

Line-transect sampling for estimating ptarmigan (*Lagopus* spp.) density

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Abstract: Current methods of estimating ptarmigan density require total counts, and hardly apply to areas exceeding 1 km². We evaluated the applicability, accuracy, and efficiency of line-transect sampling as an alternative method for estimating breeding density of male ptarmigan. We compared Hayne's and generalized Hayne's estimators with line-transect estimators based on perpendicular distance. We surveyed 6 subalpine areas in Kluane, Yukon, with 231 km of transects in 1995 and 1996, in addition to a 77-ha grid where we also conducted total counts. Estimates of perpendicular distance were accurate (bias = -3 to -7%). Their efficiency resides mainly in detecting changes in density over 2-year periods in highly or moderately fluctuating populations. Performance of Hayne's estimator was close to that of perpendicular distance (coefficient of correlation, $r = 0.95$), even if in many cases the average sighting angle was not 32.7°. The generalized Hayne's estimator was not robust; biases were up to -90%. The results of this survey, with densities ranging between 0 and 65 males/km² for similar and adjoining subalpine areas, dispute the principle that the "health" of a population can be assessed by censusing only a small area.

Résumé : L'estimation des densités de lagopèdes (*Lagopus*) se fait par décomptes totaux, ce qui s'applique mal aux aires de plus de 1 km². Nous avons évalué l'applicabilité, l'exactitude et la précision des ligne de transect comme autre méthode d'estimation des densités de lagopèdes mâles pendant la saison d'accouplement. Nous avons comparé cette méthode, basée sur les distances perpendiculaires, aux estimateurs Hayne et Hayne généralisé. En 1995 et 1996, nous avons inventorié les oiseaux dans 6 zones subalpines à Kluane, Yukon, soit 231 km de transect, et avons également compté tous les oiseaux dans une grille de 77 ha. Les estimations basées sur les distances perpendiculaires se sont avérées exactes (biais = -3 à -7%); leur précision permettait surtout de détecter les variations de densité sur une période de 2 ans au sein de populations à fluctuations moyennes ou importantes. L'évaluation des populations selon la méthode Hayne a donné des résultats semblables (coefficient de corrélation, $r = 0,95$), même si dans bien des cas, l'angle moyen d'observation n'était pas de 32,7°. L'estimateur Hayne généralisé n'était pas robuste; les biais sur les estimations pouvaient atteindre -90%. Les résultats de cet inventaire, où la densité des mâles variait de 0 à 65/km² en des zones subalpines adjacentes et semblables, remettent en cause le principe selon lequel la santé d'une population peut être jugée par inventaire d'une petite zone.

Introduction

There are no known methods for reliably estimating densities of ptarmigan (*Lagopus* spp.) populations on a large scale. This information is necessary to assess the "health" of these game bird populations and to manage them wisely on the huge area that they occupy, i.e. most of the Canadian arctic and alpine regions (Godfrey 1986). Such methods are also necessary to test fundamental ideas about factors that regulate ptarmigan breeding density in space. Present methods for estimating density of ptarmigan, typically censusing, apply only to small areas (<2 km²) and there is no evidence that this information can be extrapolated to larger areas. A census is a complete enumeration of a population, while a survey is a sample of that population (Cochran 1977). The most accurate censusing method for ptarmigan is to map

territories after all the individuals have been banded (e.g., Mossop 1987; S.J. Hannon, cited in Boutin et al. 1995). However, it is not practical to use this technique on an area larger than 100 ha, owing to the required effort. *Transect censusing*, i.e., counting every bird in a strip, using a dog for flushing (e.g., Mossop 1994), is faster and more practical, but is also limited to small areas in order to obtain reasonable accuracy. With this technique, the risk of double-counting some birds and missing others seems to increase almost exponentially with the size of area censused. Another technique, *aerial surveys*, can cover very large areas at low cost. However, when done by fixed-winged aircraft, this technique provides only indices of abundance. Pelletier (1996) showed that the technique did not provide reliable indices for comparing abundances through years, possibly because of a change in the flushing response of ptarmigan to the aircraft over years. The technique we evaluated, *line-transect sampling*, is used widely in wildlife management in aerial (e.g., Holt and Cologne 1987; White et al. 1989) and ground surveys (e.g., Kelley 1996; Sherman et al. 1995). The technique can easily be applied to large areas because it is the absolute size of the sample (the number of detections and transect lines) that is important, not the fraction of the population sampled (Buckland et al. 1993). It is an efficient way to sample elusive populations such as ptarmigan because

Received November 17, 1996. Accepted February 17, 1997.

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(i) not all of the birds need to be seen in a strip (only those directly on the centre line), and (ii) it is a self-correcting method that adjusts to variable detection conditions.

Hayne (1949) provided the first line-transect estimator with rigorous justification in statistical theory (Buckland et al. 1993); his technique was developed for flushing animals such as grouse and was based on sighting distances and angles. Nowadays, robust line-transect estimators exist that are based on perpendicular distance (see Buckland et al. 1993). By conducting a large ground survey and making comparisons with known densities on a grid, we wanted to evaluate the applicability, efficiency, and accuracy of both types of estimator for ptarmigan populations. This provides the first known field comparison of the two types of estimator (D.R. Anderson and K.P. Burnham, personal communication).

Methods

Sampling protocol

We conducted this study in the subalpine region of Kluane (61°N, 138°W), southwestern Yukon, Canada, in spring of 1995 and 1996 as part of the evaluation of an aerial survey program for ptarmigan (see Pelletier 1996). Three major plant species provide cover for the birds in the subalpine region of Kluane: willow (*Salix* spp.), dwarf birch (*Betula glandulosa*), and white spruce (*Picea glauca*). Three species of ptarmigan occur in the areas surveyed: the common willow ptarmigan (*Lagopus lagopus*) and the rarer rock ptarmigan (*Lagopus mutus*) and white-tailed ptarmigan (*Lagopus leucurus*). We started surveyed in late April of each year, once most of the males were on territories and had started to be conspicuous, and we stopped in the first week of June, shortly after the start of egg laying, when males became much harder to detect.

Two observers did line-transects in 2 areas in 1995 and in 6 areas in 1996 (transect effort in Table 1). One of the two observers changed in 1996. Line-transect sampling provided an estimate of breeding density of male ptarmigan for each of these areas (female ptarmigan are too secretive and move away from the line before detection). We sampled areas one at a time in the morning. We determined the order of sampling areas by accessibility. We did systematic transects perpendicular to the stratification of the habitat (from the treeline to the alpine area, and then vice versa). We recorded the length of each transect, and for each observation of male ptarmigan (i) the perpendicular distance between the original location of the bird and the centre line, d , and (ii) if the bird flushed, the flushing distance from the observer, r . The sighting angle, θ , could be calculated afterwards with $\theta = \arcsin(d/r)$. We used two different methods to estimate the length of transects, L : (1) topographic maps using landmarks and (2) pedometers. We calibrated pedometers on 1100-m transects set on a grid. This grid is described in the section on the test of accuracy. We used estimates from maps to help us reduce our estimates of L when walking conditions were difficult, because pedometers could then overestimate L by up to 10%. We used 30-m polyurethane or metal measuring tapes to measure d and r . We did not use dogs on the transects because the snow was too deep (1–1.25 m) and soft in early May.

Data analysis

Estimators based on perpendicular distance

Estimators using perpendicular distance (PD) are based on the concept that the detection function $g(y)$ decreases with increasing distance from the transect line (Burnham et al. 1980; Buckland et al. 1993). The general estimator of density for line transect sampling is

$$[1] \hat{D} = n_s \cdot \hat{f}(0)/2L$$

where

n_s is the sample size (number of male ptarmigan detected)
 L is the length of the transect
 $f(0)$ is the estimated value of the probability density function (PDF) of perpendicular distances at zero distance

To estimate $f(0)$, we pooled distance data over years, observers, and areas. However, we restricted the pooling to two sets, one for data gathered before snowmelt and leaf-out of willow and one for data gathered after. We preferred not to pool those two sets because visibility conditions varied between the two periods. This change is corroborated by the variation in the effective strip width (ESW). The ESW is the half-width of the strip extending either side of the transect centre line, so that as many birds are detected outside the strip to remain undetected within it (Buckland et al. 1993). The ESW was significantly lower after snowmelt and willow leaf-out (ESW = 16.6 m; 95% confidence limits (CL) = 13.9–19.8 m) than before (ESW = 24.5 m; 95% CL = 21.2–28.4 m). We truncated about 5% of distance data (the extreme distances) and left the data ungrouped. We considered all observations to be of single males (cluster size 1) even when a female was around because females, being secretive, did not contribute to the detection of males.

Of the robust models for $g(y)$ recommended by Buckland et al. (1993), we considered the half-normal key with cosine or Hermite adjustment and the hazard-rate key with cosine or polynomial adjustment. We did not consider the uniform key because it did not visually fit the distance data. Of the models considered, we selected the one with the lowest Akaike's information criterion (AIC), as implemented in the program DISTANCE version 2.1 (Laake et al. 1994) used for calculations.

Buckland et al. (1993) listed 3 critical assumptions to be made in achieving reliable estimates of density from line-transect sampling. These assumptions are given roughly in order of importance from most to least critical. All 3 assumptions can be relaxed under certain circumstances. (1) Objects directly on the line are always detected. (2) Objects are detected at their initial location, prior to any movement. (3) Distances are measured accurately. Assumption 3 is not a problem because we used 30-m metal or polyurethane measuring tapes to measure distance to the closest 25 cm. Assumption 1 is not a problem in ground counts unless assumption 2 fails. If a substantial part of the population moves farther from the line prior to detection, this movement will often be apparent when the histogram of the distance data is examined (Buckland et al. 1993). Also, if evasive movement prior to detection occurs at a high level, the estimator will be biased low.

Estimators based on sighting angles and distances

Hayne's estimator (H) is based on the concept that detection is due to the animal flushing in response to the observer (Burnham et al. 1980).

$$[2] \hat{H} = \frac{n_f}{2L} \left[\frac{1}{n_f} \sum_{i=1}^{n_f} \frac{1}{r_i} \right]$$

where

\hat{H} is Hayne's estimate of density
 n_f is the number of birds seen flushing
 L is the length of the transect
 r_i is the sighting distance to each bird, i

The basic assumption of H is that the flushing distance, r , is fixed. The critical assumption tested is that $\sin(\theta)$, θ being the sighting angle, is a uniform random variable on the interval $[0, 1]$. We tested this by testing whether the expected average sighting angle was 32.7° (Burnham et al. 1980) with

$$[3] z = \frac{\sqrt{n}(\bar{\theta} - 32.7)}{21.56}$$

If $|z| \leq 1.96$ ($\alpha = 0.05$), we used H , otherwise we tried the generalized Hayne's estimator (GH). GH is an extension of the fixed flushing radius model and allows an elliptical flushing envelope (Burnham et al. 1980), where the ratio of the major and minor axes is constant and equal to C (Laake et al. 1979). The sines of the angle can be transformed to a uniform distribution on the basis of C . A χ^2 goodness-of-fit test determines if the sample of transformed sines comes from a uniform distribution (Laake et al. 1979). We used the program TRANSECT II (Laake et al. 1979, modified by White in 1988) for the calculations of H and GH and for the tests of assumptions.

Test of accuracy

We tested the accuracy of line-transect estimators in the field thrice: once in 1995 and twice in 1996. We tested accuracy on one 0.7×1.1 km (77 ha) grid, flagged every 100 m, located on area 6. Each test consisted of a line-transect survey, with the same sampling protocol as for the large areas, followed by a total count. Transect efforts are given in Table 1.

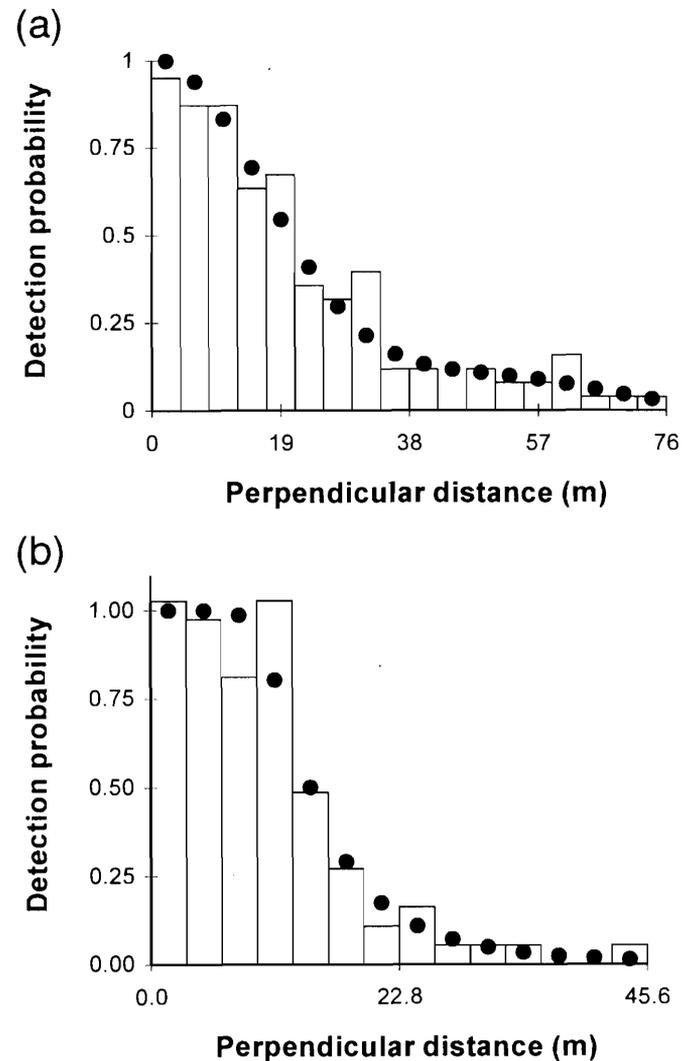
In the first week of June of both years, after we finished the line-transects on the grid, we proceeded to a total count of males present in the area, using a human chain. We used 5 observers in 1995 and 8 in 1996. Observers walked in parallel 10–20 m apart and transects covered the entire grid. We recorded every observation of a male. To prevent counting the same males twice when they flushed to an area that was not yet sampled, an observer remained behind with binoculars to observe if they flew back to their original location. The grid permitted this kind of observation from a long distance, owing to the concave topography of the area. In parts where the willow was thick and males could hide, one observer would go in and try to scare the birds out while other observers watched from the sides. Mapping of paired and single males on small parts of the grid in early May corroborated the accuracy of total counts. The relative bias of line-transect density estimates = [(estimate of density - actual density) / actual density] \times 100, where actual density = total count on the grid / size of the grid.

Precision

To decide whether the precision of the method was high enough to detect changes in density of ptarmigan populations, we used sensitivity. Sensitivity, or the detection threshold, is a measure of how small a change or difference a given study reliably detects (Eberhardt 1978a). The relative sensitivity of an estimate of density, \hat{D} = [(UCL - LCL) / \hat{D}] \times 100, where UCL and LCL are the upper and lower confidence limits of \hat{D} , respectively. We used 80% CL ($\alpha = 0.20$) to detect significant differences at roughly $\alpha = 0.10$. The difference is significant when the relative difference is equal to or greater than the relative sensitivity. This assumes that the two estimates of density for which the difference is being tested have the same sensitivity. The relative difference in density between 2 consecutive years, t and $t + 1$ = [$(\hat{D}_{t+1} - \hat{D}_t) / \bar{\hat{D}}$] \times 100, where \hat{D}_t is the estimate of density for year t and $\bar{\hat{D}}$ is the mean of \hat{D}_t and \hat{D}_{t+1} .

We tested the precision of the method by comparing the sensitivities obtained with changes that occur in natural populations of willow ptarmigan. We considered 3 classes of populations according to the intensity of their fluctuations in density over years: (1) high, (2) medium, and (3) low. Mossop's (1994) Chilkat Pass population represented 1, his Dempster and North Slope populations represented 2, and Hannon's (Boutin et al. 1995) Chilkat Pass population represented 3. For each of these population classes, we calculated the median and range of the relative differences in density between years. We assessed the precision of the line-transect method for each class from the proportion of relative differences equal to or greater than the relative sensitivity of the method.

Fig. 1. Observed perpendicular distances (histograms) and predicted detection functions (●) for line-transects of male ptarmigan. (a) Half-normal / cosine model, data pooled from areas 1, 5, and 6 and the grid 1 in 1996 ($n = 148$). (b) Hazard rate / cosine model, data pooled from areas 1 and 2 and the grid in 1995 plus areas 2, 3, and 4 and grid 2 in 1996 ($n = 94$).



Results

Estimates based on perpendicular distance

Figure 1 shows histograms of pooled distance data and the 2 PDF used for calculating the PD estimates given in Table 1. For the pool of areas 1, 5, and 6 and grid 1 in 1996, $\hat{f}(0) = 0.0408$, with 95% CL = 0.0352–0.0473. For the pool of areas 1 and 2 and the grid in 1995 plus areas 2, 3, and 4 and grid 2 in 1996, $\hat{f}(0) = 0.0604$, with 95% CL = 0.0505–0.0722. We counted 19 male ptarmigan on the grid in 1995 (24.7 males/km²) and 50 in 1996 (64.9 males/km²). The first PD estimate of 1996 for the grid was overbiased (bias = 82%; Table 1). We attribute this bias to possible double-counts of some birds during the 29 April transects. If we do not include the transects of 29 April 1996, the bias is reduced to -7%. Including the results of the other two surveys on the grid (bias = -5 and -3%; Table 1), the range of the bias is 4%.

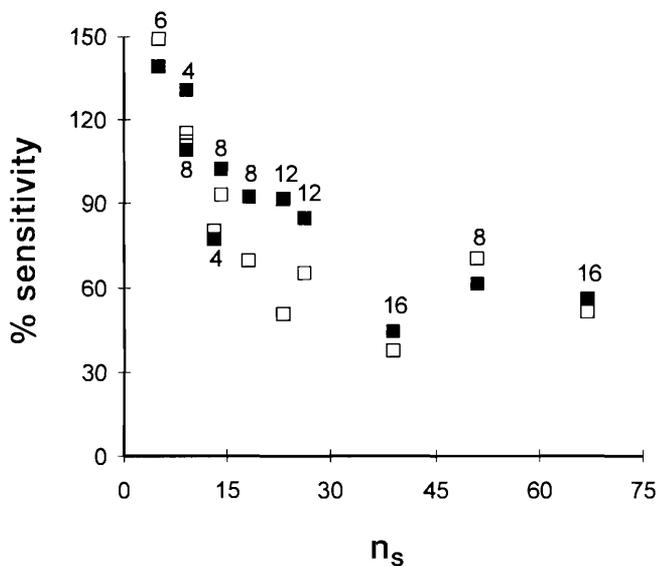
Table 1. Line-transect efforts and estimates of density based on perpendicular distance, \hat{D}_{PD} (number of male ptarmigan/km²), for areas surveyed in 1995 and 1996.

Year	Area	S^a	n_t^b	L^c	Dates	n_s^d	\hat{D}_{PD}	%CV ^e	df	LCL ^f	UCL ^g	%sensitivity ^h	%bias ⁱ
1995	1	5	4	20.0	19–20 May	9	13.6	34.5	3	7.9	23.6	116	
	2	13.5	6	17.6	23, 26 May	5	8.6	49.4	5	4.3	17.1	149	
	Grid	0.77	8	17.6	30 May, 6–7 June	14	24.0	33.2	8	15.3	37.7	93	-2.7
1996	1	5	12	26.0	24 April, 4, 12 May	23	18.0	18.7	16	14.0	23.1	50	
	2	13.5	16	45.9	28–30 May, 2 June	39	25.7	14.5	37	21.3	31.0	38	
	3	3	8	12.0	4 June	9	22.6	40.2	8	13.1	39.1	115	
	4	4	8	12.0	11 June	0	0						
	5	5	12	26.3	20, 21, 24 May	26	20.2	24.1	13	14.7	27.8	65	
	6	12	16	36.4	9, 10, 15, 16 May	67	37.5	19.3	21	29.1	48.3	51	
	Grid 1	0.77	8	8.8	29 April, 9 May	51	118.2	25.0	8	83.8	167	70	82
	Grid 1s	0.77	4	4.4	9 May	13	60.3	24.3	4	40.8	89.2	80	7.1
	Grid 2	0.77	8	8.8	8 June	18	61.8	25.1	9	43.9	86.9	70	4.8

Note: The actual densities on the grid were 24.7 males/km² in 1995 and 64.9 males/km² in 1996. For 1996, grid 1 refers to the first survey on the grid, grid 2 to the second, and grid 1s to the first without transects on 29 April.

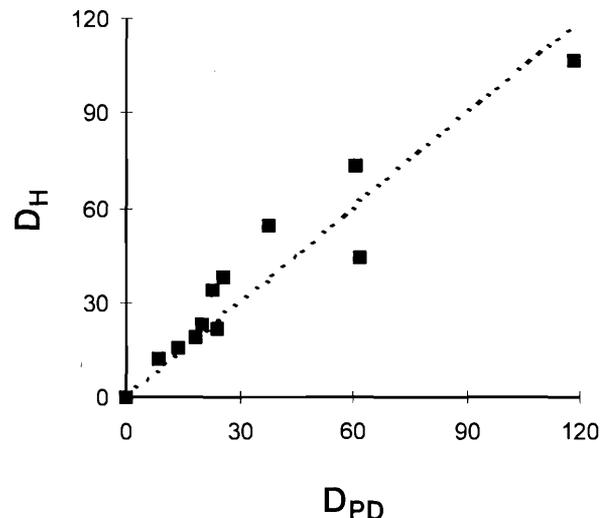
- ^aSize of the area (km²).
- ^bNumber of transects.
- ^cTotal length of transects (km).
- ^dNumber of male ptarmigan seen.
- ^ePercent coefficient of variation.
- ^fLower 80% confidence limits.
- ^gUpper 80% confidence limits.
- ^hRelative sensitivity = [(UCL - LCL)/ \hat{D}] × 100.
- ⁱRelative bias = [(\hat{D} - D)/D] × 100.

Fig. 2. Precision (sensitivity as a percentage) of line-transect estimates based on perpendicular distances (■) (Table 1) and Hayne's estimates (□) (Table 3) in relation to the number of observations, n_s . The number of transects is given above or below each set of estimates.



The precision (percent sensitivity) of line-transect PD estimates reached a plateau at 38–70%, with a mean of 55% when >20 males were detected in an area (Table 1, Fig. 2). With less than 20 detections, precision was low, with sensitivity ranging from 70 to 149%. A sensitivity of 55% is too low to detect significantly ($\alpha = 0.10$) any difference in density between years in populations with low fluctuation

Fig. 3. Correlation of Hayne's estimates of density (D_H ; Table 3) (number of male ptarmigan/km²) with estimates based on perpendicular distances (D_{PD} ; Table 1). The dotted line shows a 1:1 correlation. The coefficient of correlation, $r = 0.95$, $P < 0.001$.



(Fig. 4). With mean differences of 11 and 18% between 1- and 2-year periods, respectively, it would be hard for any sampling program to detect these changes. In moderately fluctuating populations, at a sensitivity of 55% changes begin to be detected, up to 44% of differences between 2-year periods (Fig. 4). The method works well with highly fluctuating populations, where a sensitivity of 55% detects up to 75% of differences between 2-year periods (Fig. 4).

Table 2. Hayne's (H) and generalized Hayne's (GH) estimates of density, \hat{D}_{H-GH} (male ptarmigan/km²), per area and their relative bias for surveys on the grid.

Year	Area	n_f^a	Angle ^b	Z	$P(Z)^c$	χ^2	df	$P_{(\chi^2)}^c$	Estimator	\hat{D}_{H-GH}	%CV ^d	%bias ^e
1995	1	7	30.7	-0.24	0.80	—	0	—	H	15.9	34.1	
	2	3	33.3	0.05	0.96	—	0	—	H	12.0	47.1	
	Grid	11	31.8	-0.13	0.90	0.20	1	0.65	GH	25.4	50.6	2.8
									H	21.9	36.2	-11.3
1996	1	15	48.0	2.74	0.006*	19.6	1	<0.001*	None			
	2	34	52.0	5.22	<0.001*	8.06	3	0.045*	None			
	3	8	46.1	1.75	0.08	—	0	—	H	33.9	46.2	
	4	0								0		
	5	21	49.9	3.65	<0.001*	0.90	2	0.64	GH	8.8	39.6	
	6	57	50.7	6.30	<0.001*	18.0	5	0.003*	None			
	Grid 1	36	51.5	5.23	<0.001*	19.8	4	<0.001*	None			
	Grid 1s	11	61.5	4.43	<0.001*	1.27	1	0.26	GH	6.6	41.4	-89.8
	Grid 2	9	55.8	2.83	0.005*	—	0	—	None			

Note: The average sighting angle must be 32.7° in order to use H (Z test). The transformed sines of the angles must come from a uniform distribution to use GH (χ^2 goodness-of-fit test). The actual densities on the grid were 24.7 males/km² in 1995 and 64.9 males/km² in 1996. Transect efforts are given in Table 1.

^aNumber of male ptarmigan flushed.

^bAverage angle from the transect line from which male ptarmigan flushed.

^c P value of the respective test.

^dPercent coefficient of variation.

^eRelative bias = $[(\hat{D} - D)/D] \times 100$.

*Rejected, $P \leq 0.05$; the estimator whose assumption is being tested cannot be used.

Table 3. Hayne's estimates of density, \hat{D}_H , for each area, even if the assumption that the average sighting angle is 32.7° in Table 2 is not met.

Year	Area	\hat{D}_H	%CV	df	LCL	UCL	%sensitivity	%bias
1995	1	15.9	34.1	3	7.0	24.8	112	
	2	12.0	47.1	5	3.6	20.3	139	
	Grid	21.9	36.2	7	10.7	33.1	102	-11
1996	1	19.2	33.6	11	10.4	28.0	92	
	2	38.2	16.7	15	29.6	46.7	45	
	3	33.9	46.2	7	11.7	56.0	131	
	4	0						
	5	23.1	31.2	11	13.3	32.9	85	
	6	54.4	20.8	15	39.2	69.5	56	
	Grid 1	106.2	21.7	7	73.6	138.8	61	64
	Grid 1s	73.3	24.1	3	44.4	102.2	79	13
Grid 2	44.0	32.7	7	23.6	64.4	93	-32	

Note: For details see Tables 1 and 2.

Estimates based on sighting distances and angles

The range of applicability of H and GH seems narrow because neither met its assumption in 5 out of 11 surveys (Table 2). However, after comparison with PD estimates, PD being the reference because it is more robust (Buckland et al. 1993; D.R. Anderson and K.P. Burnham, personal communication), we found that H is robust to deviations from its assumption, but GH is not. When we compared H estimates (Table 3) with PD estimates (Table 1), even when the assumption that the average sighting angle is 32.7° had failed for H , correlation was excellent ($r = 0.95$, $n = 12$, $P < 0.001$; Fig. 3). The range of biases for H estimates is 45% (-32 to 13%, not including grid 1 in 1996; Table 3). The precision (percent sensitivity) of H (Table 3) is roughly of the same order as that of PD (Table 1) (Fig. 2). On the

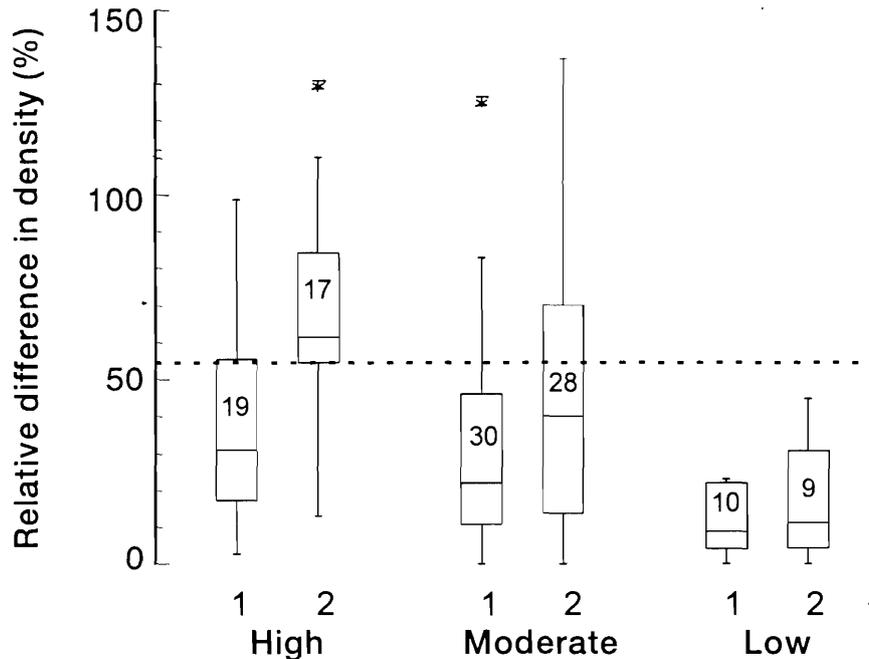
other hand, GH is not robust because there was no correlation between GH and PD estimates when the transformed sines of the angles were not always from a uniform distribution ($r = 0.22$ but not significantly different from 0, $n = 12$, $P = 0.49$). Even when GH met its assumption, it could be biased by up to 90% (Table 2).

Discussion

Accuracy and precision

Given that the assumptions of the method and the requirements concerning total sample size for estimating $f(0)$ are met (both are discussed in the next section on applicability), PD is accurate; it is also relatively efficient or precise, but only in highly and, in some cases, moderately fluctuating

Fig. 4. Box plots of relative differences in density (as a percentage) for 3 classes of willow ptarmigan populations: (i) highly fluctuating density: Mossop's (1994) Chilkat Pass population; (ii) moderately fluctuating density: Mossop's (1994) Dempster and North Slope populations; and (iii) low fluctuations in density: Hannon's (Boutin et al. 1995) Chilkat Pass population. The relative difference in density, D , between years a and $b = [(D_b - D_a) / (\bar{D}_{a-b})] \times 100$. The differences reported are between consecutive years (1) and 2-year periods (2). Inside each box is the number of relative differences for each class of populations and the median (horizontal line). The horizontal ends of the box represent the 25th and 75th percentiles. The lower fence = [(25th percentile) - 1.5(spread)] and the upper fence = [(75th percentile) + 1.5(spread)], where spread = [(75th percentile) - (25th percentile)]. The asterisks represent data values outside fences. The broken line at 55% is the average sensitivity of PD estimates with >20 detections (Table 1).



populations. Its efficiency is also mainly restricted to detecting changes in density between 2-year periods. Differences in density between 2-year periods are usually larger and easier to detect than those between consecutive years because of the cyclic nature of ptarmigan populations. These populations show 8- to 11-year fluctuations in density (Mossop 1994). Precision may be increased by increasing the number of transects and the number of detections, although it seems that these would need to be much higher to make a significant contribution, as shown by the plateau in Fig. 2. The accuracy of PD did not seem to be affected by the small number of detections, because for the 3 surveys serving for the test of accuracy, $n < 20$.

For estimators based on sighting distances and angles, H performs well, given its simplicity, but GH should not be used. On the few occasions when GH met its assumptions, GH estimates were biased. Unlike GH, H is robust. It gave similar results to PD, even when violating the assumption that $\sin(\theta)$ is a uniform random variable on the interval $[0, 1]$ (Fig. 3). This shows, as Eberhardt (1978b) indicated, that H is fairly unbiased over a range of underlying distributions.

Burnham et al. (1980) thought the value of H was overrated in the published literature, though it still had some merit, pointing to the fact that studies of inanimate objects (i.e., Robinette et al. 1974) failed to produce satisfactory results. Burnham et al. (1980) even saw GH as a substantial improvement over H . We believe our unexpected results for H and GH come from the fact that results using H and GH

cannot be simulated because they depend on the behaviour of the birds (which is still unpredictable). Only birds that flushed, i.e., that responded to the presence of an observer, could be counted, and in the present case up to 30% of observations could not be used because birds did not flush. No realistic simulation studies have yet incorporated this fact. Therefore, GH should not be used, but H could be used as a simple alternative to PD (e.g., for estimating density while in the field). PD should, however, be chosen in the end because it is more robust (Buckland et al. 1993; D.R. Anderson and K.P. Burnham, personal communication). The smaller range of bias of PD estimates, -3 to -7%, compared with 13 to -32% for H , indicates this.

Applicability

The assumptions of line-transect sampling, particularly with reference to mobility of animals prior to detection, and requirements concerning the total sample size, for estimating $f(0)$ for PD, can be met when the method is used during the male territoriality period, i.e., late April to the end of May on the areas surveyed. Mobility prior to detection is low during that period because visibility is good and because of male "antagonist" behaviour. Males seem to challenge intruders, or show that they are aware of their presence, by cackling, and when observers get too close, they flush in the air noisily. Even unpaired males show this behaviour. The distribution of perpendicular distances and the size of biases permitted us to assess the importance of mobility prior to detection in general. The distributions of perpendicular dis-

tances (Fig. 1) did not show any net movement of the birds away from the line because there is a good shoulder of the distribution close to zero distance (Buckland et al. 1993). Because the method estimates the density of all males present in an area at a given time, including both territorial and non-territorial (i.e., floater) males, we may wonder if floaters could bias the estimate by being more mobile prior to detection. This is not the case, because if they were mobile prior to detection and constituted a significant part of the population (to have an effect on the estimate), it would be visible in Fig. 1. In addition, if evasive movement prior to detection were occurring at a high level, estimates of density would be biased low (Buckland et al. 1993). The underbiases of PD estimates (Table 1) are too small (the largest bias is -7%) to indicate that mobility was a problem. However, after mid-June, males become much harder to detect and mobility prior to detection may become important.

Buckland et al. (1993) recommend a minimum total sample size of 60–80 observations for calculating $f(0)$. Because males are visible during the territorial period, it is easier to reach this number than later in summer. However, sample size could still be a problem in years of very low abundance or if applied to rock or white-tailed ptarmigan, whose populations are not as dense as those of willow ptarmigans. There are three solutions: (1) Using dogs can help to increase the number of detections and widen the shoulder of the PDF (which increases its robustness), provided the dogs stay on the transect centre line with the observers (D.R. Anderson, personal communication). (2) Line-transect sampling by helicopter would allow a large increase in transect effort. Evasive movement prior to detection may not be a problem, but a good system would be required to measure distances accurately. (3) Pooling observations over years (e.g., Kelley 1996), observers having the same capacity for detection, and areas with similar habitat types. This is the easiest solution, and is what we did.

High densities can also create problems. Line-transect sampling of really dense ptarmigan populations (e.g., >50 males/km²) requires extreme caution when territorial display is at its peak (the last week of April in Kluane) to avoid counting the same birds twice on the same transect. Otherwise, overestimation occurs, as for our first PD estimate on the grid in 1996 (Table 1). Because we usually lost track of the birds we had already counted while we were recording the distance data for another one, it would be valuable to pair up observers in this situation, one to take the measures and record them while the other keeps an eye on birds already counted. Nevertheless, this type of problem will be rare because such high densities are rare. Densities ≥ 50 male willow ptarmigan/km² occur in 7% of years and ≥ 65 in less than 3% of years (using the population trends of Hannon (Boutin et al. 1995) and Mossop (1994); $n = 72$ years).

The present results are mostly applicable to willow ptarmigan because these birds represented about 95% of observations. Not enough data for rock and white-tailed ptarmigan presently exist to test if there is a significant species-specific bias, although nothing suggested to us that there could be one, either from the flushing behaviour or the range of distance data.

The method could also be tried in fall and winter with

some adjustments. Each flock would then have to be considered a single observation and a correction in the detection function would be required for cluster size (Buckland et al. 1993).

Implications

The large-scale surveys at Kluane in 1995 and 1996 showed that it can be a mistake to characterize the "health" of a population in a whole region by extrapolating from counts on small areas, because the range of densities between similar and adjoining subalpine areas is very wide (0–65 males/km²; Table 1). The cause of these large variations in breeding density between qualitatively similar and adjoining subalpine areas is still unknown. Line-transect sampling now provides a tool that can help resolve these large-scale questions about the distribution of ptarmigan. A knowledge of the population trends of ptarmigan on a large scale will also help to increase understanding about the breeding, population trends, and distribution of their predators, e.g., golden eagles (*Aquila chrysaetos*), gyrfalcons (*Falco rusticolus*), lynx (*Lynx canadensis*), red fox (*Vulpes vulpes*), etc. For instance, in Denali, Alaska, the proportion of the territorial population of golden eagles that lay eggs each year was found to change in response to the numbers of snowshoe hares (*Lepus americanus*) and willow ptarmigan available (C. McIntyre, personal communication). Finally, accurate assessments of breeding density are also needed for management, e.g., to predict harvest limits (Mossop 1994). Wildlife biologists may be scared by the heavy theory underlying the concept of line-transects, but should not be. Recently developed software such as DISTANCE version 2.1 (Laake et al. 1994) makes this method accessible to everyone.

Acknowledgements

This study was made possible by a Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Special Project research grant to C.J. Krebs and a NSERC postgraduate scholarship and a Northern Scientific Training Program grant to L. Pelletier. We thank everyone who contributed to this work, especially Julie Sénécal.

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