# HOURLY VARIATION IN MORNING POINT COUNTS OF BIRDS

JARED VERNER AND LYMAN V. RITTER
*Pacific Southwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 2081 East Sierra Avenue, Fresno, California 93710 USA*

ABSTRACT.—We studied hourly variation in measures of the abundance of individual species and the species composition of bird assemblages in different habitats and seasons in the western Sierra Nevada of California, using 8- and 10-min point counts. Results failed to show clearly that any one of the first 4-5 h after sunrise is better than another. The advantages of more counts or more sites sampled, or both, gained by counting over several hours outweigh any advantage that might result from restricting counts to periods that give counts with lower variance. Species richness was better measured by sampling over a period of several hours than by sampling an equal period of time during any single hour. *Received 27 September 1984, accepted 16 August 1985.*

FEW studies give detailed analyses of diurnal variation in bird counts, perhaps because such information is a byproduct of studies done for other reasons. Ornithologists have long known, however, that birds are detected early in the morning more often than later in the day. Guidelines for extensive surveys account for this by recommending that counts be confined to early-morning hours (e.g. Hall 1964, Anon. 1970, Järvinen et al. 1977, Bystrak 1979, Conner and Dickson 1980).

This is not a problem for all bird species, however, as the detectability of some may be nearly constant throughout the day [e.g. Northern Cardinal (*Cardinalis cardinalis*) and Scarlet Tanager (*Piranga olivacea*), Robbins 1981]. The detectability of others can increase for several hours after sunrise [e.g. Kirtland's Warbler (*Dendroica kirtlandii*), Mayfield 1960; Eurasian Woodcock (*Scolopax rusticola*), Järvinen et al. 1977; American Goldfinch (*Carduelis tristis*), Robbins 1981; Steller's Jay (*Cyanocitta stelleri*), Skirvin 1981]. We believe that too little attention has been given to exceptions such as these, so the general guideline to "count early in the morning" is almost an unchallenged dogma.

Rapid changes in the detectability of most species near dawn might result in such high variance in counts that more effort would be required with dawn counts than with midday counts to detect significant differences between samples, even though larger numbers of birds might be detected during counts beginning at or near sunrise. Believing this to be the case, Dawson (1981) recommended counting between 0930 and 1530 for relative measures of bird populations in New Zealand forests.

Finally, sampling bird communities at different times of the day may give different conclusions about the richness and composition of those communities. If this is true, comparisons between communities should be based on samples taken during comparable periods of the day.

Our objective in this study was to quantify hourly changes in bird counts to determine the best time in the morning to count birds in forest and woodland habitats in the western Sierra Nevada of California. To accomplish this, we examined hourly trends among five measures: (1) counts of individual species, (2) variance in counts of individual species, (3) pooled counts of all species, (4) species richness, and (5) species composition.

## METHODS

*Study areas.*—Counts were done at meadow edges in the Sierra National Forest (SNF) in Fresno and Madera counties, California and in oak-pine woodlands at the San Joaquin Experimental Range (SJER) in Madera County. All counting stations ($n$ = 125) in SNF were different, randomly selected points at the edges of 32 meadows (elevation 1,280–2,225 m, $\bar{x}$ = 1,801 m, SD = 215 m), randomly chosen from a pool of 80 meadows earlier identified as suitable for the study. Most (89%) were included in the mixed-conifer forest zone (white fir, *Abies concolor;* incense cedar, *Calocedrus decurrens;* ponderosa pine, *Pinus ponderosa;* Jeffrey pine, *Pinus jeffreyi;* and sugar pine, *Pinus lambertiana*). The remainder were at higher elevations in the zone of red fir forests (red fir, *Abies magnifica;*

and white fir). All meadows had sufficient moisture to support mixtures of sedges, grasses, and forbs. Most had light to moderate shrub cover around the edges. In wet sites these included willows (*Salix* spp.), alders (*Alnus* spp.), and occasionally western azaleas (*Rhododendron occidentale*). The dominant shrub on drier areas was mountain whitethorn (*Ceanothus cordulatus*). The forest immediately surrounding most meadows included a substantial belt of lodgepole pine (*Pinus contorta*), even at lower elevations. The climate is characterized by warm, dry summers and cold winters with moderate to heavy snowfall.

Two study areas were used at SJER, where the climate is characterized by cool, wet winters and hot, dry summers. The "grazed site" (elevation 365 m) has been exposed to a moderate level of grazing almost yearly since the late 1800's. The "ungrazed site" (elevation 335 m) was fenced and set aside as a preserve in 1934; it has had no grazing, fires, or other major disturbances since that time. Both sites support extensive stands of open woodland, with interspersed and understory patches of shrubs and annual grasses. Composition of the vegetation was similar on both sites, each supporting a mixed canopy of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and digger pine (*Pinus sabiniana*). Total tree cover was 32.3% on the grazed site and 25.3% on the ungrazed site. Shrub cover was 6.6% on the grazed site and 21.8% on the ungrazed site, with a distinct browse line only on the grazed area. Principal shrub species were buck brush (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and Mariposa manzanita (*Arctostaphylos mariposa*).

*Bird counts.*—The sampling procedure in SNF was specifically designed to measure diurnal changes in counts. The study at SJER was designed to test factors other than time of day that may influence bird counts (Verner and Ritter 1985). Results, however, were typical of those normally obtained when point counts were used to measure the abundance of birds. An analysis of the SJER data therefore is included here, under the assumption that results accurately reflect diurnal influences on counts.

We avoided counting during periods of precipitation or when cloud cover exceeded 60%; the sky was no more than 5% overcast during 87% of the counts in SNF and during all counts at SJER. Maximum wind velocity during any count was 16 km/h. Counts by different observers were equalized among different hours of the day to balance potential observer bias.

One data set (SNF Meadow Edges) was obtained using 10-min point counts with unlimited distance at meadow edges in SNF during the breeding season of 1983 (14 June to 15 July), from 0500 to 1000 PST. Counts were confined within five hourly periods, beginning at 0500, and all hourly samples included 25 counts. The time of sunrise varied among the meadows sampled because they differed in their relationship to surrounding terrain and the height of nearby forests. However, all areas were past morning twilight by 0500, even though direct sunlight did not reach surrounding treetops until 0520 or later. Counting stations were located at intersections between meadow edges and lines from meadow centers on randomly chosen compass directions, subject to the constraints that no two points could be less than 400 m apart and points could not be located near major disturbances (campgrounds, heavily used roadways, ongoing logging operations, etc.). Distances from sources of disturbance varied with the amount of activity and the intensity of noise, but points were always at least 100 m from disturbances and were at least 400 m away from some, such as logging activity.

We obtained five data sets at SJER: two during the breeding season of 1980, using 8-min point counts on both plots from 14 April to 5 May ("SJER Grazed 1980" and "SJER Ungrazed 1980" data sets), and three during the winter and early spring of 1982, using 10-min point counts on the ungrazed plot only (19 January to 2 February, "SJER January 1982"; 8-19 February, "SJER February 1982"; and 9-22 March, "SJER March 1982").

Bird counts at SJER began about 15 min before sunrise each day. Counts were done on mapped grids, 300 × 660 m, used for spot-mapping. Lines were randomly selected from the long axis of the grid. Five point counts (beginning 30 m from the end of the line and spaced at 150-m intervals along the remainder of the line) were used to sample the bird community. Birds were counted along two lines, at least 90 m apart, during eight days for each data set. Each daily counting period at SJER was divided into four hourly intervals. Because the sampling routine at SJER proceeded without reference to hourly breaks, some counts overlapped two hourly periods. In those cases, counts were assigned to the hour in which more than half of the count occurred, giving unequal sample sizes in the hourly samples at SJER (see Table 1).

We compared species richness in different samples, standardized to the same effort (number of counts) by using species-accumulation curves estimated using Eq. 1. This formula is the exact expression of the estimate (a "bootstrap estimate"; Efron 1982), obtained by randomly drawing, with replacement, an infinite number of samples of size *m* from the original sample:

$$S_m = S_o - \sum_{i=1}^{S_o} (1 - p_i)^m, \qquad (1)$$

where $S_m$ = the estimated number of species, given a sample of $m$ counts; $S_o$ = the total number of species in the original sample; $p_i$ = the proportion of counts during which species $i$ was detected; and $m$ = the number of counts in the sample to be estimated. The variance is estimated by

TABLE 1. Mean number of individuals of all species combined (±2 SE) detected during point counts in successive hourly periods after dawn. (Sample sizes in parentheses beneath means.)

| Data set | Hourly period | | | | | F value |
|---|---|---|---|---|---|---|
| | First | Second | Third | Fourth | Fifth | |
| SNF Meadow Edges | 17.2 ± 1.2<br>(25) | 16.4 ± 1.5<br>(25) | 16.7 ± 1.4<br>(25) | 16.8 ± 3.2<br>(25) | 15.5 ± 1.5<br>(25) | 0.40 ($P = 0.81$) |
| SJER Grazed 1980 | 8.5 ± 1.1<br>(21) | 8.4 ± 1.0<br>(20) | 8.9 ± 1.1<br>(21) | 8.2 ± 0.9<br>(18) | | 0.25 ($P = 0.86$) |
| SJER Ungrazed 1980 | 8.8 ± 1.5<br>(22) | 7.9 ± 1.5<br>(18) | 8.1 ± 1.1<br>(23) | 7.5 ± 1.3<br>(17) | | 0.66 ($P = 0.58$) |
| SJER January 1982 | 14.5 ± 3.6<br>(17) | 12.5 ± 2.2<br>(21) | 13.2 ± 2.7<br>(16) | 13.7 ± 2.6<br>(26) | | 0.36 ($P = 0.79$) |
| SJER February 1982 | 12.6 ± 2.3<br>(22) | 16.5 ± 3.8<br>(18) | 11.4 ± 2.8<br>(18) | 9.7 ± 1.4<br>(22) | | 4.77 ($P = 0.004$) |
| SJER March 1982 | 15.5 ± 2.6<br>(22) | 14.3 ± 2.0<br>(21) | 11.8 ± 1.9<br>(19) | 13.4 ± 3.0<br>(18) | | 1.72 ($P = 0.17$) |

$$V = \sum_{i=j}\sum (1 - p_i)^{m-1}(1 - p_j)^{m-1} \cdot (w_{ij} - p_i p_j)m^2/n, \qquad (2)$$

where $n$ = the total number of counts and $w_{ij}$ = the proportion of counts during which species $i$ and species $j$ were detected. We prefer this method to rarefaction using randomly drawn samples without replacement (Simberloff 1979), because the latter method lacks an inferential basis and the direction and magnitude of bias in its estimates are unknown (Tipper 1979, James and Wamer 1982).

Species richness from counts done during the breeding season included only species known to nest in the habitats being sampled. In samples from meadow edges in SNF, we excluded known early migrants from northern latitudes (e.g. Rufous Hummingbird, *Selasphorus rufus*) and species known to wander upslope after nesting only at lower elevations (e.g. House Wren, *Troglodytes aedon*; Orange-crowned Warbler, *Vermivora celata*). At SJER, we excluded spring transients and wintering species that breed elsewhere, even though they were present during the counts. In all samples, we did not count birds that obviously just passed over the habitat being sampled.

*Analysis.*—We identify statistical tests used with the corresponding results; the alpha level for tests of significance is 0.05.

## RESULTS

*Total count.*—Highest mean total counts (all individuals of all species combined) were obtained during the first hour in four data sets and during the second and third hours in one data set each (Table 1). However, hourly differences among total counts were significant only in the data set SJER February 1982 (one-way ANOVA; Table 1). Pairwise comparisons, using the Bonferroni approach (adjusting for multiple comparisons of all pairs of means), showed only one significant difference among 40 comparisons: the total count was higher ($P$ = 0.003) in the second than in the fourth hour of the SJER February 1982 data set.

*Individual species.*—Patterns of diurnal change in hourly counts varied among species. Counts of some decreased markedly and those of others increased from early to late hours in the morning, but counts of most species showed little or no change, or the pattern of change did not conform to either a steady increase or a steady decrease in hourly counts. Among 66 species with a total count of at least 5 individuals in each of the first 4 h of sampling, the rank order from highest to lowest hourly count showed that many species had their highest counts during the first hour, many had their second-highest counts during the second hour, and so on (Table 2). However, the trend was not significant (Friedman statistic = 4.80, $P$ = 0.19) among summed ranks from the six data sets. Moreover, in 67% of the cases, species had highest counts in the second, third, or fourth hour (Table 2), and even among many of those species with highest counts during the first hour, differences between hourly counts were small.

*Variance of counts.*—Hourly variance in counts was least during the first hour for nearly twice as many species as during any other hour, and

TABLE 2. Rank order of hourly counts of individual species with a minimum count of 5 in each hour ($n = 66$), including results from all samples and standardizing all SJER samples to 25 counts.[a]

| | Hourly period | | | |
|---|---|---|---|---|
| Rank order | First | Second | Third | Fourth |
| 1 | 22 | 15 | 15 | 14 |
| 2 | 14 | 25 | 15 | 12 |
| 3 | 17 | 13 | 19 | 17 |
| 4 | 13 | 13 | 17 | 23 |
| Mean rank | 2.32 | 2.36 | 2.58 | 2.74 |

[a] For example, 22 species had their highest counts during the first hour, 14 had their second-highest counts during the first hour, etc.

the summed ranks of hourly variance showed the least variance during the first hour in three of the six data sets. Variance was least in the first hour for six of eight species in the data set SJER Grazed 1980, and hourly differences in variance were significant (Friedman statistic = 12.3, $P = 0.01$). However, hourly differences for the remaining five data sets were not significant (Friedman statistics ranged from 1.56 to 4.53, $P$ ranged from 0.21 to 0.82). Similarly, when variances were pooled by hour for all data sets combined, the variance in counts increased with each later hour of the day, but the trend was not significant (Friedman statistic = 4.44, $P = 0.22$). Because the variance in counts was unusually high among species for which flocks were detected (the three winter-period data sets for SJER), the data were reanalyzed with those species removed. These smaller data sets gave basically the same results as the complete data sets.

*Observed species richness.*—Highest mean species richness was recorded during the first hour in four data sets and during the second hour in two (Table 3). Among the six data sets, hourly totals differed significantly in three (one-way ANOVA; Table 3). As with total counts, however, most between-hour differences were small and insignificant. Bonferroni tests showed only three significantly different, pairwise comparisons among 40 possible: first vs. fourth hour, SNF Meadow Edges, $P = 0.003$; second vs. fourth hour, SJER February 1982, $P = 0.0003$; first vs. third hour, SJER March 1982, $P = 0.004$.

Species richness in the SNF Meadow Edges data set was lowest in the first hour and highest in the last; successive hourly totals were 41, 41, 47, 47, and 49. A similar direct comparison cannot be made for the SJER data sets, because the number of counts differed among hours. The next section estimates these comparisons on samples standardized to the same number of counts.

*Predicted species richness.*—Predicted species-accumulation curves (bootstrap estimates) ascended rapidly with the first 8-10 counts, after which they ascended more slowly toward the total number of species expected (Fig. 1). These estimates, standardized within each data set to the fewest counts in any hour, showed few significant differences between hours within data sets. Predicted species richness with 25 counts was greater in each of the last three hours than in either of the first two hours of the SNF Meadow Edges data set (nonoverlapping 95% confidence limits; Table 4). In the data set SJER March 1982, predicted species richness was greater in the first hour than in the third and fourth hours, and it was greater in the second than in the third hour (Table 4). No significant hourly differences occurred in any of the four remaining data sets. Species-accumulation curves using all hours combined for each data set, standardized to the same number of counts, gave greater species richness than did hourly counts in 23 of 25 cases. In 8 cases (2 first-hour

TABLE 3. Mean species richness (±2 SE) recorded during point counts in successive hourly periods after dawn. (Sample sizes are given in Table 1.)

| | Hourly period | | | | | |
|---|---|---|---|---|---|---|
| Data set | First | Second | Third | Fourth | Fifth | $F$ value |
| SNF Meadow Edges | 12.8 ± 1.1 | 12.4 ± 1.1 | 11.1 ± 0.9 | 10.5 ± 1.0 | 11.2 ± 1.1 | 3.20 ($P = 0.02$) |
| SJER Grazed 1980 | 6.3 ± 0.7 | 6.6 ± 0.8 | 6.0 ± 0.6 | 5.6 ± 0.6 | | 1.37 ($P = 0.26$) |
| SJER Ungrazed 1980 | 6.0 ± 0.8 | 5.9 ± 0.7 | 5.7 ± 0.7 | 5.9 ± 0.9 | | 0.10 ($P = 0.96$) |
| SJER January 1982 | 8.5 ± 1.4 | 8.0 ± 0.7 | 7.6 ± 0.9 | 7.3 ± 0.7 | | 1.26 ($P = 0.29$) |
| SJER February 1982 | 7.6 ± 0.9 | 8.9 ± 0.6 | 7.3 ± 1.2 | 6.3 ± 0.9 | | 4.84 ($P = 0.004$) |
| SJER March 1982 | 10.1 ± 1.1 | 9.0 ± 0.8 | 7.8 ± 1.2 | 8.2 ± 1.2 | | 3.43 ($P = 0.02$) |

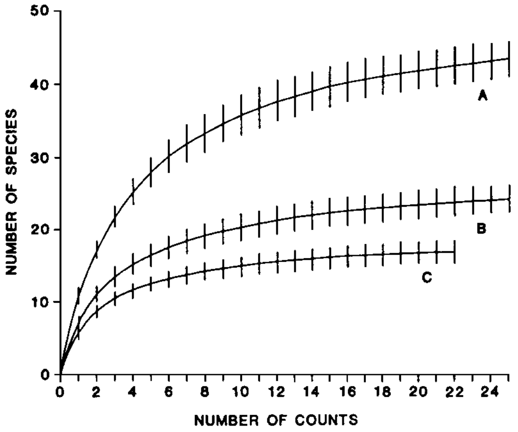

Fig. 1. Representative bootstrap estimates of species-accumulation curves for one hour in each of three data sets: A = SNF Meadow Edges, third hour; B = SJER January 1982, fourth hour; C = SJER Grazed 1980, first hour. Vertical lines are 95% confidence limits.

samples, 2 second-hour samples, 1 third-hour sample, and 3 fourth-hour samples), the 95% confidence limits of the all-hour samples did not overlap those of the individual hours (Table 4).

Summed ranks of species-accumulation curves, standardized to the lowest number of counts in any hour, also failed to show that earlier hours gave a significant advantage over later hours (Friedman statistic = 0.40, $P = 0.94$).

*Species composition.*—Species lists for each hourly period, standardized to the fewest counts within each sample, averaged 83.9% of the species detected during other hours in the same data set (SE = 0.94%, range = 59.1–100%, $n = 72$). No hour consistently included a higher proportion of species detected in any other hour (values ± 2 SE ranged from 82.8% ± 4.97 to 85.7% ± 6.03; $n = 6$ in each case). Furthermore, summed ranks of hourly percentages of the total species list detected in all data sets together, standardized to the hourly sample with fewest counts, showed no significant differences among hours (Friedman statistic = 0.50, $P = 0.92$).

## DISCUSSION

*Individual species.*—Robbins (1981) gives the best summary of hourly trends in counts, by species, showing that most species yield higher counts early in the morning, others show no marked trend, and still others give higher counts later in the morning. Similar results were reported by Skirvin (1981), and our results show the same interspecific variability. Although we found a trend toward higher counts early in the morning for many species, the tendency for species to have their highest counts during the first hour, their second highest counts during the second hour, etc. was not significant. We know of only one marked exception to this pattern of interspecific variability. Shields (1977) counted more individuals on transects begun at 0600 than at 0730 for all of 18 species reported; differences were significant in 14 cases.

Dawson's (1981) recommendation to count only during midday hours (0930–1530) to reduce the variance in counts of individual species was not supported by our results. On the contrary, the variance of our combined late-morning samples was greater than that of early-morning samples, although we did not find a significant hourly trend in variance. The advantages of having more counts or more sites sampled (or both), attainable by counting during more hours of the day, would outweigh any disadvantage that may come from counting during hours with higher than average variance.

*Total count.*—The combined total counts of

TABLE 4. Predicted species richness (±2 SE) by hourly period, standardized to the fewest counts in any hour for each sample (from bootstrap estimates).

| | | | Hourly periods | | | | |
|---|---|---|---|---|---|---|---|
| Data set | *n* | All hours combined | First | Second | Third | Fourth | Fifth |
| SNF Meadow Edges | 25 | 46.6 ± 2.0 | 37.7 ± 2.0 | 38.1 ± 2.0 | 43.2 ± 2.6 | 42.6 ± 2.3 | 43.8 ± 3.4 |
| SJER Grazed 1980 | 18 | 20.0 ± 1.0 | 17.5 ± 1.8 | 20.5 ± 1.8 | 20.3 ± 1.3 | 17.7 ± 1.2 | |
| SJER Ungrazed 1980 | 17 | 19.9 ± 1.4 | 16.6 ± 1.5 | 17.3 ± 1.2 | 18.7 ± 2.2 | 19.4 ± 2.7 | |
| SJER January 1982 | 16 | 26.2 ± 1.4 | 26.2 ± 2.4 | 24.0 ± 1.4 | 23.1 ± 2.2 | 22.5 ± 2.0 | |
| SJER February 1982 | 18 | 24.0 ± 1.5 | 22.9 ± 1.8 | 21.9 ± 1.1 | 21.7 ± 1.9 | 23.2 ± 2.2 | |
| SJER March 1982 | 18 | 29.8 ± 1.7 | 31.4 ± 2.2 | 27.3 ± 2.2 | 22.5 ± 1.4 | 24.8 ± 2.8 | |

all species showed no convincing hourly trend in our samples. These results agree with those of Hogstad (1967: fig. 2) from conifer forests in Norway. Robbins (1981: fig. 5C) reported similar results from 5-min point counts in woods along bluffs of the Patuxent River in Maryland. However, the total count declined markedly each hour after sunrise during 3-min point counts in forested floodplain habitat (Robbins and van Velzen 1970: fig. 2). Robbins (1981) concluded that the 3-min counts failed to give equivalent total counts for more hours after sunrise because count duration was too short to permit detection of many individuals during later hours, when the rate of cue production was lower. The 5-min counts, on the other hand, compensated better for the lower rate of cue production by many individuals later in the morning. This may partially explain why we, too, observed no significant decline in total counts during later hours, as our counts lasted 8 and 10 min.

Interspecific variability in hourly trends in counts probably also contributed to our failure to find a declining trend in total counts. Species with declining hourly trends compensated during early hours for those with increasing hourly trends; the reverse was true later in the morning.

*Species richness.*—Our data failed to show consistently higher species richness from early-morning counts than from counts done later in the morning. Järvinen et al. (1977) also had mixed results when comparing species richness between early- and late-morning samples in forest and open-field habitats in southern Finland. Richness was higher in early-morning samples in four of their six comparisons, but they did not test the significance of the differences. Robbins (1981: figs. 1, 5B) found no significant differences in species richness among the first four hours or more after sunrise. Mean species richness and total species richness did not differ significantly between early-morning and midday transects in two desert habitats in southeastern California (Weathers and Mayhew 1981). On the other hand, Grue et al. (1981) found fewer species during midday and evening counts than during early-morning counts in Arizona desert habitats. However, they did not show when in the morning the measures of species richness began to decline in the habitats they sampled, and they did not report confidence limits.

Surprisingly, hourly values of *total* species richness in our best data set—SNF Meadow Edges—were significantly higher (based on species-accumulation curves) in each of the last three hours than in either of the first two, in spite of the fact that mean species richness did not show this pattern. Although the assemblage of species available in each full data set appeared to be equivalently represented in the species composition of each hourly sample, one aspect of the higher species richness in later hours merits comment. Six species in the total assemblage characteristically forage on the wing, and all were recorded only in flight. These were the Red-tailed Hawk (*Buteo jamaicensis*), Common Nighthawk (*Chordeiles minor*), Vaux's Swift (*Chaetura vauxi*), White-throated Swift (*Aeronautes saxatalis*), Violet-green Swallow (*Tachycineta thalassina*), and Barn Swallow (*Hirundo rustica*). All were recorded only during the last three hours, when ambient temperatures were higher (hourly means, in order, were 5.1, 7.7, 11.2, 17.3, and 19.1°C). Most of the airborne insects needed for efficient foraging by aerial insectivores may not be flying at lower temperatures, or thermals that develop with increasing ambient temperature may be important in the flight dynamics of some of these species. We see only a hint of this pattern in the SJER data sets, but hourly temperature differences were less there because it is at a much lower elevation and counts there were done in the spring. In addition, most species of aerial foragers at SJER were often seen on perches as well as in the air.

The late-morning peak in counts of Kirtland's Warblers (Mayfield 1960) may also be a temperature-related phenomenon (J. R. Probst pers. comm.). Probst believes that research on this subject, using altitudinal and latitudinal gradients, may explain a number of apparent anomalies in peak counts of various bird species. Unfortunately, however, our samples were inadequate to examine this question properly for individual species.

*Species-accumulation curves.*—Our bootstrap estimator is negatively biased, because it shows only the number of species one would expect to detect, with a specified effort, from among those detected in the original sample. The calculations do not anticipate additional species undetected in the original sample that would likely be detected with further sampling from the same assemblage of birds. Smith and van

Belle (1984) attempted to adjust for the negative bias, but use of their method with our data gave results that were obviously biased in a positive direction, especially with small samples. We suspect that rarefaction curves using random sampling without replacement, as recommended by Simberloff (1979), James and Rathbun (1981), and James and Wamer (1982), may come closer to the real number of species expected with a given sampling effort. However, because bootstrap estimates have an inferential basis, we recommend them in favor of rarefaction for generating expected species-accumulation curves for studies using point counts or transects. These can then be used as indices to compare samples with equal effort, understanding that they are negatively biased. As with rarefaction, one can standardize bootstrap estimates by "rarefying" all samples to be compared with the smallest number of counts in any sample. However, results should be interpreted cautiously, because large samples will be less negatively biased than small samples when both are standardized to the same number of counts.

Results of this and other studies show that if study objectives require counting of selected species during optimum hours of the day, those hours should be individually determined for each species at each altitude and latitude. This information may now be available for many species, but because there is variation with habitat, season, stage of the breeding cycle, and possibly latitude and altitude, the prudent course is likely to require a pilot study. When the objective is to measure species richness or to obtain a total count of all species combined, during the breeding season, any of the first four or five hours after sunrise is equivalent in the meadow-edge and oak-pine habitats sampled in this study. Published literature shows that a similar conclusion applies in some but not all other habitats. With these questions, too, one probably should invest time in pilot studies to incorporate time-of-day considerations in the study design. Because some of our data suggest that counting during all hours may give higher species richness than an equal counting effort during any single hourly period, study designs that include counting over several hours of the day are probably better than those with counts confined to one or two early-morning hours.

In any case, selection of the best time of day to count birds should be guided by study objectives. For example, methods designed to estimate densities of birds attempt to fix locations and avoid duplicate recording of individuals. Normally, observers are within the range of detectability of most birds for a reasonable period of time (e.g. 5–10 min). Even if the rate of cue production (visual or auditory) declines during the course of a sample period, one may need to detect a bird only once to judge its location. Therefore, diurnal changes in rates of cue production may have only a small effect on the number of species recorded (Robbins 1981, Weathers and Mayhew 1981) or on estimated densities (Skirvin 1981).

Most studies, including ours, have not used counts during early-afternoon, late-afternoon, or evening hours, even though all studies using evening counts show that some species are detected more often then or only then (e.g. Hogstad 1967, Yui 1977, Tomialojć 1980, Robbins 1981, Kessler and Milne 1982). Furthermore, advantages gained from larger sample sizes or more plots sampled (or both), attainable by counting during many hours of the day, outweigh any advantage that may be gained by confining counts to hours likely to give more detections.

Future research on this problem should be designed specifically to study hourly variations in counts, rather than being a byproduct of studies designed for other purposes. A particularly interesting question concerns the effect of exposure time (count duration for point counts, walking speed for transects and mapping studies) on results obtained during different hourly periods. If, as Robbins (1981) suggested, small adjustments in exposure time can give equivalent count results over more hours of the day, this would be an extremely important aspect of any future study design.

## ACKNOWLEDGMENTS

Dawn Breese and Kathryn L. Purcell assisted with fieldwork. Dr. James Baldwin, Mark F. Bryan, and Charles J. Evans assisted with statistical analyses. Drs. Richard N. Conner, D. Heinemann, Douglas H. Johnson, John R. Probst, and Robert C. Szaro, and an anonymous reviewer made constructive suggestions on the early drafts of the manuscript. To all we express our sincere appreciation.

## LITERATURE CITED

ANONYMOUS. 1970. Recommendations for an international standard for a mapping method in bird census work. Pp. 49-52 *in* Bird census work and environmental monitoring (S. Svensson, Ed.). Bull. Ecol. Res. Comm. 9. Stockholm, Swedish Nat. Sci. Res. Council.

BYSTRAK, D. 1979. The breeding bird survey. Sialia 1: 74-79.

CONNER, R. N., & J. G. DICKSON. 1980. Strip transect sampling and analysis for avian habitat studies. Wildl. Soc. Bull. 8: 4-10.

DAWSON, D. G. 1981. Counting birds for a relative measure (index) of density. Pp. 12-16 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. No. 6.

EFRON, B. 1982. The jackknife, the bootstrap and other resampling plans. Monogr. No. 38. Philadelphia, Pennsylvania, Soc. for Industrial and Applied Mathematics.

GRUE, C. E., R. P. BALDA, & C. D. JOHNSON. 1981. Diurnal activity patterns and population estimates of breeding birds within a disturbed and undisturbed desert-scrub community. Pp. 287-291 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. No. 6.

HALL, G. A. 1964. Breeding-bird censuses—why and how. Audubon Field Notes 18: 413-416.

HOGSTAD, O. 1967. Factors influencing the efficiency of the mapping method in determining breeding bird populations in conifer forests. Nytt Mag. Zool. (Oslo) 14: 125-141.

JAMES, F. C., & S. RATHBUN. 1981. Rarefaction, relative abundance, and diversity of avian communities. Auk 98: 785-800.

———, & N. O. WAMER. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63: 159-171.

JÄRVINEN, O., R. A. VÄISÄNEN, & Y. HAILA. 1977. Bird census results in different years, stages of the breeding season and times of the day. Ornis Fennica 54: 108-118.

KESSLER, W. B., & K. A. MILNE. 1982. Morning versus evening detectability of southeast Alaskan birds. Condor 84: 447-448.

MAYFIELD, H. F. 1960. The Kirtland's Warbler. Bloomfield Hills, Michigan, Cranbrook Inst. Sci.

ROBBINS, C. S. 1981. Effect of time of day on bird activity. Pp. 275-282 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. No. 6.

———, & W. T. VAN VELZEN. 1970. Progress report on the North American breeding bird survey. Pp. 22-30 *in* Bird census work and environmental monitoring (S. Svensson, Ed.). Bull. Ecol. Res. Comm. 9. Stockholm, Swedish Nat. Sci. Res. Council.

SHIELDS, W. M. 1977. The effect of time of day on avian census results. Auk 94: 380-383.

SIMBERLOFF, D. 1979. Rarefaction as a distribution-free method of expressing and estimating diversity. Pp. 159-176 *in* Ecological diversity in theory and practice (J. F. Grassle, G. P. Patil, W. K. Smith, and C. Taille, Eds.). Fairland, Maryland, Intern. Cooperative Publ. House.

SKIRVIN, A. A. 1981. Effect of time of day and time of season on the number of observations and density estimates of breeding birds. Pp. 271-274 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. No. 6.

SMITH, E. P., & G. VAN BELLE. 1984. Nonparametric estimation of species richness. Biometrics 40: 119-129.

TIPPER, J. C. 1979. Rarefaction and rarefiction: the use and abuse of a method in paleoecology. Paleobiology 5: 423-434.

TOMIAŁOJĆ, L. 1980. The combined version of the mapping method. Pp. 92-106 *in* Bird census work and nature conservation (H. Oelke, Ed.). Proc. VI Intern. Conf. on Bird Census Work. West Germany, Univ. Göttingen.

VERNER, J., & L. V. RITTER. 1985. A comparison of transects and point counts in oak-pine woodlands of California. Condor 87: 47-68.

WEATHERS, W. W., & W. W. MAYHEW. 1981. Time of day and desert bird censuses. Western Birds 12: 157-172.

YUI, M. 1977. The census method of woodland bird populations during the breeding season. Pp. 97-112 *in* Studies on methods of estimating population density, biomass, and productivity in terrestrial animals (M. Morista, Ed.). Japanese IBP Synthesis, vol. 17. Japan, Univ. Tokyo Press.