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TECHNICAL REPORT

Evaluation of aerial surveys of ptarmigan *Lagopus* species

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Summary

1. We evaluated the reliability of aerial surveys to monitor trends in breeding population density of ptarmigan *Lagopus* spp. in south-western Yukon, Canada.
2. Aerial surveys provided repeatable indices of density.
3. Aerial indices of density were positively and linearly related to density between areas within the same year.
4. However, aerial indices of density were not positively related to density between years because the aerial index was lower in 1996 than in 1995, while in fact the density of ptarmigan increased. This could be explained by a reduction in the flushing response of ptarmigan in 1996.
5. We caution wildlife managers against a possible inter-year variation in the number of animals that can be seen from the air when conducting aerial surveys.

Key-words: calibration, counting bias, repeatability, survey errors, Yukon.

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Introduction

Aerial surveys are used or tried on a multitude of organisms that can be seen from the air. Many types of errors can alter the reliability of estimates generated from these surveys. Accidental errors include random-sampling error and editing errors (errors introduced in editing, coding and tabulating the results; Cochran 1977). Non-accidental errors include counting bias (errors of measurement; Cochran 1977), sampling bias (Jolly 1969), estimator bias (Jolly 1969; Cochran 1977) and non-response bias (failure to measure some of the units in the chosen sample; Cochran 1977). Finally, the total survey error includes rounding error (Bjerhammar 1973). For a detailed review of the different types of survey errors, refer to Pelletier (1996). Of all these errors, random-sampling error and counting bias are probably the most important types of errors affecting aerial survey estimates.

Counting bias is a main source of negative error in aerial surveys (Jolly 1969; Cook & Jacobson 1979) and results in an underestimation of the actual population size (Caughley 1974; LeResche & Rausch 1974; Wolfe & Kimball 1989). Counting bias has two components that may vary across surveys (Marsh & Sinclair 1989): (i) an availability bias, i.e. animals are concealed by other animals or the environment; and (ii) a perception bias, i.e. animals are potentially visible to observers but are not seen.

Much has been written about the need to improve the precision of population estimates (by reducing the random-sampling error) in order to improve the power of surveys to detect trends in abundance (Siniff & Skoog 1964; Caughley 1977; Kraft *et al.* 1995). Much has also been written about the need to correct for the perception bias in order to eliminate errors in counting that can be attributed to poor or variable visibility conditions between surveys (Caughley 1974; Caughley & Grice 1982). However, the problem of fluctuating availability bias has received far less attention. The problem is relevant to all aerial surveys where there is a portion of the population concealed and which do not use the double-sample (Jolly 1969) or mark–recapture method (Packard, Summers & Barnes 1984) to correct for availability bias. Other correction methods, such as line-transects (Buckland *et al.* 1993) and double-counts (Cook & Jacobson 1979; Graham & Bell 1989), correct only for the perception bias. With line-transects, the availability bias is made up of animals missed on the centreline.

The objective of this study was to evaluate the reliability of aerial surveys to monitor trends in breeding population density of ptarmigan *Lagopus* spp.

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over large areas ($>30\,km^2$). Presently, the only reliable large-scale surveying technique for ptarmigan is line-transect sampling on foot (Pelletier & Krebs 1997). This method accurately estimates male ptarmigan density during the breeding season, but is slow and demanding in terms of efforts compared to aerial surveying. On the other hand, aerial surveys of ptarmigan may be unreliable because the counting bias may be large and variable due to the elusiveness of ptarmigan and poor visibility conditions.

To evaluate the reliability of aerial surveys of ptarmigan we used a three-step protocol of evaluation: (i) a reduction of the main sources of errors, (ii) a test of the repeatability, and (iii) a calibration. Repeatability indicates how reproducible the survey estimate is under conditions where the population parameter estimated is assumed not to vary. In the calibration, estimates from a relatively cheap survey method are compared to estimates from a reliable, but more expensive, survey method (Dodd & Murphy 1995; Rodgers, Linda & Nesbitt 1995; Prenzlow & Lovvorn 1996). This protocol permits detecting errors often overlooked, such as a fluctuation of the availability bias.

Methods

AERIAL SURVEY PROTOCOL

Each year between 24 April and 8 May, from 1990 to 1996, the Kluane Boreal Forest Ecosystem Project (Boutin *et al.* 1995) has conducted aerial surveys in the subalpine region of Kluane (61°N, 138°W), southwestern Yukon, Canada, to track population trends of the breeding population of willow ptarmigan *Lagopus lagopus* (L.). A few rock ptarmigan *Lagopus mutus* (Montin) and white-tailed ptarmigan *Lagopus leucurus* (Richardson) were present in the areas surveyed and were included in the counts. These two species accounted for less than 5% of all counts. Three major plant species provide cover for the birds: willow *Salix* spp., dwarf birch *Betula glandulosa* (Raup) and white spruce *Picea glauca* (Voss). The height of the vegetation protruding out of the snow pack is low (<1 m) and does not provide much cover for the birds. Snow cover varied from year to year, and ranged from 25% to 100%. Willow ptarmigan did not use snow holes during the period when surveys were conducted.

We sampled seven distinct areas, with size ranging between 3 and $13{\cdot}5\,km^2$. Natural features such as ridges and streams were used to delineate the areas. Not all of the areas were sampled each year. The number of transects per area was determined by the width of the area, with two to five transects per area, spaced about 300–500 m apart. Transects were 1·5–10 km long and were parallel to contour lines. It was not possible to survey the same transects each year because flight conditions were too variable. Details of the sampling protocol are presented in Table 1.

Three observers counted ptarmigan in a Helio-courier aircraft: one at the front at the right hand side of the pilot, and two on the back seats, one on each side. The pilot did not take part in counts. Speed (80–160 km h^{-1}) and elevation (20–50 m) were kept as constant and low as possible, but still varied because of wind gusts. Because the field of vision of observers varied a great deal, counts were considered unbounded. The farthest observations were about 100 m from the centreline, so that these birds were too far to be counted again from the adjacent transects. For each transect, each observer recorded (i) the number of birds seen, (ii) if they were singles, in a pair or in a flock, and (iii) flushed or on the ground. Until 1995, (ii) and (iii) were not recorded systematically. Since the rates of encounter were low, the two observers sitting on the right hand side of the plane used a simple method similar to the one of Graham & Bell (1989) to avoid double-counting. In the plane, observers were linked by intercom. Whenever the back seat observer detected a ptarmigan, he/she spoke into the microphone about one second later. The front seat observer noted whether or not he/she had made the same observation. This lapse of one second was short enough to make sure that the front seat observer counted as a distinct individual another bird seen a few seconds after or before. Because counts were unbounded and transects were of unequal lengths, we expressed aerial counts as encounter rates, i.e. number of observations per kilometre of transect, using the ratio estimator.

AERIAL SURVEY INDEX OF DENSITY – RATIO ESTIMATOR

The ratio method (Cochran 1977) weighs the number of observations per transect by the length of the transects. The ratio estimator for simple random sampling $\hat{R}$ is:

$$\hat{R} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i} \qquad \text{eqn 1}$$

where y_i = number of observations in transect i, x_i = length of transect i, and n = number of transects. We used the jack-knife ratio estimate, $\hat{R}_Q$, as the index of population density for the aerial surveys. $\hat{R}_Q$ is the average of the n quantities:

$$\hat{R}'_j = n\hat{R} - (n-1)\hat{R}_j \qquad \text{eqn 2}$$

where $\hat{R}_j = \hat{R}$ computed after omitting transect j (Cochran 1977). An unbiased estimate of the variance of $\hat{R}_Q$ is:

$$\text{var}(\hat{R}_Q) = \frac{\sum^{n}(\hat{R}'_j - \hat{R}_Q)^2}{n(n-1)}. \qquad \text{eqn 3}$$

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Table 1. Transect efforts and indices of abundance per survey, $\hat{R}_Q$, for aerial surveys of ptarmigan in Kluane, Yukon, from 1990 to 1996

Year	Survey	Date	n_t*	L†	n_s‡	$\hat{R}_Q$§	%CV	Sensitivity¶
1990	1	8 May	9	25·5	17	0·677	35·5	132
1991	1	27, 29 April	19	65·7	132	2·003	35·5	123
1992	1	30 April	19	67·7	76	1·135	16·7	58
1993	1	6 May	20	63·9	9	0·140	50·0	173
1994	1	2 May	10	33	14	0·440	74·8	274
1995	1	29 April	19	64·3	53	0·824	33·5	116
	2	1 May	12	48	34	0·708	34·6	124
	Mean					0·766	10·7	
1996	1	24 April	28	93·5	25	0·268	28·1	96
	2	27 April	28	93·5	37	0·394	22·1	75
	3	3 May	28	92·5	44	0·478	22·9	78
	4	6 May	28	94·5	17	0·180	22	75
	5	8 May	28	95·5	33	0·346	20·8	71
	Mean					0·333	34·4	

* Number of transects.
† Total length of transects (km).
‡ Number of ptarmigan sightings per survey.
§ Jack-knife ratio estimate (ptarmigan seen km^{-1} of transect) = index of abundance.
¶ Sensitivity = $[(95\%\text{UCL} - 95\%\text{LCL})/\hat{R}_Q] \times 100\%$.

We used the Student's t distribution to compute 95% confidence limits for $\hat{R}_Q$:

$$\hat{R}_Q \pm t_{0{\cdot}05(2),n-1}\sqrt{\mathrm{var}(\hat{R}_Q)}. \qquad \text{eqn 4}$$

COUNTING BIAS

We did not correct aerial indices of abundance for counting bias. We could not use the simultaneous double-count method (Magnusson, Caughley & Grigg 1978; Cook & Jacobson 1979; Caughley & Grice 1982; Graham & Bell 1989) to correct counting bias because the number of double-counts was less than seven in most surveys, which caused a high error in correction factors. The modified Petersen estimator for small samples requires at least seven recaptures to be unbiased (Krebs 1989). Line-transects would not work because an unknown number of birds is missed on the centreline and birds move prior to detection. Mark–recapture is time-consuming (trapping the birds each year) and costly in material (radiotelemetry equipment). Only double-sampling remained as a method to correct the counting bias, but we used the ground counts for the calibration. For a review of correction methods, see Pollock & Kendall (1987).

REPEATABILITY

A survey technique provides repeatable estimates if the variability between estimates taken in a window of time, when the population parameter estimated is assumed not to have varied, is lower than the variability between estimates taken over a period of time when the population parameter estimated could vary. To estimate repeatability, we conducted the aerial survey five times in 1996 between 24 April and 8 May. s^2_{intra} is the variance between the five $\hat{R}_Q$ of 1996, and s^2_{inter} is the variance between the $\hat{R}_Q$ from 1990 until 1996. We tested H_o: $s^2_{inter} \leqslant s^2_{intra}$ with a one-tailed variance ratio test where $F = s^2_{inter}/s^2_{intra}$ ($\alpha = 0{\cdot}05$). If H_o is not rejected and the power is sufficiently high ($\beta < 0{\cdot}40$), the technique is not repeatable because there is as much absolute variability (opposed to relative variability) within the replicated indices of abundance of a given year as there is between 7 years of counts.

To assess the relative variability attributable to daily factors (e.g. wind, sunny/overcast sky, snow cover, biological timing), we used a two-layered replication procedure in 1996. In each of the five surveys of 1996, we surveyed six of the seven areas once and the other area twice. From survey to survey, a different area was sampled twice. This provided an estimate of the variance between two aerial estimates $\hat{R}_Q$ for the same day. The first $\hat{R}_Q$ was calculated using combined counts from all first samplings of areas sampled twice; the second $\hat{R}_Q$ from all second samplings of areas sampled twice. The relative variability attributable to daily factors ($CV_{daily\ factors}$) is the difference between the relative variability between the $\hat{R}_Q$ from replicate surveys done over 2 weeks (CV_{intra}) and the relative variability between the $\hat{R}_Q$ from replicate counts in the same areas on the same day ($CV_{same\ day}$). So: (i) $CV_{daily\ factors} = CV_{intra} - CV_{same\ day}$, and (ii) the percentage of total variability depending on daily factors $= CV_{daily\ factors}/CV_{intra}$.

CALIBRATION

Ground counts

Ground counts were used as best estimates of the actual density for the calibration. Details of the ground counts methods and results are presented in Pelletier & Krebs (1997). As a summary, two observers undertook ground counts, using line-transect sampling (Buckland *et al.* 1993), from late April to early June in two areas in 1995 and in six areas in 1996. This provided an accurate estimate of the breeding density of male ptarmigan for each of these areas (bias = −3 to −7%; Pelletier & Krebs 1997).

We also conducted one total ground count on a 77-ha grid in 1995 and one in 1996 (details in Pelletier & Krebs 1997). The grid was located in one of the seven areas. We treated these total counts as Poisson counts.

Geometric mean regression

We calibrated the aerial indices of some of the areas of 1995 and 1996 (means of the replicate surveys per area) with the ground counts. The use of the geometric mean regression (GMR) was necessary for the calibrating model because of errors in both variables (Ricker 1973, 1984): x the estimates of density from ground counts and y the aerial indices of abundance. The slope of the central trend line is given by:

$$\hat{v} = \frac{\hat{b}}{r} = \sqrt{\frac{\hat{b}}{\hat{d}}} \qquad \text{eqn 5}$$

where $\hat{v}$ = estimated slope of the GMR, $\hat{b}$ = estimated slope of least-squares regression of y on x, r = correlation coefficient between x and y, and $\hat{d}$ = estimated slope of the least-squares regression of x on y (Ricker 1973). The 95% confidence limits of $\hat{v}$ are:

$$\hat{v} \pm s_{\hat{v}} t_{0\cdot05(2),\mathrm{df}} \qquad \text{eqn 6}$$

where $s_{\hat{v}} = s_{\hat{b}}$ (Ricker 1973). We set the intercept of the regression = 0 (at a true density of 0, no ptarmigan can be seen) so that the no-intercept GMR model is:

$$\hat{\hat{R}}_Q = \hat{v}\hat{D} \qquad \text{eqn 7}$$

where $\hat{\hat{R}}_Q$ = estimate of the aerial index of abundance, and $\hat{D}$ = estimate of density from ground counts. We provide, in addition, a GMR model with a y intercept, y_0, estimated from the data:

$$y_0 = \bar{y} - \hat{v}(\bar{x}) \qquad \text{eqn 8}$$

where $\bar{y}$ and $\bar{x}$ are, respectively, the observed mean values of y and x (Ricker 1973).

Results

REPEATABILITY

The technique was repeatable because the variance between the five survey indices of 1996, $s^2_{\mathrm{intra}} = 0{\cdot}0131$, was significantly lower than the variance between years, $s^2_{\mathrm{inter}} = 0{\cdot}396$ ($F = 30{\cdot}2$, d.f. = 6, 4, and $0{\cdot}005 > P > 0{\cdot}0025$). The intra-year variance between indices of abundance s^2_{intra} was only 3·3% of the inter-year variance s^2_{inter}. With CV_{intra} = 34·4% (Table 1) and $CV_{\mathrm{same\ day}}$ = 10·0%, 71% of the variability between replicate surveys in 1996 could be attributed to daily factors.

CALIBRATION

Aerial indices were positively ($\hat{v} > 0$; $t = 8{\cdot}427$, $n = 7$, $P < 0{\cdot}001$) and linearly related to density (no-intercept GMR model of Fig. 1a). The GMR model with intercept [$\hat{\hat{R}}_Q = -0{\cdot}0329 + 0{\cdot}0147(\hat{D})$] also provided a positive ($\hat{v} > 0$; $t = 4{\cdot}181$, $n = 7$, $P < 0{\cdot}01$) and linear relationship except that the fit of this model with the data was poorer ($r^2 = 0{\cdot}71$) than the fit of the no-intercept GMR model ($r^2 = 0{\cdot}92$).

The positive and linear relationship between aerial indices and density occurred only within years and not between. The mean aerial index of 1996 [$\bar{\hat{R}}_Q = 0{\cdot}333 \pm 0{\cdot}051$ (SE)] was significantly lower than in 1995 ($\bar{\hat{R}}_Q = 0{\cdot}766 \pm 0{\cdot}058$) using a two-tailed t-test ($t = 3{\cdot}092$, d.f. = 5, $P = 0{\cdot}027$) (Table 1). But densities on the ground were significantly higher in 1996, in two out of three areas (Table 2). Therefore, the change in aerial index was negatively related to the change in density between 1995 and 1996. The calibrating model of Fig. 1a did not apply between years. After removal of the single 1995 data point we had included in the calibrating model of Fig. 1a, the no-intercept GMR model basically stayed the same: $\hat{\hat{R}}_Q = (0{\cdot}0137)\hat{D}$, where the slope $\hat{v} > 0$ ($t = 8{\cdot}954$, $n = 6$, $P < 0{\cdot}001$). Thus, the survey technique could detect differences in density in a given year, in this case 1996. That is, even at different densities, a constant but unknown proportion of the population was detected. The positive relationship between the aerial index and density may still be true for years other than 1996, except that the slope of the relationship may vary. Figure 1b presents the calibrating model using only sightings of ptarmigan flushed by the aircraft (the birds more readily seen from the aircraft), the slope $\hat{v} > 0$ ($t = 8{\cdot}238$, $n = 6$, $P < 0{\cdot}001$).

The proportion of aerial counts accounted for by ptarmigan that did not flush in response to the aircraft increased significantly between 1995 and 1996. In 1995, 8·8% ± 12·5% (SE) of ptarmigan detected from the air did not flush. In 1996, this number rose to 44·7% ± 21·0%. Using a 2-tailed t-test with the arcsin transformation: $t = 2{\cdot}583$, d.f. = 5, and $P = 0{\cdot}049$.

Discussion

VALIDITY OF THE REPLICATION OF THE 1996 AERIAL SURVEY

Two factors may have had an impact on the validity of the replication procedure. Ptarmigan may have

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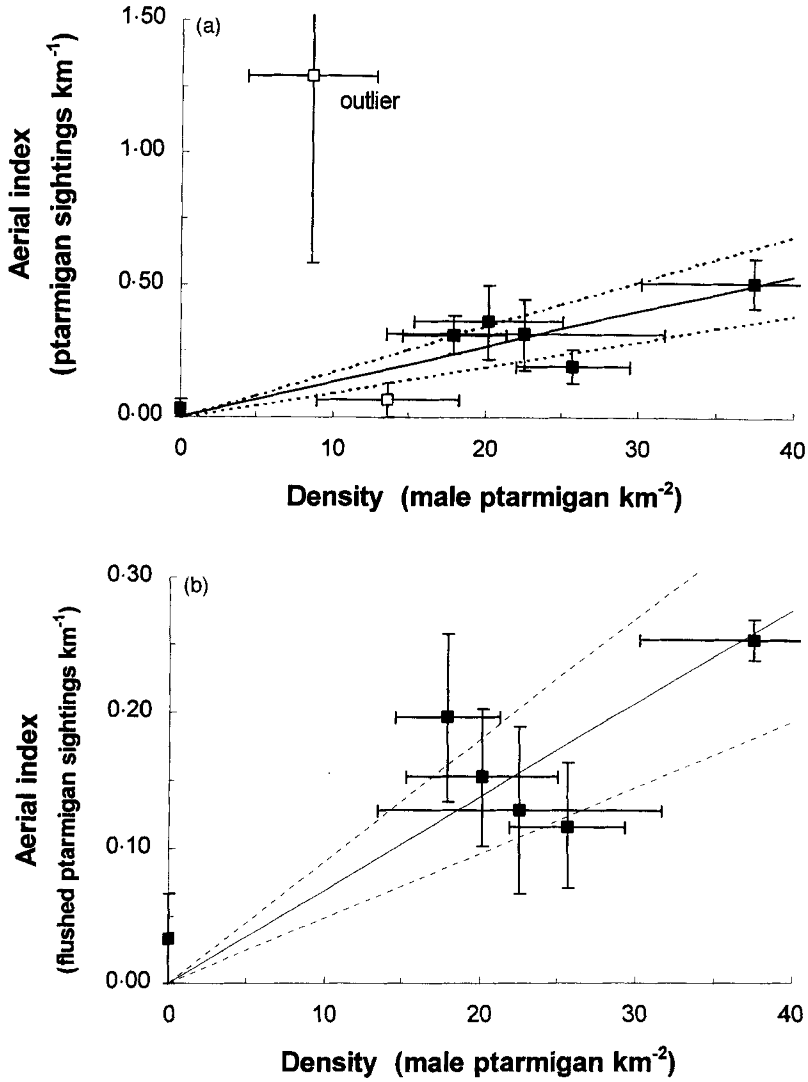

Fig. 1. Central trend line of the geometric mean regression (solid line) ± 95% confidence limits (dotted lines) for the calibration of the aerial index of abundance R_Q (ptarmigan sightings km^{-1} of transect) vs. density (male ptarmigan km^{-2}) from ground counts in Kluane, Yukon, in 1995 and 1996. Each data point represents the mean and standard error (error bars) of repeated survey estimates for individual areas in 1995 (□) and 1996 (■). (a) Aerial counts including all sightings of ptarmigan: $\hat{\hat{R}}_Q = (0{\cdot}0134)\hat{D}$, and $r^2 = 0{\cdot}92$. The outlier was not included in the regression since its standard error in y was too large, which may be because this 1995 aerial index was based on only two aerial surveys, compared to five or six for the 1996 indices. (b) Aerial counts including only sightings of ptarmigan that flushed in 1996. $\hat{\hat{R}}_Q = (0{\cdot}00691)\hat{D}$, and $r^2 = 0{\cdot}93$. Details of ground counts are in Pelletier & Krebs (1997).

Table 2. Inter-year comparisons of the estimated density $\hat{D}$ of ptarmigan (males km^{-2}) between 1995 and 1996 in two areas of Kluane, Yukon, with two-tailed t-tests, and of total counts on a grid using Poisson. For area 1, the power of the test = 0·447

Area	$\hat{D}_{1995}$	SD	$\hat{D}_{1996}$	SD	d.f.	t	P
1	13·6	4·69	18·0	3·37	19	0·546	0·591
2	8·6	4·24	25·7	3·70	42	2·154	0·037*
						z	P
Grid	24·7	–	64·9	–	–	4·25	<0·0001*

* Significant statistical difference ($\alpha = 0{\cdot}05$).

become habituated to the aircraft and the two observers that did the five surveys may have improved their counting skills during the surveys.

The repetition of the aerial surveys over a short time could have habituated ptarmigan, making them less prone to respond (i.e. flush) to the aircraft. This would have potentially decreased the availability of the birds and increased the variability between replicate counts. There was no evidence that habituation occurred. The five surveys were spaced by 2–6 days and the location of transects varied by up to 100 m, so different birds could be flushed from time to time. Only one transect was static (marked with 4-m^2 fluorescent orange boards on the ground) and on this transect, the number of birds flushed increased through surveys (0–0–0–0–4). Ground transect observations showed that birds flushed once were just as easy to flush a second or even a third time. Ptarmigan did not even seem to habituate on a short time-scale since the relative variance between replicate counts done on the same day was only 10% (CV).

The two observers who did the five surveys could have become more skilled through surveys, but there was little time for it. The total number of hours of aerial surveying amounted to about 6 hours in 1996, split into five surveys. There was still a possible gain in experience throughout surveys, but it probably had less effect on the counts than the natural detection ability of the observers. At worst, the two factors could have increased the variance between replicate surveys, resulting in a conservative evaluation.

CALIBRATION

Results showed that we could not use the calibrating model found with 1996 data (Fig. 1a) to compare indices of abundance between years because the relationship between indices of abundance and density, based on inter-year results, was the reverse. What could explain the lower 1996 aerial index compared to 1995 when density was higher in 1996? The lower aerial index was not due to (i) less visibility (e.g. more snow cover) or (ii) less experienced observers in 1996 vs. 1995 because birds that did not flush accounted for a significantly higher proportion of the aerial counts of 1996 compared to 1995 (44·7% in 1996 vs. 8·8% in 1995), and birds staying on the ground are more difficult to detect from the air than birds that flushed. One remaining explanation is that there was a change in the flushing behaviour of ptarmigan: they flushed less in 1996 and, thus, aerial counts were lower.

Reduced flushing could not be a consequence of increased density (e.g. from stress effects) or of low willow cover (1996 was a late year for the melting of snow), but it may have been a consequence of increased avian predation pressure. If increased density were the cause, the slope of the calibration based only on sightings of birds that flushed (Fig. 1b) would have been negative, which is not the case. Low willow cover could not be the cause, either, because the flushing did not increase in the last 1996 survey when only about 25% of snow cover remained on most areas. In fact, we had hypothesized the influence of willow cover to be the opposite: when willow is high enough to provide a good cover, birds should sit tight rather than flush when the plane flies overhead (F.I. Doyle, personal communication). However, ptarmigan could flush less because of increased avian predation pressure. In the study area, golden eagles *Aquila chrysaetos* (L.) and northern goshawks *Accipiter gentilis* (L.) are the main species of raptors to prey on adult ptarmigan during breeding. We did not formally survey those two species because we did not suspect their potential role at that time, but there were more sightings of golden eagles in 1996 than in 1995; there were also four or five suspected active nests in 1996 compared to two in 1995. Another argument that points to an increase in the golden eagle population in 1996 is that at Denali, Alaska, the proportion of the territorial population of golden eagles that lays eggs each year is known to change in response to the numbers of snowshoe hares *Lepus americanus* (Erxleben) and willow ptarmigan available in the area (C. McIntyre, National Park Service, personal communication). In Kluane, the snowshoe hare (C.J. Krebs, unpublished data) and ptarmigan populations did increase in 1996.

For this change in flushing to occur, ptarmigan may have adapted their behaviour individually, or the composition of the ptarmigan population may have changed, new individuals not tending to flush. This last hypothesis is realistic in ptarmigan populations because the turnover of individuals can be high, with adult mortality rates between 40% and 60% per year (Mossop 1987) and an average of three offspring fledged per clutch (Martin, Hannon & Rockwell 1989).

In summary, the variability of the counting bias was low within a given year, as demonstrated by the test of repeatability. On the other hand, between years the counting bias varied highly and in unexpected ways, as demonstrated by the comparison of the positive slope of the calibration vs. the decrease in density between 1995 and 1996.

IMPLICATIONS

This survey programme was based on the assumption that the behaviour of ptarmigan in response to the aircraft does not change from year to year. This was apparently incorrect. This type of assumption is common in wildlife surveys. For instance, estimates of density of small mammals based on trapping assume an equal catchability from year to year (Krebs 1989). Therefore, we caution wildlife managers against a possible fluctuation of availability bias between years.

If availability bias fluctuates between years, it is mandatory to use a correction method that corrects for the entire counting bias, not just for the perception bias as the double-counts and line-transect methods do. The double-sampling and mark–recapture methods are the only ones that can efficiently correct for the entire counting bias with fixed-winged aircraft sampling.

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