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Effects of Survey Frequency on Bird Density Estimates in the Shrub-Steppe Environment

Abstract

An assumption underlying the valid use of repeated line transect surveys is that the detectability of animals does not vary during the survey period. We conducted a line transect study of shrub-steppe birds to examine the relationship between the temporal sampling regime and the consistency of the resulting counts. Total counts of birds nesting in the sampled habitat were found to be significantly lower when sampling was repeated on a daily interval than on a weekly interval. Counts of birds not nesting in the habitat were unaffected by the sampling regime. We attribute this effect to changes in behavior of nesting birds in response to the repeated presence of the observer: western meadowlarks (*Sturnella neglecta*) were more likely to be silent and sage sparrows (*Amphispiza belli*) were probably temporarily leaving their territories when an observer reappeared on consecutive days. The temporal patterning of samples may therefore affect the mean and variability of density estimates using any of the available line-transect algorithms.

Introduction

Obtaining accurate density data is essential to studies dealing with wildlife demography and population change. Such data are often obtained by line transect counts, in which sightings of individuals are recorded whenever they are detected on or within a specified distance of a line of predetermined length. Line transect methods have long been used to estimate numbers of birds in terrestrial habitats (e.g., Merikallio 1951), and a great deal of attention has been given to improving estimates by modifying field methods (e.g., Emlen 1971) and analyses (e.g., Eberhardt 1978, Anderson *et al.* 1979).

The accuracy of density estimates derived from transect counts reflects the degree to which the assumptions of the method are met. The primary assumptions are: 1) individuals are randomly distributed within the sampled space; 2) the probabilities of observing an individual declines from unity immediately on the transect to zero at some distance at right angles to the transect; 3) no errors occur in measurement; 4) individuals are counted only once; 5) the behavior of individuals in one portion of the transect does not influence the detectability of individuals in other portions of the transect; 6) individuals are not likely to escape detection as a response to the observer; 7) detectability does not change during the sampling period; and 8) detectability does not vary with age or sex (Burnham *et al.* 1980, Franzreb 1981a).

A number of studies have examined the robustness of various transect methods to violations of underlying assumptions (e.g., Franzreb 1981a, Tilghman and Rusch 1981, Ekman 1981). The nonrandom distribution of individuals is generally recognized (Eberhardt 1978) and is countered by randomly locating transects within the sampling space. The nonconstant probability of detection versus distance from the transect is generally dealt with using any of several probability functions (e.g., Burnham *et al.* 1980) or correction factors (e.g., Emlen 1971). Similar correction factors are employed to correct counts for differences in detectability due to age or sex (e.g., Emlen 1977). Measurement errors are acknowledged but are less important with certain transect methods (Franzreb 1981a). Assumptions regarding behavior constancy of the individuals being sampled are dismissed less readily and often receive less scrutiny in study designs and analyses.

In 1986, one of us initiated a study of shrub-steppe birds using a line transect methodology. The purpose of this study was to evaluate habitat associations and time-trends in bird abundances and to assess statistical properties of the sampling regime itself. The present paper describes statistical properties related to the time interval between successive samples.

Methods

Study Area

The study area is located in the Cold Creek Valley on the U.S. Department of Energy's Hanford Site near Richland, Washington (Figure 1). The valley is composed of relatively undisturbed shrub-steppe

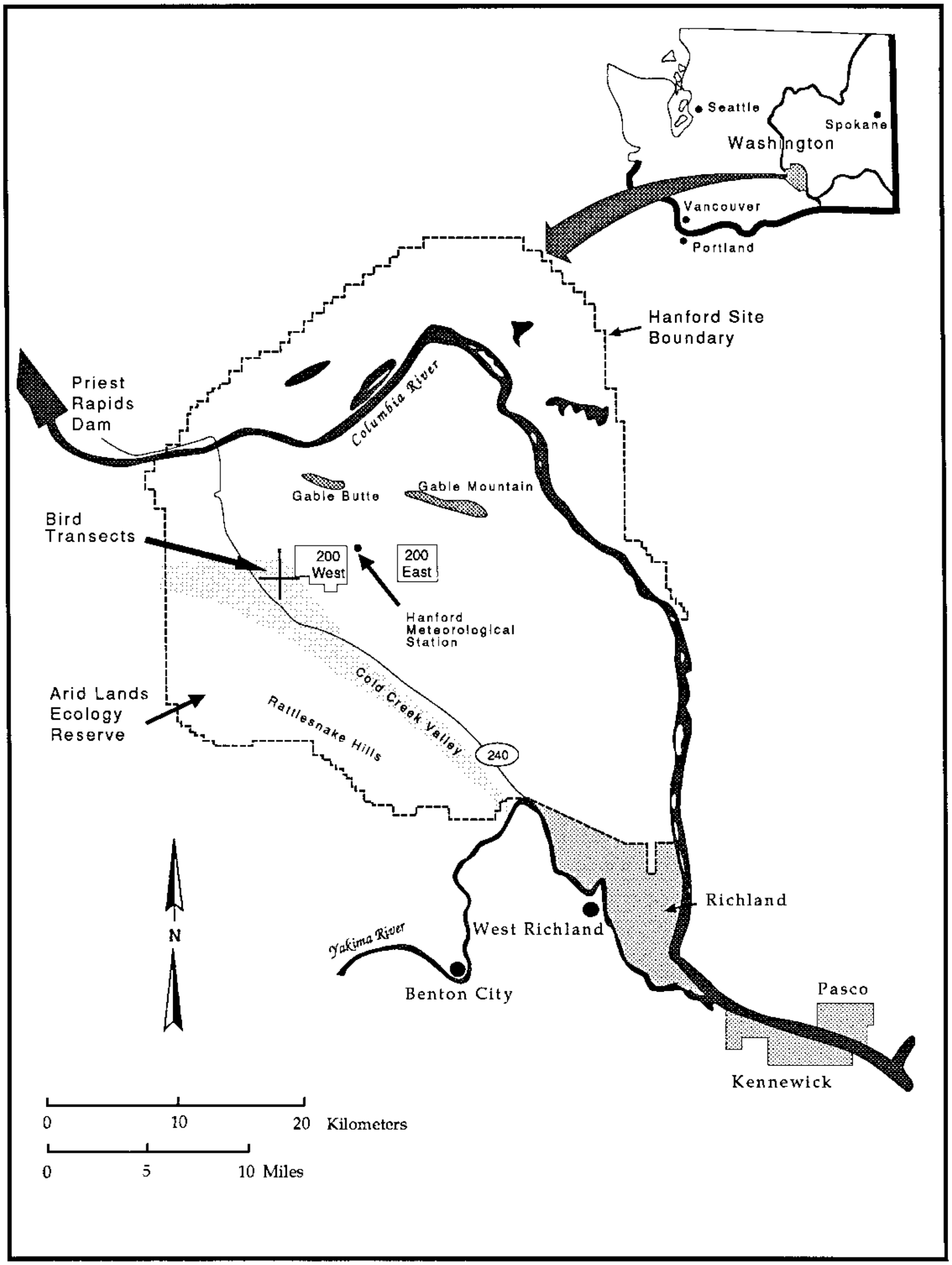

Figure 1. Location of study on the Hanford Site.

habitat dominated by annual and perennial grasses, especially cheatgrass (*Bromus tectorum*) and Sandberg's bluegrass (*Poa sandbergii*), with an overstory of widely spaced shrubs, including big sagebrush (*Artemisia tridentata*), spiny hopsage (*Grayia spinosa*), gray rabbitbrush (*Chrysothamnus nauseosus*), and green rabbitbrush (*C. viscidiflorus*).

Transect Surveys

Four line transects were established in 1986 along cardinal compass points. The lengths of the east and west transect were 1.69 km; the north and south transects were 2.66 km in length. Vegetation types traversed by the transects included big sagebrush/cheatgrass, spiny hopsage/Sandberg's bluegrass, and cheatgrass only (burned areas). Transect lines were marked with stakes at 0.1 km intervals within homogeneous habitat.

All transects were surveyed within 2 hrs of sunrise twice each week on consecutive days. These 24 hr surveys were repeated at approximately 1-week intervals for 30 weeks between 10 March and 2 October, 1987. Two observers performed the surveys simultaneously, with transects assigned to observers on a random basis each sampling day. On the first survey of the week, observations started first on randomly selected ends of each transect. On the subsequent day, the observers walked the halves of the transect in the reverse direction. In this fashion, observer identity was randomized over both transects and transects were sampled at equivalent times over the duration of the study period. Transects were walked at an approximate rate of 2.4 km/h.

The numbers, species, and distances from the transect of birds observed within 80 m of either side of the transect were recorded for each 0.1 km segment of each transect. Birds were identified to species using visual and aural cues. Bird behavior was recorded when the bird was first observed. Behavioral categories included Flyby (bird crossing the transect ahead of observer), Flush (bird flushing within 30 m of the observer), Sing (perched bird singing), and Perch (bird perched and silent). Categories were mutually exclusive, such that a singing bird was recorded under Sing and not also under another category, such as Perch; flushing birds that crossed the transect were recorded under Flush. Birds were not counted twice; the openness of the habitat and the habits of the birds allowed accurate tracking of individuals.

Data Reporting and Analysis

Data are reported as counts summed over all segments of both transects. Statistical analyses included time series analysis, Wilcoxon signed-ranks analysis, paired *t*-tests, and Chi-square tests for goodness-of-fit. Two-by-two contingency tables with fixed marginals (i.e., weeks versus sign of difference between counting periods) were analyzed using Fisher's exact test. Parametric analyses of counts were conducted on data transformed to square roots to normalize distributions. Two-tailed tests were applied in all cases of primary analysis, with a Type I error rate of 0.05 constituting a significant departure from the null. One-tailed tests were used where the null hypotheses included a direction.

Results

All Birds

Thirty-five bird species were observed during the transect walks (Table 1). Nine of these species nested in the shrub-steppe vegetation along the transects. The most frequently sighted birds were western meadowlarks and sage sparrows. European starlings were the most common species sighted that did not nest in shrub-steppe vegetation.

An average of 49.3 birds of all species were counted per survey during the study period when estimates from all surveys were included. However, when average counts were estimated using only the first of the consecutive surveys each week, the average for the survey period was 55.1 birds per survey. On a monthly basis, first-day counts were higher than mean counts based on two-day samples 7 months out of 8, the exception being March (Figure 2). Counts based on both sample sets showed similar trends over the study period, with peak numbers in April and a second peak in June. Counts declined from June to October for both sample sets.

During a period of declining population numbers, survey counts and resulting density estimates based on second-day surveys are expected to be lower than estimates based on first-day surveys throughout the decline phase. The average expected difference between the two estimates during any time period is the average daily rate of decline during that period (see Appendix A). For the present study, the differences in monthly bird counts between first-day and second-day samples

TABLE 1. Average number of birds counted on suveys from 10 March through 2 October 1987.[a]

Common Name	Scientific Name	Mean Count/ survey	Surveys when species detected
Shrub-steppe birds nesting along the transect			
western meadowlark[b]	*Sturnella neglecta*	12.04	60
sage sparrow	*Amphispiza belli*	5.44	51
burrowing owl	*Athene cunicularia*	1.32	44
horned lark	*Eremophila alpestris*	1.24	28
long-billed curlew	*Numenius americanus*	1.15	24
mourning dove	*Zenaida macroura*	0.75	24
loggerhead shrike	*Lanius ludovicianus*	0.75	22
lark sparrow	*Chondestes grammacus*	0.22	7
common nighthawk	*Chordeiles minor*	0.18	10
Other birds			
white-crowned sparrow	*Zonotrichia leucophrys*	5.03	6
European starling	*Sturnus vulgaris*	4.69	37
black-billed magpie	*Pica pica*	1.00	18
American robin	*Turdus migratorius*	0.51	9
barn swallow	*Hirundo rustica*	0.46	12
rock dove	*Columba livia*	0.39	4
common raven	*Corvus corax*	0.35	17
western kingbird	*Tyrannus verticalis*	0.35	13
brown-headed cowbird	*Molothrus ater*	0.19	8
savannah sparrow	*Passerculus sandwichensis*	0.13	3
American kestrel	*Falco sparverius*	0.08	6
Swainson's hawk	*Buteo swainsoni*	0.06	5
Townsend's solitaire	*Myadestes townsendi*	0.04	1
sage thrasher	*Oreoscoptes montanus*	0.04	3
northern flicker	*Colaptes auratus*	0.03	2
red-winged blackbird	*Agelaius phoeniceus*	0.03	2
Brewer's blackbird	*Euphagus cyanocephalus*	0.03	1
house finch	*Carpodacus mexicanus*	0.03	1
Brewer's sparrow	*Spizella breweri*	0.01	1
chipping sparrow	*Spizella passerina*	0.01	1
northern harrier	*Circus cyaneus*	0.01	1
northern oriole	*Icterus galbula*	0.01	1
red-tailed hawk	*Buteo jamaicensis*	0.01	1
rough-legged hawk	*Buteo lagopus*	0.01	1
Say's phoebe	*Sayornis saya*	0.01	1
vesper sparrow	*Pooecetes gramineus*	0.01	1

[a] Total number of surveys = 60.

[b] Species underlined were seen on at least 15% of surveys.

were much lower than the average rate of decline for all months when numbers were declining. The greatest rate of decline occurred between April and May, when numbers declined at a rate of 1.8 per day. However, monthly bird numbers based on second-day surveys during that period were lower than first day estimates by 29.9 ($\bar{x}_{day1} = 103.4$, $\bar{x}_{day2} = 73.5$).

The pattern of fluctuation in daily estimates departed significantly from random (runs test: $z = 2.424$, $P = 0.0156$). Counts fluctuated more frequently than expected based on a random model. Estimates were subjected to time series analysis to identify the strongest periodicity in the data. The greatest level of autocorrelation was for a lag of one ($r = 0.429$, SE = 0.129). The autocorrelation for lag of two was 0.289 (SE = 0.151). Autocorrelations for lags of greater time were all less than 0.135. Fourier transformation of the time series identified the primary cycle as the N_t to N_{t+1} signal, with the factor weighting over 7 times any other weighting.

The sample-to-sample differences identified in the time series analysis were examined further

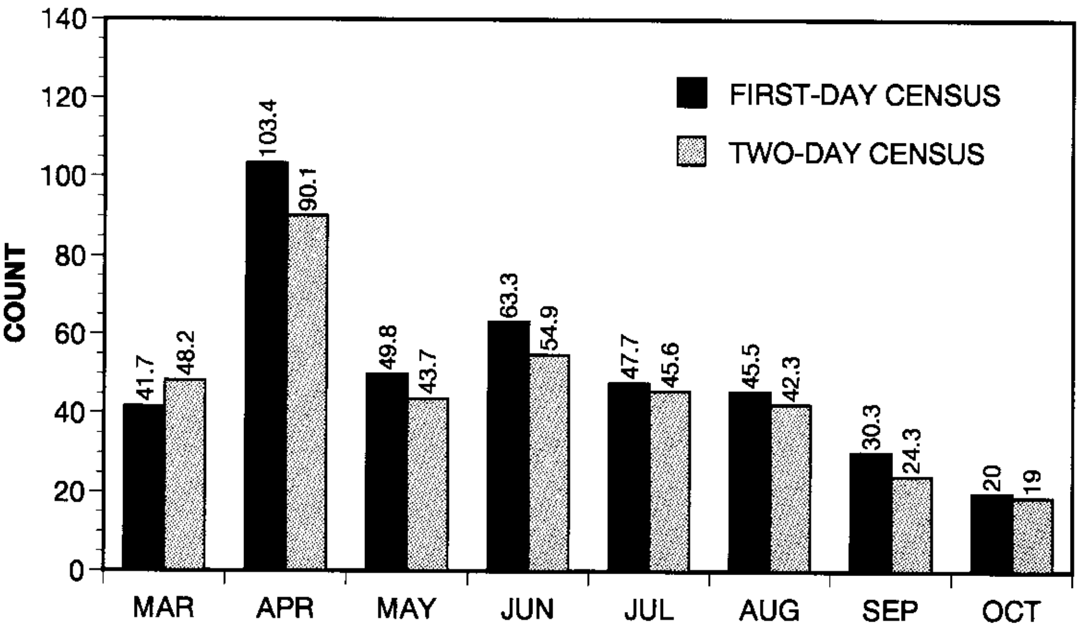

Figure 2. Average counts of all birds seen in the sampling transects based on weekly and twice-weekly samples.

using paired comparisons in a one-tailed test with the null hypothesis that second-day counts were no lower than the previous or subsequent estimates. The null hypothesis was rejected: Average counts on the second survey of the week were significantly lower than counts obtained the previous day (paired *t*-test: $t = 2.449$, $df = 29$, $P < 0.012$). Average counts were also lower on the second survey of the week than they were on the subsequent survey approximately six days later (paired *t*-test: $t = 1.751$, $df = 28$, $P = 0.045$).

The behavior of survey estimates was examined further by subdividing birds into two groups: those that nested in the shrub-steppe habitat along the transects and those that nested elsewhere, but which visited the area. Monthly estimates of nesting species exhibited a temporal pattern similar to the estimates for all birds, without the large peak in April (Figure 3). Estimates based on two samples per week were smaller than estimates based on the first sample each week for all months except March. In all cases when estimates were declining, the difference in estimates based on first-day versus second-day samples were greater than the average decline rate. Partial autocorrelations from the time series analysis showed the primary cycle to be between one sampling period and the next ($r = 0.255$, SE $= 0.129$). Fourier transformation weighted the first element over ten times that of any other. Runs test analysis, however, did not show a significant departure from random ($z = 0.758$, $P = 0.44$).

Survey counts of species that did not nest in the shrub-steppe habitat were less constant over time compared to the nesting species (Figure 4). Numbers of visiting species peaked dramatically in April, when large flocks of birds, probably migrants, made temporary appearances on the transects. Monthly estimates based on first-day samples were no larger, on average, than were estimates based on all samples. Paired comparisons showed no significant difference between first-day and second-day estimates ($t = 0.027$, $P = 0.978$). Autocorrelations were low for all time lags, although the greatest correlation was between one sample period and the next ($r = -0.208$, SE $= 0.153$). Fourier transformation weighting of the one-day lag was only twice that of the 2-period and 3-period lags. Thus the period-to-period cycle was much less strong for visitors than for birds nesting in the shrub-steppe habitat.

This difference was further explored using only those 14 species that were detected on at least 15% of the surveys (Table 1). Of these, 8 nested in the shrub-steppe and 6 were visitors. Counts for 7 of

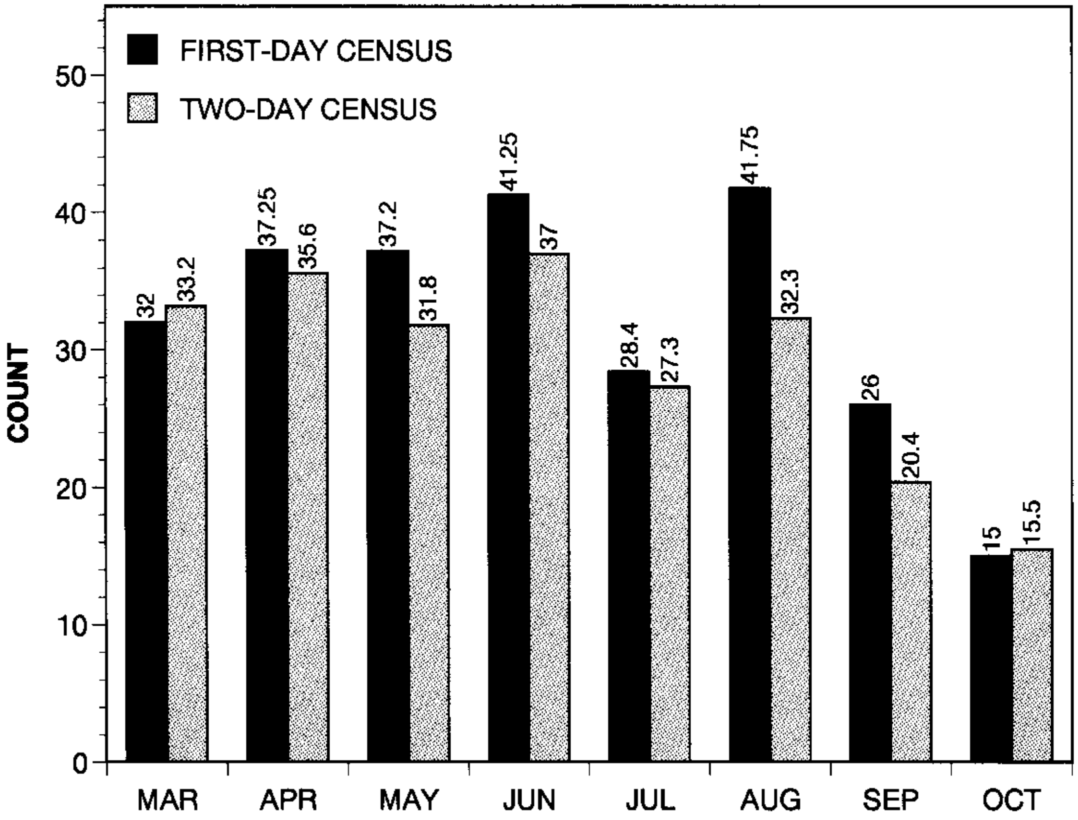

Figure 3. Average counts of birds nesting on the sampling transects based on weekly and twice-weekly samples.

the 8 species nesting in the shrub-steppe were greater on the first sample day than on the subsequent sample day for the entire study period (binomial $P = 0.035$). Only 2 of the 6 visitor species showed the same trend (binomial $P = 0.344$). The difference in counts for the 2 groups of species approaches significance (Fisher's Exact $P = 0.063$).

Western Meadowlarks

Western meadowlarks were the most abundant species on the transects, composing nearly one-third of all sightings. Average estimates of western meadowlarks on second-day samples (14.1 birds/survey) were significantly lower than counts on the previous day (18.1 birds/survey; paired-$t = 2.628$, $df = 29$, $P < 0.014$). One observation on day 200 (first-day sample) constituted a significant outlier that could not be normalized using standard transformations. Subsequent comparison using the nonparametric Wilcoxon signed-ranks test supported the conclusion made on the basis of parametric tests ($z = -2.408$, $P < 0.016$). Deletion of the outlier and its pair (day 201) from the parametric analysis did not affect the significance of the conclusion (paired-$t = 2.113$, $df = 27$, $P < 0.028$).

During the period from nesting to fledging (1 April to 30 June), counts were greater on the first survey of the week on 9 weeks, with the opposite occurring only on 2 weeks (binomial $P = 0.033$). During the flocking period after 30 June, first-day counts were greater than second-day counts during 8 weeks, with the opposite occurring on 5 weeks (binomial $P = 0.291$).

Counts of meadowlarks classed as singing and flyby during the entire study period were significantly smaller on the second day than on the first day of the week, although the likelihood that second-day counts would be lower than on the previous day was not significant (Table 2). Differences for other behavioral categories were not

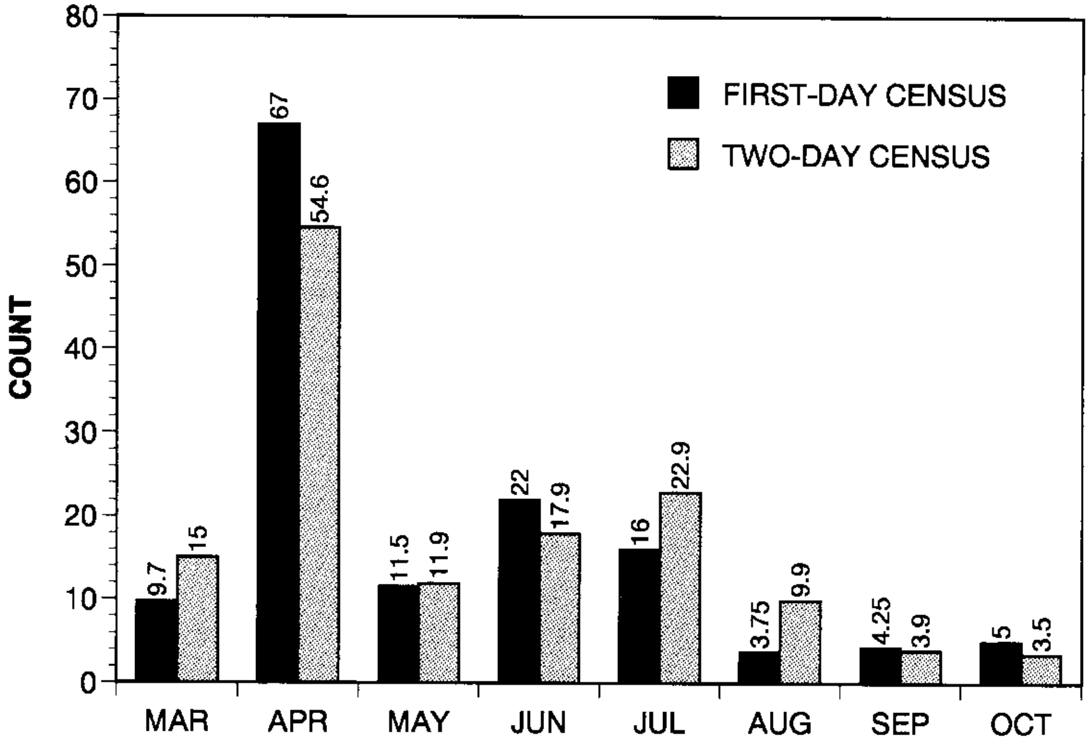

Figure 4. Average counts of birds visiting (not nesting on) the sampling transects based on weekly and twice-weekly samples.

TABLE 2. Analysis of western meadowlark counts according to activity at sighting.

	Sing	Perch	Flyby	Flush
Average First-Day	6.4	2.0	4.2	5.6
Average Second Day	5.3	2.2	1.9	4.6
Wilcoxon *Z*	−1.736	−0.436	−1.724	−0.555
One-tailed *P*	0.041	0.33	0.043	0.29
No. Day 1 > Day 2	15	12	17	14
No. Day 1 < Day 2	9	15	10	15
χ^2	1.500	0.926	1.815	0.034
P	>0.1	>0.1	>0.1	>0.5

significant. Counts of singing birds were lower on the second day than the first day during the nesting-to-fledging period on 9 weeks, with the opposite obtaining on 3 weeks (binomial $P = 0.073$). During the flocking period, no differences were observed for singing birds on first-day versus second-day samples on 5 weeks; first-day counts of singing birds were greater than second-day counts on 5 weeks, with the opposite occurring on 4 weeks (binomial $P = 0.5$). Comparisons for other behavioral categories did not depart significantly from random.

Sage Sparrows

Sage sparrows were detected during all but nine surveys and were the second most abundant bird on average. Counts of sage sparrows early in the study period were almost entirely of singing birds. After 9 July, no singing was heard, and subsequent counts were either of perching or flushing birds. No sage sparrows were counted after 4 September.

Counts of sage sparrows on the first survey of the week ($\bar{x} = 9.4$ birds/survey) were significantly greater than on the subsequent survey ($x = 7.7$ birds/survey, paired-$t = 2.497$, $df = 24$, $P < 0.02$). Counts on first-day surveys were more frequently higher than counts on the following day but the difference was within the realm of sampling error (14 counts higher versus 8 counts lower, Binomial $P = 0.143$). No portion of the study period existed in which bird counts on any given pair of survey dates were more likely to show a common trend.

TABLE 3. Analysis of sage sparrow counts according to activity at sighting.

	Activity at Sighting			
Statistic	Sing	Perch	Flyby	Flush
$\bar{x}_{day\ 1}$	6.1	1.8	0.2	1.4
$x_{day\ 2}$	5.6	1.2	0.2	0.7
Wilcoxon Z	−0.643	−0.679	−0.632	−1.512
One-tailed P	0.261	0.248	0.264	0.066
No. samples Day 1 count > Day 2 count	10	8	2	9
No. samples Day 1 count < Day 2 count	7	9	5	3
Binomial P	0.315	0.500	0.227	0.073

Analysis of counts according to the activity of the birds when first sighted shows no significant differences between paired survey dates for any activity (Table 3). Sage sparrows were rarely counted as flybys (8 of 48 surveys), so comparisons on this variable are not reliable. Counts of birds in other activity categories were lower on the second survey, though only the counts for flushing birds neared statistical significance. There was no significant tendency for trends from first-day to second-day samples to differ between nesting/incubation and flocking periods (Binomial $P > 0.3$).

Density Estimates

Density estimates are generally derived from line-transect survey data by applying a correction factor to observed counts (Burnham *et al.* 1980). This correction factor utilizes information on the distance from the transect to the observed individual to determine the expected number of individuals that are undetected, assuming that the probability of detection declines with distance from the transect according to some standard decay function (see Seber 1973, Burnham *et al.* 1980). Density estimates from consecutive surveys could therefore remain invariant despite differences in counts if average distances of sighted individuals from the transect increased on the second survey. This possibility was not upheld: no significant differences in average distance from the transect to the sighted individuals were found for shrub-nesting species as an aggregate or for any individual species (binomial $P > 0.5$).

Discussion

Selection of an appropriate sampling frequency for repeated transect surveys is crucial to obtaining accurate indices of density. Our analysis indicates that bird density indices derived from surveys repeated on a short-duration cycle can be significantly below estimates made from surveys on a longer duration cycle. In the present study, the average weekly bird count was consistently lower by more than 10 percent when surveys were taken on consecutive days rather than 1 week apart.

Differences in counts from first-day to second-day samples are expected when population numbers (or estimates of those numbers) are declining; however, the difference in estimates in the present study could not be explained by population decline alone. Remaining potential causes for the observed difference are limited to real differences in numbers or artificial differences resulting from bird behavior, observational conditions (e.g., poor weather on the second day), and/or sampling technique (e.g., the tendency for more-competent observers to sample on the first day of the week transects with higher bird densities). The only periodic aspect of the sampling design was that transects were walked in the reverse direction from one sample to the next. However, since starting points were chosen at random, it is highly unlikely that direction of travel would produce the trend observed. Weather conditions were random with respect to sample date, and timing of samples were constant with respect to sunrise.

Differences in bird numbers between first and second day samples were thus either a consequence of real differences or differences in detectability. In both cases, differences would be a function of observer-bird interaction. Real differences in numbers are unlikely unless the birds were more likely to leave the sampled area earlier in response to the approaching observer on the second survey than on the first survey. Most birds are detected on transects by song alone (Cyr 1981). Thus differences in counts could also arise if normally singing birds were less likely to sing as a consequence of the repeated appearance of the observer. This change was noted for western meadowlarks during the nesting period.

In contrast to counts of meadowlarks, counts of singing sage sparrows showed no significant differences between first-day and second-day surveys. Counts of sage sparrows for all behavior categories were generally lower on the second day than on the previous day, although not significantly so, which is consistent either with the hypothesis that fewer sage sparrows were present on the second survey of the week, or the hypothesis that sage sparrows became less conspicuous on the second day by moving under cover.

There were no significant differences in counts between first-day and second-day surveys for species that visited the area of the transects but did not nest there. This is consistent with the suggestion that the difference detected for birds nesting in the shrub-steppe was a consequence of repeated bird-observer interaction on a short time frame. Visiting birds are less likely to be present in the same area day after day, in contrast to resident nesting birds.

Changes in behavior in response to repeated disturbance may be attributed either to habituation or conditioning. Habituation is the waning of response to a particular stimulus pattern presented repeatedly over sufficiently short intervals. Conditioning refers to the adoption of a particular behavior pattern as a result of associating a particular stimulus with a certain reinforcement. Habituated behavior patterns are readily restored by relatively short intervals without the stimulus. Conditioned responses are less readily extinguished (see Staddon (1983) for definitions and characteristics). Given that bird counts returned to higher levels within 5 days of the previous survey, habituation of resident birds to the observer rather than conditioning is likely to be the cause for lower counts. On daily surveys, nesting birds may cease to associate the observer with a potential predator or competitor. Consequently, birds may be less likely to exhibit warning displays (e.g., singing by western meadowlarks) or to stay on their territories (e.g., sage sparrows) during the second survey when the observer approached.

A few density estimation techniques explicitly take advantage of the alarm or territorial defense response of animals to human intrusions (e.g., territory mapping, Wiens 1969). Most techniques rely implicitly on behavioral patterns to allow infallible detection in at least some portion of the survey area (e.g., variable-strip and fixed width line transect methods, Emlen 1971, Burnham *et al.* 1980; variable circular-plot methods, Reynolds *et al.* 1980). Such complete detection regions serve as the basis for deriving either a spatial detection function or a "coefficient of detectability," which is then used to "correct" counts from portions of the sampling region where the probability of detection is assumed to be less than unity (e.g., Burnham *et al.* 1980). Even with such corrections, density estimates from transect or plot sampling schemes are consistently lower than estimates from spot mapping for all but the most conspicuous species (Franzreb 1981b, DeSante 1981, Tilghman and Rusch 1981). Habituation may further bias density estimates below true values.

An assumption essential to transect or plot-sampling techniques is that the detectability of the study population does not change during the sampling period (Seber 1973, Franzreb 1981a). Detectability varies with individuals (Diehl 1981), sexes (Mayfield 1981), and season (Ekman 1981), and various techniques have been proposed to correct for or minimize such variation. Less attention has been paid to the role of habituation as a source of error. As demonstrated in the present study, repeated sampling and resulting behavioral changes in birds can produce significant biases in counts of birds nesting on line transects. Subsequent estimates of bird density based on any of the available algorithms (see listing in Tilghman and Rusch 1981) will not only under-represent reality, but will be unstable because standard errors will depend on the mixture of sampling periodicities involved in the estimate. Standard errors will be smallest when habituation is low in all samples, and maximal when half the samples are affected by habituation and half are not. Standard errors will be low when habituation is common, but density estimates will be maximally biased. The birds nesting in shrub-steppe habitat in the present study exhibited behavioral changes when sampling periods were 24 hours apart. Shorter time intervals are likely to be even more effective at inducing such behavioral changes. Counts remained at high levels when sampling periods were at least 5 days apart; longer sampling intervals may lead to even higher counts per transect.

Habituation attenuates with time; it may also be abolished by altering the stimulus or its background (Hale and Almquist 1960). For example, an animal habituated to a noise may show renewed response when the noise is accompanied by a novel visual stimulus (Staddon 1983). It is, therefore, likely that habituation in transect sampling may be overcome by similar means. Determining these means presents some interesting experimental challenges.

Acknowledgments

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APPENDIX A

For any period undergoing linear decline in numbers, the expected count on day t is estimated by

$$N_t = N_0 - t\frac{dN}{dt} + e \qquad (1)$$

where N_t = number of individuals on day t,

N_0 = number of individuals on day t = 0,

t = day since start of period,

$\frac{dN}{dt}$ = rate of change in numbers, and

e = random error.

Thus a series of w weekly samples would have an expected value during the sample period of:

$$\overline{N_1} = \frac{N_0 + (N_0 - 7\frac{dN}{dt}) + (N_0 - 14\frac{dN}{dt}) + \ldots + (N_0 - 7(w-1)\frac{dN}{dt} + we)}{w}$$

$$= N_0 - 3.5(w-1)\frac{dN}{dt} \qquad (2)$$

A comparable set of w weekly samples obtained the day after each of the previous samples would have an expected value of:

$$\overline{N_2} = \frac{(N_0 - \frac{dN}{dt}) + (N_0 - 8\frac{dN}{dt}) + (N_0 - 15\frac{dN}{dt}) + \ldots + (N_0 - (7(w-1)+1)\frac{dN}{dt})}{w}$$

$$= N_0 - 3.5(w-1)\frac{dN}{dt} + \frac{dN}{dt} \qquad (3)$$

Then, because the expected value of the difference between two random variables is the difference in their expected values,

$$\overline{N_1} - \overline{N_2} = (2) - (3) = \frac{dN}{dt} \qquad (4)$$