Hourly variation in transect counts of birds

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We examined hourly variation in numbers of birds detected during morning line transect counts in northern Wisconsin and Upper Peninsula Michigan. We analyzed hourly variation by month (May–September), year (1986, 1987; 1985–June only), and state. Mean number of individuals detected generally was highest during the first or second hour in each state. Hourly differences in total individuals were significant in 1 of 11 monthly samples in Wisconsin and in 4 of 11 in Michigan. Lowest counts of total individuals were recorded during the fourth hour. No significant difference among hours was detected in mean number of species detected per hour in Wisconsin. Differences were significant in three Michigan samples and approached significance (P < 0.06) in a fourth. Lowest counts of total species occurred during the fourth hour. Individual species varied in hourly trends; some increased during the morning, some decreased, and others showed no consistent pattern in number of individuals detected per hour. Hourly differences in abundance of individual species were significant in 12 of 61 comparisons (20%) in Wisconsin but in only 1 of 62 (2%) in Michigan.

1. Introduction

Many factors influence the probability of detecting birds, including habitat structure, weather (e.g. wind, rain), time of day, season, and speciesspecific differences in behavior (Järvinen et al. 1977, Verner 1985). Temporal variation in detectability is an important consideration when estimating numbers of birds (Shields 1979, Robbins 1981a, Verner 1985). Some studies have reported significant changes in numbers of birds detected over the course of a morning (e.g. Järvinen et al. 1977, Skirvin 1981) while others have not detected such changes (e.g. Verner & Ritter 1986). Detections of some species increase throughout the morning, others decrease, and some show no consistent pattern of detection (Robbins 1981a). Seasonal changes in bird behavior (e.g. rate of song production) are pronounced and likely influence diurnal patterns of detectability (Best 1981). Because of variations in song activity throughout the day, an understanding of this variation is essential. Järvinen et al. (1977) concluded that an international standard for censusing hours is urgently needed.

We have been sampling birds in northern Wisconsin and Upper Peninsula Michigan as part of a study designed to evaluate potential effects of the United States Navy's ELF (extremely low frequency) transmission facilities on birds (Blake et al. 1988). Although not designed to study hourly trends in bird detections, our sampling procedure allowed us to examine such changes at both community and species levels.

2. Study areas and methods

2.1. Study sites

Birds were sampled in northwestern Wisconsin (Ashland, Bayfield, and Sawyer counties) and in Upper Peninsula Michigan (Dickinson and Marquette counties) (approximately 46° to 46°15'N, both states). Wisconsin and Michigan study areas were approximately 240 km apart. Primary habitats in both regions included upland and lowland forests (deciduous, coniferous, and mixed deciduous-coniferous). Principal tree species included sugar maple (Acer saccharum), balsam fir (Abies balsamea), birch (Betula papyrifera and B. lutea), red maple (Acer rubrum), black ash (Fraxinus nigra), aspen (Populus tremuloides and P. grandidentata), black spruce (Picea mariana), cedar (Thuja occidentalis), and red pine (Pinus resinosa).

2.2. Methods

2.2.1. Bird samples

We established 20, randomly selected 4.35-km transects, including 10 in Michigan and 10 in Wisconsin (e.g., see Järvinen & Väisänen 1975). Five transects in each state were located adjacent to ELF transmission lines (treatments) and five in areas unaffected by electromagnetic fields produced by the ELF system (controls). Detailed descriptions of selection procedures are in Blake et al. (1988) and in Hanowski et al. (1990). Transects were distributed over approximately 860 km² in Wisconsin and 1,500 km² in Michigan. Thus, the data are representative of the region and do not reflect purely local effects.

Each 4.35-km transect consisted of eight 500m segments arrayed in a single line; segments were separated by a 50-m buffer. We tested the independence of adjacent 500-m segments using runs tests and correlation tests (Hanowski et al. 1990). Most analyses (> 90%) indicated that adjacent segments were independent (P < 0.05).

We counted birds along each transect once per month from May to September. Counts were started about 0.5 hr before sunrise and continued up to 4.5 hr after sunrise on days with little wind (< 15 km/hr) and little or no precipitation. Starting times, relative to actual sunrise, sometimes were delayed (usually < 15 min) because of early morning rain or heavy cloud cover. Consequently, sample sizes per hour were uneven in some months. Segments sampled in the fifth hour were not included in analyses due to small sample sizes. We estimated wind speed at the start of each transect segment and noted starting times for each segment.

Two 4.35-km transects were sampled daily, with counts conducted simultaneously. Each observer walked at a rate of 1 km/hr and recorded each bird detected (by sight or sound) within 100 m of the transect center line. All observers were experienced in identifying birds characteristic of the region and training sessions were conducted prior to censusing to standardize methods. In addition, analyses of data collected by observers on simultaneous counts of the same set of transects (N = 32) (Blake et al. 1988) did not reveal any significant observer differences in numbers of birds or species of birds counted. Further, observers conducted counts simultaneously on two transects so that no observer counted birds more often either early or late in the morning. End points of most transects were not readily accessible (i.e. without walking the entire transect) and it was not practical to alternate starting points at either end of each transect.

2.2.2. Habitat structure

Differences in habitat may influence hourly trends through effects on bird activity and detection levels. Because we located our transects randomly, we assumed that different habitats would be distributed randomly along each transect. To test this assumption, we sampled vegetation along each transect in each state. Sampling methods reflected needs of the primary study (effects of the ELF system; Blake et al. 1988).

Vegetation in Wisconsin was sampled at 25m intervals along each transect. Densities of trees, downed logs, and shrubs were calculated using the point-centered quarter method (Mueller-Dombois & Ellenberg 1974). Trees (> 2.5 cm diameter at breast height [dbh]) were identified to species and dbh and height were measured. Ground and water cover were visually estimated within $1-m^2$ quadrats centered on each sample point and water depth was measured. Canopy cover over each point was measured using a spherical densiometer (Lemmon 1956).

Detailed habitat measurements were not required in Michigan. Instead, we classified vegetation into one of 19 different habitat types (e.g. upland or lowland coniferous or deciduous forest) at 25-m intervals along each transect (Blake et al. 1988). Occurrence of each habitat type was summed for each segment. Goodness-of-fit tests were used to test for differences among segments censused during different hours, using counts of the 19 habitat types observed.

2.2.3. Statistical analyses

We combined adjacent 500-m segments to allow comparisons based on 1-hr samples (i.e. samples are based on 1-km sections of the 4.35-km transects). Sample sizes were not sufficient for accurate density estimates for most species (e.g. Burnham et al. 1980), so we used total number of birds observed as our estimate of abundance. Total counts and density estimates are likely to be highly correlated and, thus, likely to produce similar results (Raphael 1987). Also, by using total observations within a set distance we reduced the potential for observer bias in estimating distances; each observer had to decide only if a bird was within 100 m of the transect.

We used one-way analysis of variance (ANOVA; Sokal & Rohlf 1981) to examine hourly variation in (1) mean number of total individuals, (2) mean number of total species, and (3) mean number of individuals for each species with a mean of more than two observations per km. Multiple comparisons among means were based on a Scheffé test and were done if one-way ANOVA indicated a significant overall difference among hours. Variables were tested for normality (Wilks–Shapiro test) and equality of variances (Bartlett's test) and were transformed (e.g. square root, logarithmic) when necessary. Nonparametric tests (e.g. Kruskal– Wallis test) were used for variables that did not meet assumptions, even after transformations.

3. Results

3.1. Habitat differences

Differences in habitat along Wisconsin transects were not pronounced among areas censused during different hours. Average tree height on areas sampled during the first 2 hours (11 m) was higher (P < 0.05) than on areas sampled during the last 2 (9 m). Other variables used to describe habitat structure in Wisconsin showed no difference and we assumed that habitat had little effect on hourly variation in bird detections in Wisconsin.

Despite the fact that we selected transect locations randomly, the distribution of several habitats differed among areas sampled during different hours in Michigan. The most pronounced difference involved the distribution of recently logged areas dominated by short (3 to 10 m) *Populus tremuloides*. Such habitats accounted for about 5% of all points on segments sampled during the first 2 hours but about 19% on segments sampled during the last 2 hours. To eliminate the potential influence of this habitat difference on hourly variation in bird detections in Michigan, we omitted from all analyses those samples dominated by aspens 3 to 10 m tall.

3.2. Total individuals and species

Distribution of high counts (hour during which the greatest number of individuals was recorded) differed among hours in each state ($\chi^2 \ge 9.5$, P < 0.05, each state); most high counts (64%) occurred during the second hour. Distribution of low counts did not differ among hours in Wisconsin ($\chi^2 = 0.3$, P > 0.9) but did in Michigan, where 8 of 11 low counts occurred during the fourth hour ($\chi^2 = 13.4$, P < 0.005). A significant difference among hours in mean number of individuals was noted in Wisconsin only during June 1987 (Table 1). Significant differences among hourly counts occurred during 4 months in Michigan; means were lowest in the fourth hour. Distribution of high and low counts for total number of species was the same as that for total individuals, in both states. High similarity in distribution among hours of high and low counts of individuals and species reflected the high correlation between number of individuals and species recorded per hour in Michigan (Pearson's r = 0.98, P < 0.001) and Wisconsin (r = 0.95, P < 0.001). No significant differences among hours in mean number of species recorded were noted in Wisconsin. Differences among hours were significant during three samples in Michigan and approached significance (P < 0.06) in a fourth (Table 2). In all cases, lowest values were obtained during the fourth hour.

3.3. Individual species

Temporal patterns of detectability varied among species. The proportion of species that showed a significant difference in mean number of individuals observed per hour was greater in Wisconsin (12 of 61 comparisons) than in Michigan (1 of 62 comparisons; $\chi^2 = 10.6$, P < 0.005; Table 3). Most species that showed a significant difference among hours in mean number of individuals observed did not consistently increase or decrease in abundance during the 4 hours sampled (Table 3). Counts were highest during the fourth hour in seven cases and during the first hour in three. Hourly differences were more pronounced during May, June, and July than during August and September.

4. Discussion

4.1. Total individuals

Hourly variation in numbers of birds recorded during censuses has been reported by some authors (e.g. Hogstad 1967, Järvinen et al. 1977, Robbins 1981a, Skirvin 1981). Verner & Ritter (1986) suggested that species-specific differences might have contributed to their failure to detect significant hourly declines in total number of individuals when all species were combined.

Table 1. Mean number of individuals (\pm 1 S.E.) detected during transect counts done during successive hourly periods. Significant results only are shown. Sample sizes (number of counts) are in parentheses below means. ^{a,b} Within rows, means not sharing the same letter differ, (P < 0.05), multiple comparison among means test.

State	Hourly period				F	Р
Sample	First	Second	Third	Fourth		
Wisconsin						
June 1987	37.8±1.6ª (20)	37.5±2.0 ^{ab} (20)	34.7±2.2 ^{ab} (18)	30.7±1.8 ^b (20)	3.12	< 0.03
Michigan						
May 1987	24.9 <u>±</u> 2.2ª (19)	24.4±2.4 ^{ab} (18)	20.2±2.3 ^{ab} (16)	16.2±1.8 ^b (14)	3.13	< 0.04
June 1986	31.9±1.6ª (18)	32.2±2.0ª (19)	27.0±2.0 ^{ab} (17)	23.0 ±3.l ^b (7)	3.40	< 0.03
July 1987	35.1±1.8ª (19)	[`] 32.5±3.1 ^{ab} (18)	27.8±2.4 ^{ab} (17)	24. <u>9±</u> 2.7 ^ь (13)	3.16	< 0.04
August 1987	18.4±1.4ª (19)	19.7±2.4ª (19)	16.6±2.4 ^{ab} (17)	9.3±1.3 ^b (12)	4.26	< 0.01

Significant declines from first to fourth hour were noted by Skirvin (1981) for total individuals; numbers of detections of most, but not all, species also declined from early to late morning. Järvinen et al. (1977) listed similar declines from early to late morning, but their data also were gathered throughout the day. Counts were lowest in the afternoon and in the evening. Results from Wisconsin (this study) also failed to demonstrate significant hourly trends in total numbers of birds detected, although hourly totals were highest most often in the first two hours; highest totals (all species combined) never were recorded during the fourth hour. In contrast, our data from Michigan demonstrated more hourly variation in bird counts, particularly in 1987, and illustrate the need to assess hourly trends in different areas. In all cases where significant differences among hours were noted, the fewest birds were detected during the fourth hour of counting. Results were not, however, consistent from one year to the next.

Our results are based on transect counts and may not be directly comparable to studies based on point counts (J. Verner, pers. comm.) because of differences in probable length of time that birds are within the hearing range of observers. Robbins (1981a), for example, found marked de-

clines in number of individuals detected after the second hour after sunrise when analyses were based on 3-min counts. There was little change during the morning (0600 to 0900) when analyses were based on 5-min counts. He attributed much of the difference to greater likelihood of detecting individuals during a longer count. Verner & Ritter (1986) used 8- and 10-min counts and did not detect significant hourly declines in numbers of individuals recorded. Our rate of travel (1 km/hr) meant that most birds probably were within hearing range for at least 5 minutes, assuming that most vocalizing individuals could be heard at distances of at least 80-100 m. Some species undoubtedly were within hearing range for longer periods (e.g. Blue Jay Cyanocitta cristata).

4.2. Total species

Järvinen et al. (1977) found a decrease in species diversity as the day progressed, but many studies have not found consistent differences in mean number of species detected in early versus midto late morning counts (see Verner & Ritter 1986). We also failed to detect any significant difference among hours in number of species detected in Wisconsin. Our data from Michigan, how-

Table 2. Mean number of species (± 1 S.E.) detected during transect counts done during successive hourly
periods in Michigan. Results are shown only for samples with a significant (or nearly so, $P < 0.06$) difference.
No significant differences among hours were detected in Wisconsin. Sample sizes (number of counts) are in
parentheses below means. ^{a, b} Within rows, means not sharing the same letter differ (P < 0.05), multiple
comparison among means test. ^c Multiple comparison among means test not significant.

			Hourly period			Р
Sample	First	Second	Third	Fourth		
May 1987	10.6±0.8ª (19)	10.8±0.8ª (18)	9.4±1.0 ^{ab} (16)	7.4±0.8 ^b (14)	3.24	< 0.03
June 1986	12.7±0.7ª (18)	13.7+0.8ª (19)	11.2±1.0 ^{ab} (17)	8.7 <u>±</u> 2.1 ^b (7)	3.43	< 0.03
July 1987	14.5±0.7 (19)	14.2±1.1 (18)	12.4±1.0 (17)	10.9±1.1 (13)	2.64	< 0.06 ^c
Sept. 1987	6.1 <u>±</u> 0.5 ^{ab} (19)	6.6±0.7ª (18)	5.3±0.5 ^{ab} (17)	4.3±0.4 ^b (13)	2.95	< 0.04

ever, indicate that such differences may occur; lower species counts were obtained during the fourth hour in 4 of 11 samples. Verner & Ritter (1986) reported significantly higher total species

counts (but not mean/hour) during later morning hours. They attributed much of this difference to late morning appearance of species that typically forage on the wing.

Table 3. Mean number of individuals (\pm 1 S.E.) of species detected during transect counts done during successive hourly periods. Only species showing significant differences are shown. Sample sizes (number of counts) are in parentheses below means. ^{ab} Within rows, means not sharing the same letter differ, (P < 0.05), multiple comparison among means test. ^c Multiple comparison among means test not significant. ^d Kruskal-Wallis test.

State		Hourly period					P
Species	Sample	First	Second	Third	Fourth		
Wisconsin							
Black-capped Chickadee Parus atricapillus	July 1986	0.7±0.3ª (20)	1.2±0.4 ^{ab} (20)	2.3±0.8 ^{ab} (12)	2.6±0.6 ^b (18)	2.97	0.04
Red-breasted Nuthatch Sitta canadensis	Aug. 1987	2.1±0.4 (20)	2.0 ±0.4 (20)	2.1±0.4 (18)	0.8±0.3 (15)	2.72	0.051°
Hermit Thrush <i>Catharus guttatus</i>	June 1987	2.2±0.4ª (20)	1.5±0.4 ^{ab} (20)	1.1±0.3 ^{ab} (18)	0.8±0.3 ^b (20)	3.37	0.02
	July 1986	2.1±0.3ª (20)	1.3±0.3 ^{ab} (20)	1.3±0.4 ^{ab} (12)	0.8±0.2 ^b (18)	3.70	0.02
Red-eyed Vireo Vireo olivaceus	July 1986	3.1±0.7 ^{ab} (20)	4.4±0.7ª (20)	3.8±0.9 ^{ab} (12)	1.4±0.5 ^b (18)	4.44	0.007
	July 1987	3.0±0.6 (19)	3.2±0.6 (20)	1.7±0.4 (20)	1.1±0.3 (15)	3.22	0.028 ^c
Nashville Warbler Vermivora ruficapilla	May 1987	4.8±0.8 ^{ab} (20)	2.5±0.5 ^b (20)	4.6±1.0 ^{ab} (18)	5.8±0.8ª (16)	3.51	0.02
Chestnut-sided Warbler Dendroica pensylvanica	May 1987	1.0±0.3ª (20)	1.9±0.4 ^{ab} (20)	0.9±0.3ª (18)	3.1±0.8 ^b (16)	3.28	0.03
Black-and-white Warbler Mniotilta varia	May 1987	0.6±0.2ª (20)	1.0±0.2 ^{ab} (20)	1.1±0.3 ^{ab} (18)	2.1 ±0.4 ^b (16)	5.16	0.003
Ovenbird <i>Seiurus aurocapillus</i>	June 1987	4.7±0.8ª (20)	4.8±0.9ª (20)	4.2±0.8 ^{ab} (18)	2.2±0.5 ^b (20)	3.17	0.03
White-throated Sparrow Zonotrichia albicollis	May 1986	1.1±0.4ª (18)	2.5±0.7 ^{ab} (17)	2.0±0.5 ^{ab} (15)	3.2±0.8 ^b (17)	2.58	0.045
	July 1986	1.9±0.5 ^{ab} (20)	2.8±1.6 ^{ab} (20)	1.0±0.4 ^b (12)	3.6±0.7ª (18)	2.96	0.04
Michigan							
Least Flycatcher Empidonax minimus	June 1985	0.3±0.1ª (19)	1.2±0.4 ^{ab} (18)	0.8±0.5 ^{ab} (17)	1.9±0.5 ^b (14)	8.12	0.025 ^d

4.3. Individual species

Results from several studies have indicated that while many species are detected more frequently early in the morning, detections of other species are likely to increase through the morning, whereas other species show no marked or consistent trends among hours in number of detections during morning hours (e.g. Robbins 1981a, Skirvin 1981, Verner & Ritter 1986, but see Shields 1977). Our results generally agree with previous studies. Most species showed no consistent or significant hourly trends and few showed significant hourly variation in more than one sample.

More species showed significant hourly variation in Wisconsin than in Michigan and this difference may account partially for the difference between regions in hourly trends of total individuals detected. Hourly trends for individual species were significant in only one instance in Michigan and a lack of offsetting trends among species may have allowed detection of hourly trends in total number of birds detected. Conversely, a greater number of hourly trends were significant in Wisconsin. Variation among species may have resulted in the general lack of significance noted for overall hourly trends (Verner & Ritter 1986).

4.4. Hourly trends in bird detections

Many factors influence detectability of birds and may contribute to hourly variation results. Seasonal changes in bird behavior - e.g. declines in nesting and singing, fledging of young, changes in foraging behavior and patterns of habitat occupancy - may influence diurnal trends observed at different times of the year. Flocks, for example, frequently are more conspicuous than individual birds, particularly when birds are not singing, and a greater incidence of flocks in late summer and early fall might increase probabilities of detecting individual birds. At the same time, a high incidence of flocks also might promote a higher variance in number of birds detected within 1-hr samples and may reduce the probability of detecting hourly trends without substantially larger sample sizes.

Weather and habitat also influence detectability of birds and, if confounded with time of census, might influence hourly trends. Several studies have demonstrated depressed counts during periods of increased wind (e.g. Hogstad 1967, in Verner & Ritter 1986, Dawson 1981, Emlen & DeJong 1981). We did not count birds on days when wind exceeded about 15 km/ hr to reduce the potential bias due to wind. Wind speeds often increased from early to late morning and may have contributed to hourly declines in number of birds detected during some samples, particularly in Michigan. However, samples with significant differences among hours in number of birds detected did not always show pronounced changes in wind speed during the morning, nor were low counts always associated with greater wind speeds. Thus, although wind undoubtedly influenced our ability to detect birds, differences in wind speed likely were not responsible for differences observed in this study.

Bird activity also may be influenced by temperature (Robbins 1981b), with effects varying among species. High temperatures may cause declines in singing activity of some species and thereby influence hourly trends in bird detections (J. Verner, pers. comm.). Effects of temperature are not likely to be severe, however, within the range normal for the region (Robbins 1981b).

Habitat influences an observer's recognition and location of sounds (e.g. Richards 1981) and ease of seeing some birds (Dawson 1981) because of structural differences (e.g. height, foliage density, patchiness of vegetation), noise, and terrain (Yui 1977, in Verner & Ritter 1986, Gill 1980). Yui (1977, in Verner & Ritter 1986), for example, found marked and consistent differences in detectabilities of most species depending on height of vegetation. If the hourly sequence of samples is confounded by changes in vegetation, comparisons of bird abundance may be suspect. Most studies address this problem by rotating starting order among different points or transects. In our study, we were not able to alternate starting locations because of the length of our transects (4.35 km). Instead, we attempted to control for effects of habitat on bird detections through random placement of transects and by eliminating segments in Michigan that showed large differences in habitat. Nonetheless, some habitat effects might have remained. If habitat was a primary cause of hourly differences in number of birds detected, however, results should be similar between years; that was not the case.

Observer fatigue also may influence number of birds detected per hour. Observers are more likely to maintain a higher level of concentration early in a sample than later, particularly if counts continue for several hours. Fatigue may be aggravated by increased abundance of bothersome insects during late morning, as frequently occurred in our areas.

5. Conclusions

Potential effects of time of day must be considered in any study designed to sample bird abundance (Järvinen et al. 1977, Shields 1979, Verner 1985, Verner & Ritter 1986). Selection of census times will depend on objectives of individual studies. If the research focuses on a specific species or group of species, census times can account for species-specific differences in hourly activity levels. Our results generally agree with those of Verner & Ritter (1986) that, for most species, hourly variation, particularly within the first three hours of the morning, is not large or consistent enough to warrant limitation of bird counts to shorter periods. For some species, however, hourly trends may be pronounced and counts should be timed accordingly (Robbins 1981a).

Selostus: Kellonajan vaikutus linjalaskennan tulokseen

Kirjoittajat tutkivat kellonajan vaikutusta aamulla suoritetuissa laskennoissa havaittujen lintujen määrään Wisconsinissa ja Michiganissa. Kellonajan vaikutusta verrattiin kuukausien (toukosyyskuu), vuosien (1986 ja 1987; 1985 havaintoja oli vain toukokuulta) ja tutkimusalueiden välillä. Laskennan ensimmäisen ja toisen tunnin aikana havaittiin keskimäärin eniten yksilöitä. Laskentatuntien väliset erot olivat Wisconsinissa merkitseviä 1 tapauksessa 11:stä ja Michiganissa 4 tapauksessa 11:stä. Pienimmät yksilömäärät havaittiin laskennan 4. tuntina. Havaittujen lajien määrä ei Wisconsinissa eronnut laskentatuntien välillä. Erot olivat merkitseviä kolmessa Michiganin näytteessä ja lähes merkitseviä (P < 0.06) yhdessä näytteessä. Havaittujen lajien määrä oli pienin laskennan 4. tuntina. Toisten lajien yksilömäärät kasvoivat laskennan kuluessa, toisten vähenivät. Osalla lajeista ei havaittu minkäänlaista selkeätä vaihtelua laskentatunnin suhteen. Wisconsinissa 12 tapauksessa yksittäisten lajien yksilömäärien erot laskentatuntien välillä olivat merkitseviä (20%, 61 vertailua), mutta vain yhdessä tapauksessa Michiganissa (2%, 62 vertailua).

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