during the resighting census (Table 1). Although the estimate using the fixed-wing aircraft was larger and less precise than the estimate obtained via helicopter, the difference was not significant ($Z = 1.11$, $P = 0.26$). Mean population size from the 2 estimates was 20,958 animals (95% CI = 2,536).

During the resighting surveys, the ratio of marked to unmarked animals (i.e., resightability) ranged from 3.5 to 11.4%, while the fraction of marked individuals resighted from the marked population (i.e., resighting rate) varied from 10.7 to 58.5% (Table 1). As expected, the data suggested the degree of precision was correlated with resightability and resighting rate. However, due to the mathematical interdependence among n_1, n_2, and m_2, performing a correlation analysis on ratios of these variables could produce spurious results. For example, although there was no association between n_1 and n_2 ($P = 0.10$), m_2 was directly correlated with n_1 ($P = 0.02$) and n_2 ($P < 0.01$). A more statistically valid technique for investigating the relation between precision and these variables is to use multiple regression of integers.

Partial correlation analysis indicated the degree of precision (i.e., CV) was strongly associated with variation in the number of resighted animals with marks ($r = -0.95$, $P < 0.01$, $n = 12$), and was less dependent on the total number of animals resighted ($r = -0.20$, $P = 0.04$, $n = 12$; Fig. 2). There was no significant correlation, however, between precision and the initial number of animals marked after statistically controlling for the effect of n_2 and m_2 ($P > 0.15$). In addition, precision was independent of the estimate of population size ($P > 0.20$). These results suggest the degree of precision was influenced primarily by the number of animals resighted with marks, and secondarily by the total number of animals resighted (i.e., a measure of resighting effort).

DISCUSSION

Appropriate mark–resight techniques used to estimate population size should possess the following properties: (1) violate few assumptions, (2) generate precise and unbiased estimates, and (3) be cost effective. These features are not mutually exclusive, particularly (1) and (2), but they should be examined to assess the suitability of mark–resight methods. Although we were unable to determine fully the accuracy of the population estimates generated by marking caribou with spray paint, we were successful at evaluating several other properties of this novel approach. Our results indicate the method used here produced precise and likely unbiased population estimates for free-ranging caribou herds in insular Newfoundland.

Obtaining accurate and precise population estimates from mark–resight methods depends primarily on the extent to which the assumptions are violated (Seber 1982, Krebs 1989). Observations of radiocollared animals suggested the populations were closed and marks were not lost between the initial marking and resighting surveys (i.e., 2–3 weeks). Although we tested these 2 assumptions only on the Middle Ridge Herd in 1985, our experience indicates mortality and movement among herds is infrequent during mid- to late winter (see also Fong et al. 1990). In addition, these assumptions should be particularly robust given the short interval between censuses. We did, however, have to exercise caution when marking caribou because inaccurate application of paint can lead to misclassifying animals as marked or unmarked (Mercer et al. 1990), and biased population estimates can occur when individuals are incorrectly classified with regard to marks (Bear et al. 1989).

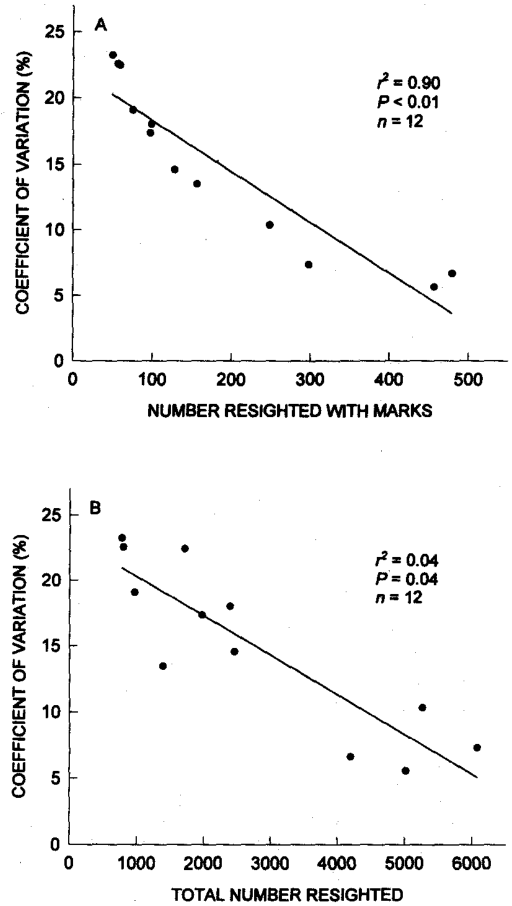

Fig. 2. Partial regressions for the relation between the coefficient of variation in caribou population estimates and number of animals resighted with marks (A) and total number of animals resighted (B).

Heterogeneity in sighting probabilities of marked animals is the principal factor responsible for biased and imprecise population estimates. Sighting probability may be affected by group size and age- and sex-specific differences in spatial distribution (Sage et al. 1983, Peterson and Page 1993, Vincent et al. 1996). Although we did not investigate the influence of age and sex on resighting probabilities, results showed the distribution of marked individuals was homogenous among group sizes. Thus, the probability of resighting a marked animal was independent of group size, which further increases confidence in population estimates. In addition, because caribou were invariably sighted before marks were actually observed, behavioral analogues of "trap shyness and happiness" would have had a negligible effect on the estimates.

During the mark–resight period, visibility of caribou on the snow-covered barrens was optimal. High visibility likely generated marginal sightability bias and possibly produced reliable population estimates. Although a more rigorous evaluation of the bias associated with this method is required, a previous study on a small, isolated caribou population of known size indicated the method produced unbiased estimates when the proportion of animals marked in the population was 83% (Mercer et al. 1990). Future work should also involve the use of different colored paint to determine if resighting probabilities are affected by age and sex differences. However, we believe this study has unequivocally demonstrated the ability of this technique not to violate the fundamental assumptions of mark–resight methods.

The degree of precision (CV) for the caribou population estimates was dependent primarily on the number of animals resighted with marks (m_2), and secondarily on the total number of animals resighted (n_2). Other studies have also linked width of confidence interval with m_2 (Bartmann et al. 1987, Bear et al. 1989, Neal et al. 1993). Increasing resighting effort (i.e., n_2) is also a standard procedure for generating more accurate and precise estimates (Seber 1982, Krebs 1989). Importantly, the number of animals initially marked (n_1) had no significant effect on precision of caribou population estimates. This result suggests the fraction of marked animals in each population (range = 4–11%) was likely not limiting precision, at least for the distribution of population size and n_1 examined here. Theoretically, accuracy and precision decrease hyperbolically as a function of n_1. Hence, once the asymptote is reached, bias and precision will be unaffected by increasing the number of animals marked. Similar results have been obtained in fallow (*Cervus dama*) and white-tailed deer (McCullough and Hirth 1988, Vincent et al. 1996). Finally, results from the Middle Ridge Herd in 1985 showed that combining a number of resighting surveys produced narrower confidence intervals.

The efficiency of marking a large number of caribou in a relatively short period to obtain population estimates is among the most salient features of this technique. High efficiency largely occurred because there was virtually no handling time involved while applying marks. Mercer et al. (1990) reported a marking rate of 1.1 caribou/min when caribou density was 4.7/km^2. The rate of marking decreased proportionately with a decline in density. Because there is no physical handling of animals, spray painting likely causes less stress than other mark–recapture procedures. We have also observed no pathological effects from the paint (Mercer et al. 1990). The method provides a practical and cost-effective alternative to more traditional marking techniques such as radiocollars, colored collars, and ear tags.

MANAGEMENT IMPLICATIONS

Biologists managing wildlife populations are constantly searching for mark–resighting methods that provide reliable estimates for a minimum cost. The method applied here for woodland caribou complied with the fundamental assumptions of the Petersen estimate. Analysis also revealed the degree of precision was strongly dependent on the number of animals resighted with marks (m_2; Seber 1982). However, after statistically controlling for m_2, precision was also correlated with resighting effort (n_2), but was independent of the number of caribou initially marked (n_1).

These results have general implications for mark–resighting methods. There is likely a sharp truncation in the relation between accuracy and precision and the fraction of animals marked in the population (i.e., the asymptote is approached rapidly). Consequently, after some threshold value, increasing only the number of marked individuals in the population will have little effect on reliability of the estimate. Precision and accuracy then become limited by the number of animals resighted with marks, which is partly a function of resighting effort. Money and time saved by efficiently marking a large number of animals with pressurized paint can be used to increase resighting effort. The method evaluated in this study may provide reliable and cost-effective population estimates for many ungulates and other large mammals (e.g., brown bears [*Ursus arctos*] and polar bears [*U. maritimus*]) inhabiting semiopen areas during part of the year.

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