# Monitoring vertebrate populations using observational data

**Wesley M. Hochachka, Kathy Martin, Frank Doyle, and Charles J. Krebs**

**Abstract**: Methods for monitoring temporal changes in population size vary from intensive and potentially expensive to less intensive and more easily implemented techniques. In this paper we evaluate the utility of a monitoring technique that can be used to follow many vertebrate species simultaneously at low cost and requires little training of personnel. Observers record the number of individuals seen per hour in the field and these rates of encounter are used as an index of population size. We examine whether encounter rates reflect population size by comparing them with independent censuses of three species over a 7-year period in the boreal forest near Kluane Lake in the southern Yukon Territory. Encounter rates were generally an accurate reflection of variation in population size. In our study system, inter-observer variability did not influence our ability to detect fluctuations in population size: the underlying fluctuations were detected whether data from all or only a group of "high-quality" observers were used. In our study, the benefit of using all available data outweighed the cost of variation among observers because sample sizes were large (averaging over 1200 data points from 33 observers per year). Variation in the length of observation periods did not affect the chance of detecting animals in our study. Encounter rates provide a reasonable index of variation in population size, although caution should be used with species that are uncommon or difficult to detect.

**Résumé** : Les méthodes d'estimation des changements temporels de taille des populations vont des méthodes intensives, potentiellement onéreuses, aux méthodes moins intensives souvent plus faciles à utiliser. Nous évaluons ici une méthode d'estimation adaptée à suivre plusieurs espèces de vertébrés simultanément, méthode qui ne coûte pas cher et qui requiert peu d'entraînement de personnel. Les observateurs notent le nombre d'animaux aperçus en 1 h sur le terrain et ce nombre sert d'indice de la taille de la population. Nous examinons si la fréquence de ces rencontres reflète la taille des différentes populations en comparant les chiffres obtenus avec les résultats de recensements de trois espèces effectués indépendamment pendant une période de 7 ans dans la forêt boréale de la région du lac Kluane, dans le sud du Yukon. La fréquence des rencontres est généralement un indice assez exact de la taille des populations. Dans notre système, la variabilité inter-observateurs n'influence pas la capacité de détecter les fluctuations dans l'effectif des populations : les fluctuations de la taille de la population ont été détectées dans les cas où les données de tous les observateurs de « haute qualité » ont été utilisées aussi bien que dans les cas où seulement celles d'un groupe d'entre eux ont été utilisées. Dans cette étude, les avantages à utiliser toutes les données disponibles excèdent les coûts reliés à la variation entre les observateurs, à cause de l'importance des échantillons (en moyenne, plus de 1200 données enregistrées par 33 observateurs par année). La variation dans la durée des périodes d'observation n'affecte pas la probabilité de détecter la présence d'un animal. La fréquence des rencontres donne des indices réalistes de la variation de la taille des populations, mais il faut user de prudence dans le cas d'espèces peu communes ou difficiles à repérer.

[Traduit par la Rédaction]

## Introduction

Numerous techniques have been developed for estimating abundance in animal populations, and they vary in the amount of effort required to conduct the work. Direct census (e.g., Falls 1981) and mark—recapture (e.g., White et al. 1982; Pollock et al. 1990; Krebs 1999) provide data on actual numbers of animals but require intensive effort to obtain information on one or a few species. Other highly standardized monitoring methods such as the North American Breeding Bird Survey (e.g., Robbins et al. 1986) and constant-effort mist-netting (e.g., Ralph et al. 1993) provide indices of abundance for several species simultaneously, but still require a considerable amount of effort directed specifically towards the census work. However, there are circumstances in which information on relative population size is required but it is logistically impossible to expend the time and effort solely on intensive censusing. One type of census

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data requiring a low intensity of specifically directed effort is a tally of random encounters with animals (e.g., Swenson and Anglestam 1993): counts are converted to rates that provide an index of population size. These data have the advantage that they can be gathered during other fieldwork, have a simple protocol for collection, and can be collected by both professional and amateur biologists with very little prior experience in animal censusing.

Using rates of encounter with animals as an index of population size is not without potential problems, both methodological and biological. Methodological problems could be caused by factors such as differences in ability of field workers or variability in effort of observers. Even highly skilled field observers will not see the same animals at the same place and time (Källander and Rydén 1974), and combining data from observers with different levels of skill may only elevate measurement error. Variation in effort or tasks carried out by individual observers among days may also elevate measurement error by changing the likelihood of observers seeing a species, depending on the task at hand. Problems could also arise because of the biology of the species: changes in behaviour or habitat use through time can affect detectability and invalidate the assumption that the encounter rate reflects the actual abundance of species. While all of these confounding factors undoubtedly affect the accuracy of encounter rates as an index of population size, their importance has never been assessed.

In this paper we ask whether encounter rates provide a useful index of changes in population size for species that were part of an ecosystem-level study in the boreal forest in the southern Yukon Territory of Canada. The keystone animal in this system is the snowshoe hare (*Lepus americanus*), a medium-sized herbivore that fluctuates cyclically and dramatically in population size over 9- to 11-year periods throughout the boreal forests of North America (e.g., Keith 1963, 1990). Although data on population fluctuations of many species were required, it was only logistically feasible to study 12 vertebrate species intensively (Boutin et al. 1995; Krebs et al. 1995). To index abundances of other species we turned to measures of encounter rates, and the utility of this approach is the subject of this paper. In our evaluation we examined data from three species, and found that inter-annual variation in encounter rates followed the same population trends shown by independent measures of population size. Additionally, we examined whether inter-observer variability or variation in effort within observers affected the accuracy of our estimated encounter rates. Data from a fourth species was added to our analyses of within-observer variation. We also looked for evidence that detectability of species varied over the course of the study. Our results indicate that encounter rates provide a biologically meaningful index of changes in population size. We suggest circumstances under which this conclusion should hold.

## Methods

The data used in this paper are from a large-scale, long-term ecosystem study at Kluane Lake in the southern Yukon Territory (Boutin et al. 1995; Krebs et al. 1995). Population sizes of the intensively studied species were estimated by various means. In addition to the intensively studied species, there were over 25 species for which information on population fluctuations was also desired, in order to determine the extent to which these species are linked with the snowshoe hare cycle.

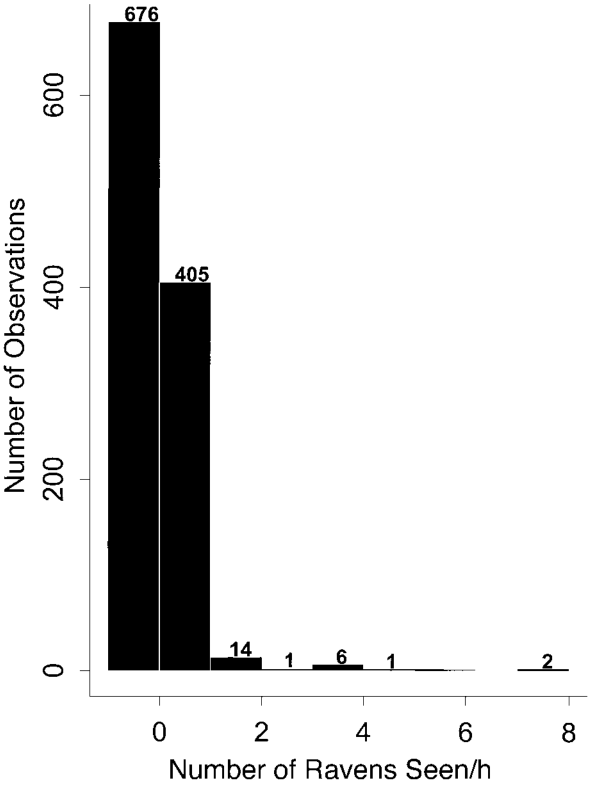
Field workers kept records of observations of more than 25 less intensively studied species during routine work on other aspects of the project. All field workers were trained to identify the species with which encounters were recorded. At the end of each day (if >30 min were spent in the field), all field workers recorded the time that they spent in the field, their mode of transportation (foot, road vehicle, snowmobile), and the number of animals of each species of interest that they saw. All times were recorded in tenths of an hour. Only animals seen during daylight hours were recorded. Visual and not auditory detection was required in order to count an individual. Encounter data were collected throughout the year from 1988 to 1994 by 12–45 observers annually (160 observers during this study). Although some observers were present throughout the study, the set of observers varied both seasonally and inter-annually. Data collection represented between 780 and 11 600 person-hours annually (mean ≈ 7700/year). In this paper we use data only from observers traveling on foot, collected from May through August of each year, the time during which the greatest number of people were working at Kluane Lake. Each observer-day was treated as a separate data point; when field workers were together, only one observer recorded observations. Data were standardized to number seen per hour. We used data from spruce grouse (*Falcipennis canadensis*), common raven (*Corvus corax*), and coyote (*Canus latrans*) to test the use of encounter rates as an index of population size. These species were chosen for comparisons because we had measures of population size that were independent of encounter rates, although independent data for ravens were not available from the entire study. The independent measures of population size for each of these three species differed because of variation in the research being conducted on each species (Boutin et al. 1995). The spruce grouse and coyote represent species that are encountered relatively infrequently during normal fieldwork and are potentially highly cryptic (averaging fewer than 0.05 encounters/h). The common raven was chosen as an example of a more observable species, given its habit of searching for food on the wing. Data from a fourth species, the red-tailed (Harlan's) hawk (*Buteo jamaicensis harlani*), were also used in an analysis that examined whether variation in observers' time in the field affected their propensity to detect species. The red-tailed hawk was a species with relatively high probabilities of encounter (11.9% of person-days) but a low rate (0.035 birds/h).

In some analyses we compared inter-annual variation in encounter rates from all observers with a subset of "high-quality" observers. The first step in defining high-quality observers was to produce a set of four criteria or "rules" for use in selecting this subset of observers: (1) so far as possible, the same group of observers was maintained from one year to the next; (2) the observers forming the selected group had roughly the same probability of seeing an animal; (3) the group of observers had a relatively high average probability of seeing the species in question; (4) the group of observers represented a large number of data points.

The reasons for choosing these four rules were as follows. Rule 1 represented the most direct way to control for inter-annual variation in encounter rates, owing to changing observers and the resultant changes in the probability of observers detecting a given species. Intra-annual variation was decreased by reducing variation among observers within a single season (rule 2). We also wanted data from observers that were consistently looking for and keeping records of a particular species; we assumed that a high probability of detection (rule 3) resulted from such behaviour on the observers' part. All other things being equal, larger amounts of data (rule 4) will reduce confidence limits around estimates of encounter rate.

We used cluster analysis (e.g., Gauch 1982, pp. 197–200) to identify groups of observers in an objective manner. We had to produce a separate group of high-quality observers each year be-

**Fig. 1.** Distribution of random encounter rates with the common raven, an abundant species in the Kluane study area. Data ($n$ = 1105 observations) are from 1992. Bars denote numbers of ravens in the following groups: $n = 0$, $0 < n \leq 1$, $1 < n \leq 2,\ldots,7 < n \leq 8$. Numbers above the bars are sample sizes.



cause the individuals constituting our total group of observers were not identical among years. We described the distribution of daily encounter rates for each observer using the following metrics: mean, median, standard deviation, skewness, kurtosis, minimum value, and maximum value. Similarity in observers' probabilities of detecting a species was determined by clustering observers on the basis of these metrics. Among observers, we standardized each of these statistics to a mean of 0 and a standard deviation of 1. The standardization insured that each of the statistics was treated as equally important in clustering observers. Euclidean distance was used as our "distance" measure for clustering, and farthest-neighbour (complete) linkage was used to form clusters of observers. Farthest-neighbour linkage created clusters with the greatest possible similarity between even the most dissimilar of a cluster's members.

Once observers were clustered on the basis of their encounter rates with an animal, our procedure for selecting a group of observers became more subjective. Our first step was to examine the data set to determine which observers had the highest overall mean encounter rates with a species (rule 3). Generally, these observers fell into one or two tight groups. Next, we looked at the number of data points that each group represented (rule 4). Often, one set of observers clearly represented larger sample sizes. When forced to choose between groups of observers, we chose the group representing the larger sample sizes. If all other criteria failed to differentiate between groups, we chose the group for which most members were also present in other years of the study (rule 1). We noticed that there were usually a few observers who often came for short periods and saw larger numbers of individual animals than anyone else. Typically, these were observers who were specifically studying the species in question, therefore encounters were non-random. Data from these observers were removed as outliers if they did not cluster with those from other observers, even though the discarded observers had seen far more individual animals than anyone else. For the data we examined, sample sizes for the select group averaged less than 25% of the total data set for each species and year (range 14–58% for the three species examined).

The same group of observers could not be used as a selected group for analyzing data from all species, even within a single year. For example, the groups of high-quality observers differed from species to species in 1990: the selected observers for the raven (4) and coyote (4) had no person in common, and the raven group had only one person in common with the selected observers of the spruce grouse (9).

We provided measures of confidence in our estimates of encounter rates by plotting 95% confidence limits around each estimated encounter rate. We could not use conventional, parametric methods for calculating confidence intervals because our data were collected from species that were not observed on the majority of days. As a result, data were skewed (Fig. 1), and whether untransformed or transformed, they did not conform to either normal or Poisson distributions. Thus, we calculated confidence intervals by bootstrapping the data, using the bias-corrected and accelerated correction factor in the bootstrapping of the confidence intervals (Efron and Tibshirani 1986). Preliminary analyses indicated that this correction was required in order to produce unbiased confidence intervals by bootstrapping. The random number generator central to the bootstrapping program was RAN1 from Press et al. (1992). All bootstrapped confidence intervals were calculated using 5000 samples from the data sets, the upper and lower 95% confidence intervals being the 2.5 and 97.5% quantiles of the distribution of the 5000 bootstrapped mean encounter rates. See Potvin and Roff (1993) and Manly (1991) for introductions to bootstrapping and other computer-intensive techniques for biologists.

## Results

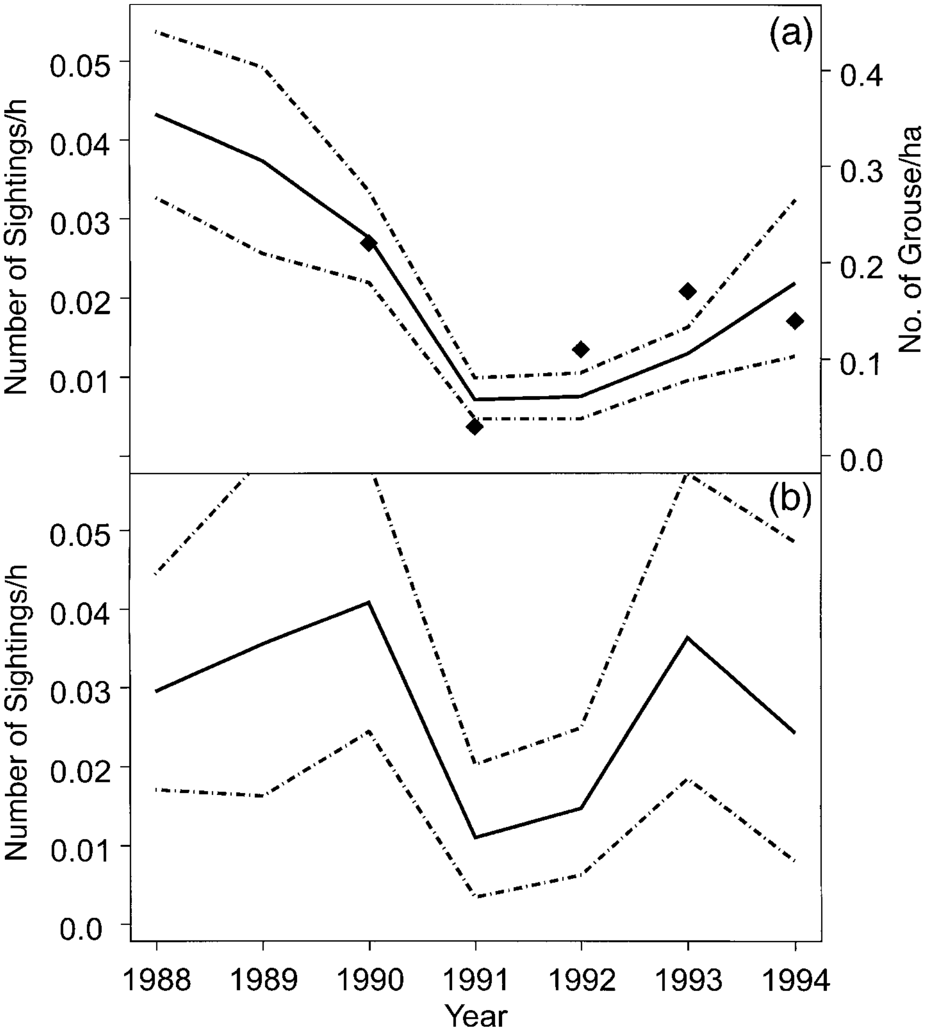
### Variation in encounter rates among observers

*Variation in ability among observers*

In our study, the trends in encounter rates for all observers combined mirrored variation in independent census data (Figs. 2*a* and 4*a*). We tested the benefits of limiting calculated encounter rates to a small group of high-quality observers by comparing the correlation between population size and encounter rate when data from all observers were used, with the same correlations when encounter rates were calculated using only data from a smaller group of highly skilled observers.

Inter-annual variation in encounter rates mirrored inter-annual variation in population sizes for the three target species examined, and the effort of screening and choosing observers was not required in our study. For the spruce grouse and raven (Figs. 2 and 3), the patterns of change in population size were similar whether the whole data set or data from the selected group of observers were used. Population indices from all observers and from high-quality observers were highly correlated for the two bird species (inter-annual correlations, $r = 0.61$ for spruce grouse and $r = 0.94$ for ravens), and both encounter rates were well correlated with the independent estimates of population size (Figs. 2 and 3). Further, note that for spruce grouse (Fig. 2), the constant decline and then rise in numbers estimated using all observers' data more closely follow the expected pattern (independent census data) than does the double-peaked population trajectory estimated using data from only the smaller set of

**Fig. 2.** Variation in abundance of spruce grouse in summer (1988–1994). (*a*) Data from all observers, given as the mean (solid line) and bootstrapped 95% confidence intervals (broken lines). Independent census data (◆, right-hand *y* axis) are plotted to evaluate the accuracy of inter-annual variation in encounter rates. (*b*) The same data from a subset of observers selected as being most likely to observe grouse. Independent census data were correlated with all encounter data ($r$ = 0.80) and data from selected observers ($r$ = 0.94).



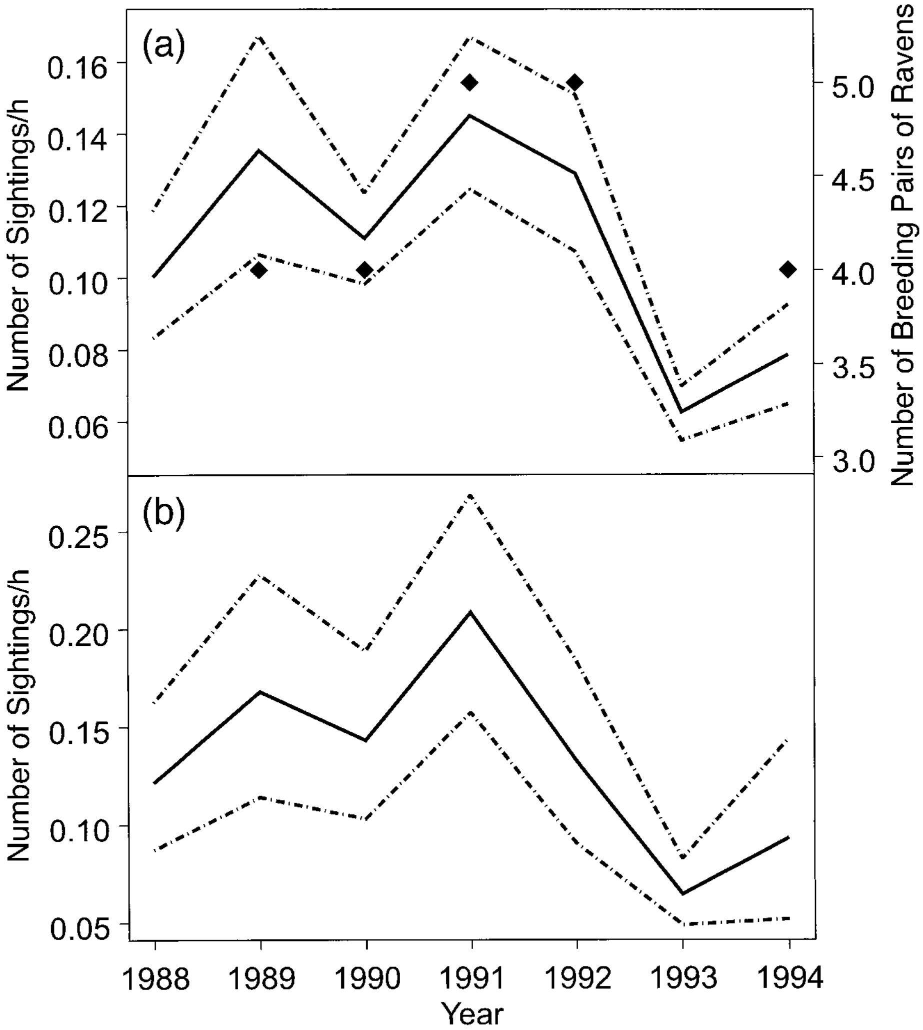
selected observers. In the case of the coyote, encounter rates for the entire group of observers and the selected group were relatively uncorrelated ($r$ = 0.13), and the data from all available observers better matched the actual numbers of animals present (Fig. 4). The average encounter rate was slightly higher for the selected observers, as would be expected on the basis of our selection criteria. However, because of the larger sample sizes with the entire data set, confidence limits were narrower, allowing detection of more subtle population trends than was possible with the selected group of observers.

### *Lengths of observation periods*

We tested for biases in encounter rates with varying amounts of time spent in the field by relating time spent in the field to the proportion of days on which a target species was observed (Table 1). We made these calculations for 5 observers, each of whom represented ≥90 days of data in one specific year. Our prediction was that the probability of seeing animals would increase with time spent in field activity, and bias would be indicated by a nonlinear relationship between time and probability of seeing animals (tested as a quadratic term in a polynomial regression). Least-squares regression rather than logistic regression was used because we were particularly interested in distinguishing between linear and nonlinear effects, and even the simplest logistic regression attempts to fit a sigmoidal and not a linear relationship to data. While, theoretically, time spent in the field was an almost continuous variable, observers' times spent in the field fell into a finite number (25–47) of discrete categories per observer, with multiple days of data from most time categories.

The majority of regressions (Table 1) showed that longer field days typically led to higher probabilities of seeing animals; however, very few of the regressions were statistically significant, and 12 of 17 positive correlations is not significantly different from random (sign test). There was no indication that the probability of detecting animals changed according to time spent in the field: quadratic terms in these regressions (indicators of bias) were all at $P \geq 0.15$, and

**Fig. 3.** Variation in abundance of common ravens in summer (1988–1994). (*a*) Data from all observers, given as the mean (solid line) and bootstrapped 95% confidence intervals (broken lines). Independent census data (◆, right-hand *y* axis) are plotted to evaluate the accuracy of inter-annual variation in encounter rates. (*b*) The same data from a subset of observers selected as being most likely to observe ravens. Independent census data were correlated with all encounter data ($r$ = 0.60) and data from selected observers ($r$ = 0.46). Note the difference in scale on the left-hand *y* axis when comparing panels.



quadratic terms always had lower statistical significance than linear terms within a regression. However, given the small sample sizes (Table 1) and resultant low statistical power, all we can conclude is that daily variation in observers' time spent in the field was not a major source of bias in our data sets. Note that the most significant regression result was opposite to our predicted pattern, suggesting that not all observers behaved in a similar manner in the field. The unexpected, negative correlation was found for the raven. One observer was less likely to see ravens as the observer's time in the field increased, and this was the only result that remained statistically significant even after Bonferroni correction of probabilities for multiple comparison (Rice 1989).

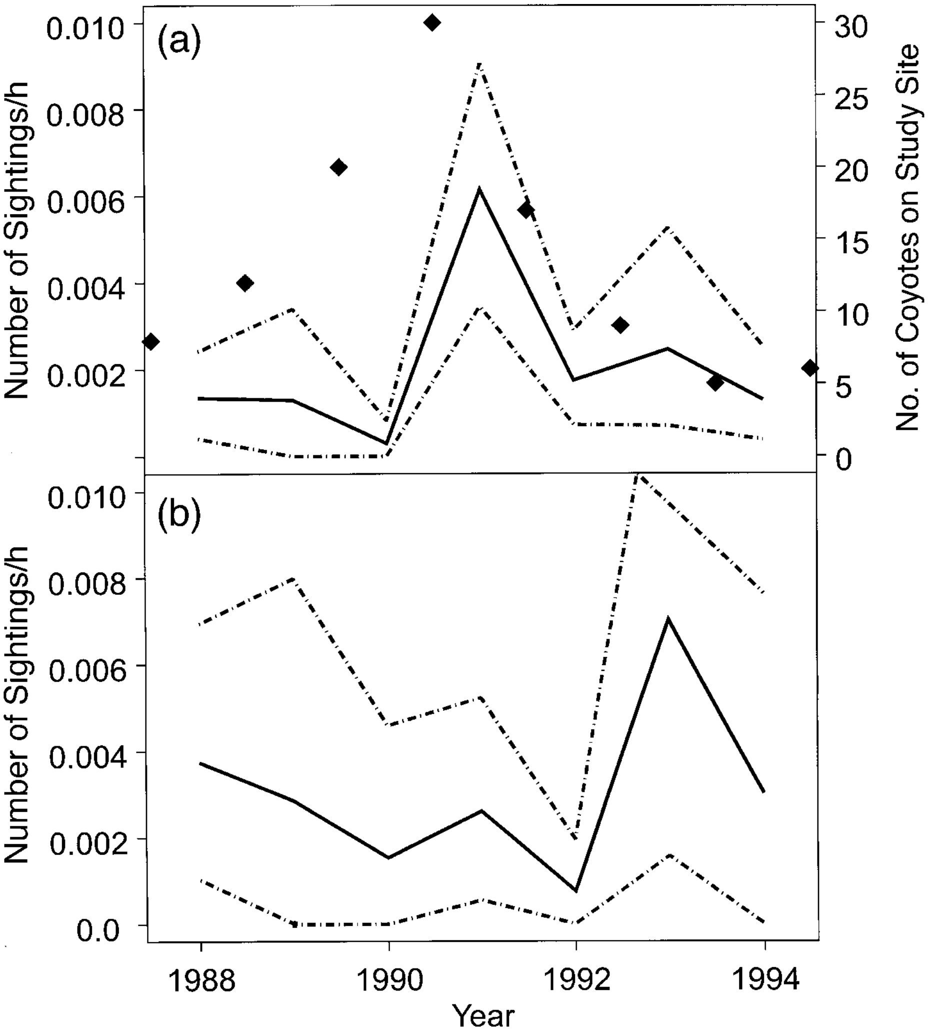
### Variation in detectability of animals

There was a suggestion that detectability varied among years for the coyotes and raven, even though some sources of variation in detectability were eliminated by excluding sightings based on vocalizations and analyzing data obtained only during the breeding season. For the coyote, encounter rates closely followed numbers estimated from independent censuses, except in 1990 (Fig. 4). The same discrepancy may also have occurred for the raven (Fig. 3), although encounter rates for both 1989 and 1990 are at odds with the independent census data. We know of no reason why our independent census measures would have been biased in these years.

## Discussion

The use of encounter rates as a coarse index of population size appeared viable in our study system. Encounter rates provided an index of population size that tracked the changes in population size observed in our study, although the degree of accuracy varied for the different species (Figs. 2–4). However, in all three cases the dominant features of population dynamics, a change in population size re-

**Fig. 4.** Variation in abundance of coyotes in summer (1988–1994). (*a*) Data from all observers, given as the mean (solid line) and bootstrapped 95% confidence intervals (broken lines). Independent census data (◆, right-hand *y* axis) are plotted to evaluate the accuracy of inter-annual variation in encounter rates. (*b*) The same data from a subset of observers selected as being most likely to observe coyotes. Independent census data were correlated with all encounter data ($r$ = 0.65) and data from selected observers ($r$ = –0.45). Data from the independent censuses are plotted midway between the summer encounter rate estimates because the independent census data were obtained in winter.



lated to the peak in numbers of snowshoe hares in 1990 and the low in hare numbers in 1993–1994, can be seen in the encounter rates as well as in the more intensively gathered census data. However, our results also indicate that caution is required in using encounter rates as an index of population size. In particular, the magnitude of each of the following potential problems has to be assessed: changes in behaviour and detectability of animals through time, within-observer variation in the likelihood of detecting animals, and variation in skill among observers.

Detectability of animals can vary through time, and such behavioural variation needs to be taken into account (Martin 1999). Our analyses are based only on data from May through August of each year, to eliminate differences in detectability between the breeding season and winter. Basing detection on visual and not auditory cues was also important for some species, because animals varied in their level of vocalization both within and among years at our study site. For example, ravens were less visible and vocal when eggs were being incubated and more vocal and visible when nestlings and fledglings were being fed by parents (personal observation). Fluctuation in numbers of snowshoe hares was related to dramatic variation in vocal behaviour of other species, with great-horned owls (*Bubo virginianus*) not vocalizing or nesting when hare densities were lowest (C. Rohner, unpublished data). Attempts to control for variation in some behaviours (i.e., vocalization rates) may not have completely controlled for variation in detectability in our study. The coincidence of the start of declines in hare numbers with sudden changes in encounter rates with coyotes (predator and scavenger) and ravens (scavenger) may indicate that the latter two species altered their behaviour and detectability in response to a novel food source (Figs. 3 and 4). At the start of the decline in numbers of snowshoe hares, carcasses of hares, killed but not completely eaten, were present throughout the study site. Note, however, measuring variation in

**Table 1.** Variation in observers' propensity to detect animals as a function of time spent in the field.

| Observer No. | Year | *n* | Common ravens | Spruce grouse | Coyotes | Harlan's hawks |
|---|---|---|---|---|---|---|
| 1 | 1988 | 31 | –0.180 | 0.196 | 0.116 | 0.159 |
| 2 | 1990 | 47 | 0.017 | 0.114 | –0.215 | 0.329* |
| 3 | 1992 | 25 | 0.120 | 0.084 | 0.045 | 0.378 |
| 4 | 1992 | 25 | 0.203 | — | — | 0.302 |
| 5 | 1993 | 27 | –0.598*** | –0.022 | — | –0.288 |

**Note:** Data presented are correlations between time spent in the field and proportion of days on which at least one individual of a species was seen. Positive correlations indicate that the observer was more likely to encounter a given species when a longer time was spent in the field. Data are presented from 5 separate observers, each of whom spent over 90 days in the field during the summer (May through August). These observers were chosen because they represented the largest data sets collected by any individual field workers. *n* is the number of distinct time intervals that each observer spent in the field. A dash indicates that the observer saw no individuals of that species.

*$P \leq 0.05$.

***$P \leq 0.001$.

encounter rates as variation in detectability levels may be an asset in some circumstances. For example, changing activity (and presumably detectability) levels of predators (a functional response) may be more important to prey than the actual numbers of predators, or may give information on a predator's perception of the abundance of prey (Hik 1995).

Given random encounters of observers with animals, we expected that as observers spent longer periods of time in the field, they would have higher probability of encountering at least one individual of a species. While this was the general trend (the majority of correlations in Table 1 are positive), the paucity of significant correlations indicates that there was high variability in encounter rates even within observers and years. The nonsignificant correlations suggest that encounters between observers and animals were not completely random. One general factor that may have reduced the correlation between time spent in the field and encounter rates is a systematic change in the behaviour of animals through the day. Ravens hunting along roadsides mainly in the morning and evening (personal observation) and red-tailed hawks soaring only when thermals are available in the middle of the day are two examples of animals' behaviours that would prevent longer times spent in the field from always resulting in a higher likelihood of seeing an animal. The behaviours of individual observers likely also increased the variance of our results. For example, the only relationship (Table 1) that was significant after Bonferroni correction of probabilities indicated that one observer was less likely to observer ravens on days when more time was spent in the field. One explanation for this unexpected pattern may be a difference in that observer's motivation or focus between short and long observation periods. Another possible explanation for this unusual correlation is provided by the behaviour of ravens: they hunt along the edges of roads in the southern Yukon, and longer periods in the field would allow an observer to travel farther from a road (all study sites were accessed from roads). Note, however, that only 1 of 5 observers showed this pattern of significantly fewer raven sightings with more time spent in the field. Nevertheless, nonrandom encounter rates of observers with animals is a reality, and in studies with smaller sample sizes than ours, one may need to be aware of differences in both animal and observer behaviour throughout the day.

Differences in ability and behaviour among observers can affect rates of encounter with animals. Even for individual observers, our data showed variation in ability: an observer who is good at finding one species may be less likely to detect other species. Nevertheless, confidence limits were wider and more variable when data from only highly skilled observers were used, and in our case inter-annual trends based on the complete data set generally matched the independent census data better than did trends based on the restricted data sets (Figs. 2–4). This result is undoubtedly aided by our large sample sizes. We suggest that in smaller studies with fewer field workers, a consistent and highly experienced group of observers should be maintained in the field throughout a study.

In addition to the biological considerations noted above, the usefulness of encounter rates is also affected by statistical considerations. The first consideration is that encounter data are not equally accurate, and spending longer periods of time in the field increases the accuracy of daily-encounter data when these encounters are turned into rates. In the process of calculating encounter rates, the numbers of animals observed during long periods of time are divided by some factor in order to calculate an encounter rate, while data from time periods that are sufficiently short are multiplied (i.e., divided by fractions of hours). These are simple data codings (e.g., Zar 1984, p. 36) in which variances change in proportion to the multiplicative factor. Data from shorter time periods will have a greater variance around them; for example, all else being equal, the mean number of animals seen during a half-hour period will have twice the variance of the mean from 1-h observations. Thus, a larger number of data points is required to produce a narrow confidence limit if the majority of individual data points come from short sampling periods. In our data sets, 5.7% of observations were from periods lasting 1 h or less, although observation periods were as long as 22 h. Hence, there are substantial differences in error variance across the available lengths of observation periods in our data. Alternative approaches to dealing with the intrinsically high variance in rates from short observation periods include (*i*) combining data from several days into a single data point, (*ii*) eliminating all data points from observation periods of less than some arbitrary duration, (*iii*) using the data as they are, or (*iv*) weighting each observation by its expected precision (an option that we did not explore). Options *i* and *ii* would decrease sample sizes and option *i* additionally assumes that encounter rates are uniform from one day to the next (e.g., they represent data representing the same weather and habitat), which we view as unrealistic. The only weakness with option *iii* is that using all observations will introduce a larger random error into the data set and hence inflate confidence intervals. However, given the large sample sizes available to us (over 1200 data points per year, on average), confidence intervals were still relatively small (Figs. 2–4). We felt it simpler to use all the data available from our study rather than make arbitrary corrections to the data set. In smaller studies, however, encounter rates should be collected over long and relatively consistent periods of time in order to maximize the accuracy of each daily encounter rate.

Another statistical consideration is that average encounter rates should only be used in association with confidence limits around these estimates, otherwise it will be impossible to distinguish true variation in encounter rates from noise resulting from sampling error. The sample sizes required for narrow confidence limits depend on the distribution of encounter rates, at least if confidence intervals are calculated by bootstrapping (unpublished data). If daily encounter rates follow a normal distribution, then smaller sample sizes are required in order to calculate a narrow confidence limit than if the distribution of daily encounter rates is highly skewed. Viewed another way, the minimum required sample size depends in part on the distribution of the data that make up the total sample of encounter rates. Group-living species that are rarely encountered will require particularly large samples in order for encounter rates to obtain narrow confidence limits around estimated rates.

The use of encounter rates as an index of population size may not be appropriate for all species or study systems. Where possible, variation in encounter rates should be validated against independent measures of population size as a preliminary step in designing a study (e.g., Dodd and Murphy 1995). If such validation is not possible even for a subset of the data, the validity of using encounter rates in a given system cannot be assumed. Encounter rates are unlikely to be an accurate measure of abundance for uncommon species or species that are difficult to find. Also, large fluctuations in abundance are more likely to be detected than subtler changes in population size. Care must be taken that changes in detection rate are not due to changes in behaviour of animals. Given the caveats outlined above, we believe that using rates of encounter as an index of variation in population size is a useful tool in field ecology. The low cost in directed effort and the large range of taxa that can be monitored simultaneously make encounter rate an attractive and appropriate measure. The major strength of encounter rates is that they can be calculated for many moderately abundant species simultaneously across a large range of taxa. Our experience is that large sample sizes (many days of field observation) are required in order for encounter rates and the confidence limits around these rates to accurately and precisely reflect changes in population sizes of animals. While encounter rates can provide a useful large-scale or auxiliary index of trends in population size, they are not a general substitute for more sophisticated measurement techniques (e.g., Buckland et al. 1993).

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