

SEASONAL CHANGES IN DETECTION OF INDIVIDUAL BIRD SPECIES

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ABSTRACT.—Changes in frequency and distance of detection during the breeding season (considering both singing-male and all observations) are documented for selected species occupying deciduous forest habitats. Several general patterns are identified in the seasonal profiles of detection and in mean detection distances. The following factors influencing seasonal changes in detection are explored: frequency of song, stage of the breeding cycle, nesting synchrony, breeding season length, flux in community composition, habitat, and weather. The function of song influences persistence of singing throughout the breeding season. Singing frequency and likelihood of escaping detection during counts vary with stage of the breeding cycle; unmated males are most conspicuous. Nesting synchrony depends upon arrival times of males and females and on nesting success. Clumping patterns of count observations are influenced by season length. Seasonal profiles of detection can be used to determine the optimal period to schedule counts for individual species. General application of a series of such profiles depends upon additional research to develop profiles for other species and habitats and to determine the consistency of profiles for individual species.

Estimating the size of avian populations is an integral part of many field studies. Usually, the results and conclusions drawn from such studies depend heavily upon the accuracy of the census procedure. Important considerations in developing census methodology are the number and distribution of counts during the study period. Seasonal changes in kinds of cues emitted by birds, emission frequency, and attenuation have been alluded to in the literature, but efforts to quantify these changes and to use this knowledge in designing census schedules are rare.

The objectives of my study were to (1) document changes in detection during the breeding season of selected species occupying deciduous forest habitats, (2) develop seasonal profiles of detection and explore factors responsible for seasonal changes, and (3) discuss the general application of such information in planning census schedules. The discussion will focus primarily on passerines and other passerine-like species that breed in North America, although much of the information has broader application.

STUDY AREAS AND METHODS

Count data used in this report were obtained from two separate studies. Most information came from an investigation of avian communities breeding in habitats adjoining streams in central Iowa (Stauffer and Best 1980). Specific habitats included open-canopy (noncontiguous tree crowns) upland woodland, closed-canopy (contiguous crowns) upland forest, and closed-canopy floodplain forest. The vegetation composition of these habitats is given in Stauffer and Best (1980). (The two upland habitats mentioned here are included in the upland woodland category described by Stauffer and Best.) Each study plot consisted of 1-5 transects, marked at 25 m intervals, that paralleled the stream channel; successive transects were 50 m apart. The

length and number of transects per plot were determined by the extent of relatively homogeneous habitat. Breeding birds were censused on all plots by using the Spot-mapping Method. Counts were begun 15-30 minutes before sunrise and were not conducted on days with rain or strong wind. During a count, transect lines were followed until the plot had been completely traversed. The location and behavior of birds observed on either side of the transects were recorded on grid maps of the plots. Counts were conducted on a rotational basis from mid-April to mid-July until each plot had been covered 12 times. Perpendicular distances of count observations from transect lines were measured on the grid maps for each study plot and then scaled to actual ground distances.

The second study was of a marked population of Field Sparrows (see Table 1 for scientific names) occupying old field (shrub-grassland) habitat in central Illinois (Best 1975). The study plot was gridded throughout at 25-m intervals; vegetation composition of the plot is described in Best (1977). Counts were conducted from 06:00 to 09:00 several times each month from May through August. During each count, the grid lines were followed in a north-south direction until the plot had been completely covered, alternately walking the even- and odd-numbered lines on successive counts. All Field Sparrows seen during each count were recorded on a grid map. Because this was part of an intensive study of Field Sparrow breeding ecology (Best 1977, 1978), the mating and nesting status was known for all territorial males/pairs during each count.

For determining seasonal patterns of detection, only initial observations were used; sightings made after an initial observation were not considered. I reasoned that the circumstances under which birds are first observed are influenced less by the observer's presence, and consequently, provide the best index to seasonal changes in detection.

Seasonal Profiles of Detection (hereafter abbreviated as SPDs) were constructed for selected species on the basis of the number of singing-male observations and all observations recorded for each species during half-month intervals within a given habitat (Fig. 1). For the Iowa study, each interval included results from two counts, except for late April, which included

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only one, and late June, which included three. Only species where at least 10 territorial males/pairs were estimated to be in a given habitat (using the Spot-mapping Method) were included in the analysis. For some species, this involved using count data from a single study plot; for others, it required combining results from two or more plots of similar habitat. All SPDs were standardized to the same scale; the number of observations made of each species during each half-month interval was expressed as a proportion of the total for the time interval with the highest count. Thus, curves for all species reach values of 1.0.

RESULTS AND DISCUSSION

GENERAL PATTERNS OF SEASONAL PROFILES OF DETECTION

The SPDs for 16 bird species that commonly nest in deciduous forest are illustrated in Figure 1. Frequencies of detection from late April through early July vary substantially among the species. Greater variation in a SPD represents greater disparity in the number of birds observed per count. The SPDs provide information on both the general seasonal pattern as well as the magnitude of variation in frequency of detection.

Seasonal changes in frequency of detection may be associated with fluctuations in population density, but they also may occur independently of population size and may be caused by factors such as variations in behavior associated with different stages of the breeding cycle, foliation of vegetation, or seasonal weather patterns. The degree to which SPDs reflect actual change in population size cannot be ascertained directly. Usually, this is not critical because the objective of most breeding-bird studies is to determine population density at the peak of the breeding season when the number of territorial males/pairs is largest. SPDs indicate clearly the period when the greatest number of individuals of each species is likely to be observed and, hence, the optimal time to schedule counts. A decline from this optimum, whether caused by flux in population density or by some other factor, reduces efficiency in detecting the total number of breeding birds.

Most SPDs take one of several general forms. All, except those of year-round residents, begin at zero, provided that counts are started early enough in the year. Probably the most common pattern is for frequency of detection to increase gradually to a peak, followed by a decline. The period over which detection remains at or near the peak (duration of optimal detection) varies greatly among species. The Great Crested Flycatcher and Rose-breasted Grosbeak are examples of species with relatively brief peaks in detection. In other species (e.g., EWP, HW, GC, C, IB; abbreviations for common names are giv-

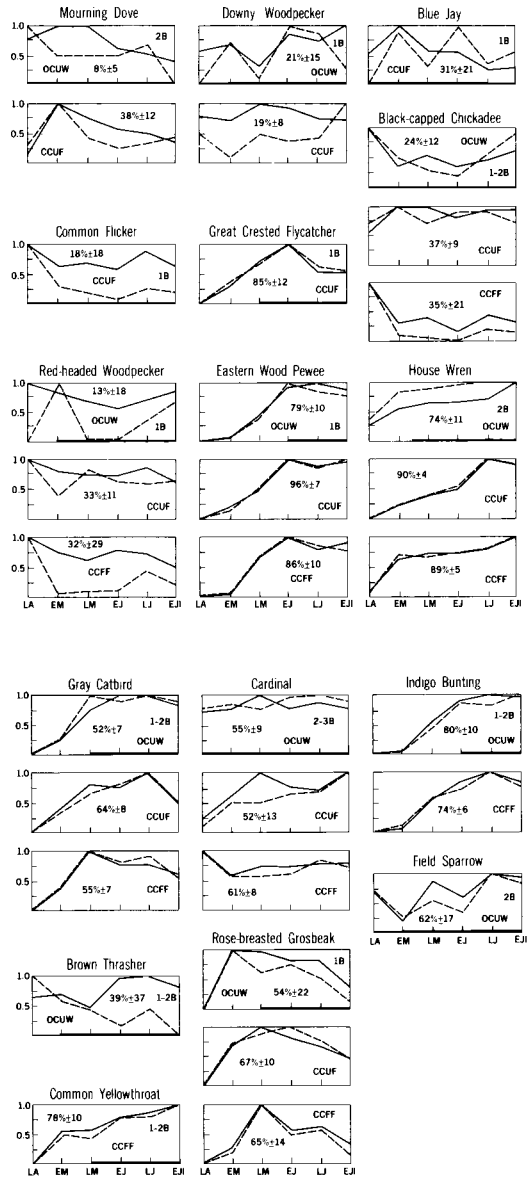


FIGURE 1. Seasonal Profiles of Detection for selected species breeding in open-canopy upland woodland (OCUW), closed-canopy upland forest (CCUF), and closed-canopy floodplain forest (CCFF). The sample units are half-month intervals covering from late April through early July. Values are proportions of the maximum half-month count of singing males (dashed lines) and of all observations combined (solid lines). The percentage that singing-male observations constituted of all observations (X ± SD), the usual number of broods per season (designated by "B"), and the nesting season length (horizontal bar) are also given. Broods per season were obtained from Forbush (1927, 1929).

en in Table 1) frequency of detection increases to a relatively high level and then remains quite constant (at least over the interval that I censused). Cardinals and, to a lesser degree, House Wrens and Gray Catbirds, have relatively protracted periods of optimal detection (OD). In nearly all cases, SPDs ultimately decline, but the more important concern is duration of OD.

Some species show rather consistent patterns of seasonal decline or seasonal increase in detection. The Brown Thrasher is a good example of the former (on the basis of singing observations), and the Common Yellowthroat exemplifies the latter.

The Field Sparrow SPD illustrates the effect of multiple nestings. The somewhat cyclic pattern of detection coincides with stages of the nesting cycle that are repeated throughout the breeding season (see "Factors influencing seasonal changes in detection"). Highs and lows in the SPDs of other species also may be associated with different stages of the nesting cycle.

Some species seemingly lack any consistent seasonal pattern of detection. This is particularly true for the Red-headed and Downy Woodpeckers and the Black-capped Chickadee, and also may be true for the Mourning Dove. It is noteworthy that, while the SPDs of Red-headed and Downy Woodpeckers lack consistency among habitats, they are somewhat similar within the same habitat.

The disparity in detection profiles for singing-male versus all observations vary considerably among species. In some instances, the two curves essentially coincide (e.g., GCF, EWP, HW, GC, CY, IB), whereas in others, they seem to fluctuate independently (e.g., MD, RHW, BT). In general, the greater the percentage that singing males constitute of all observations, the more congruent are the two curves. This is evident even within the same species, comparing among different habitats (e.g., HW, RBG). Singing-male observations generally constitute less of all observations in open-canopy woodlands than in closed-canopy forests. This probably is because birds in more open habitat are more visible, resulting in less reliance on aural observations.

The percentage that singing-male observations constitute of all observations varies throughout the season, although the amount of seasonal variation differs among species. For some species, seasonal variation is considerable (e.g., BT), whereas for others, it varies little (e.g., HW, GC). The general pattern of this variation is indicated by the direction and magnitude of disparity between the curves for singing-male and all observations. The more the singing-male curve is displaced below that for all observa-

tions, the smaller is the percentage that the former constitutes of the latter.

The degree of similarity in SPDs for the three habitats differs among species. For some species (e.g., EWP, GC, IB) SPDs are nearly identical among the habitats; for others (e.g., MD, RHW, DW, BCC), they differ greatly. Dissimilar SPDs among habitats for a species could indicate that (1) habitat per se has a significant influence on behavior and observability of that species or (2) the species does not exhibit any predictable pattern of detection regardless of habitat. The woodpeckers and Mourning Dove (all nonpasserines), in particular, suggest the latter. Not only are their SPDs inconsistent among habitats, but the curves for singing-male and all observations differ considerably.

SEASONAL CHANGES IN DETECTION DISTANCES

Not only may the number of birds observed change seasonally, but also the distance at which they are detected. The magnitude and pattern of seasonal change in mean distance of detection varies among species. Measurements for all observations are presented in Table 1. Mean detection distances of singing males generally were slightly longer than those for all observations, but rarely by more than 3 m. Small variations in mean distances probably are attributable to sampling error.

Detection distances for some species remain essentially constant throughout the breeding season (e.g., BJ, GC, CY, RBG). For others, there is an initial decline, followed by relatively stable distances (e.g., BCC, HW, C). The decline probably results from plant foliation and growth. Several species begin breeding after most plant foliation and growth have occurred; thus, plant development does not appreciably influence their detection. The shortest distances of detection for some species (e.g., MD, RHW, GCF, BT) occur midway through the breeding season. In some instances (particularly single-brooded species), shorter distances may coincide with the presence of fledglings.

FACTORS INFLUENCING SEASONAL CHANGES IN DETECTION

Frequency of song

In many breeding-bird studies, singing-male observations constitute the most important criterion for determining population size (Enemar 1959:89). Song has different functions for various species, and the persistence and frequency of song throughout the breeding season depend upon its function(s). Two functions particularly pertinent to bird detection during counts are (1) song used to advertise and defend a territory and

TABLE 1
MEAN DISTANCES OF DETECTION (M) OF SELECTED SPECIES IN THREE HABITAT TYPES DURING DIFFERENT PERIODS OF THE BREEDING SEASON^a

Species	OCUF						CCUF						CCFF						
	LA	EM	LM	EJ	LJ	EJI	LA	EM	LM	EJ	LJ	EJI	LA	EM	LM	EJ	LJ	EJI	
Mourning Dove—MD ^b (<i>Zenaida macroura</i>)	— ^c	18	16	13	18	—	—	23	21	14	17	—	—	—	—	—	—	—	—
Common Flicker—CF (<i>Colaptes auratus</i>)	—	—	—	—	—	—	23	23	18	24	19	19	—	—	—	—	—	—	—
Red-headed Woodpecker—RHW (<i>Melanerpes erythrocephalus</i>)	—	24	20	14	18	18	23	17	17	12	16	20	29	18	21	17	17	17	17
Downy Woodpecker—DW (<i>Picoides pubescens</i>)	—	21	—	18	18	16	—	24	23	19	20	18	—	—	—	—	—	—	—
Great Crested Flycatcher—GCF (<i>Myiarchus crinitus</i>)	—	—	—	—	—	—	—	—	20	24	15	20	—	—	—	—	—	—	—
Eastern Wood Pewee—EWP (<i>Contopus virens</i>)	—	—	15	18	19	16	—	—	24	21	18	22	—	—	11	19	22	16	16
Blue Jay—BJ (<i>Cyanocitta cristata</i>)	—	—	—	—	—	—	22	22	22	18	21	22	—	—	—	—	—	—	—
Black-capped Chickadee—BCC (<i>Parus atricapillus</i>)	19	17	15	13	15	15	—	18	15	16	18	16	26	18	14	14	15	14	14
House Wren—HW (<i>Troglodytes aedon</i>)	24	15	15	17	16	17	—	17	16	17	18	19	—	20	16	18	18	18	18
Gray Catbird—GC (<i>Dumetella carolinensis</i>)	—	16	17	14	17	16	—	20	18	20	16	16	—	16	13	14	15	15	15
Brown Thrasher—BT (<i>Toxostoma rufum</i>)	—	18	15	11	13	14	—	—	—	—	—	—	—	—	—	—	—	—	—
Common Yellowthroat—CY (<i>Geothlypis trichas</i>)	—	—	—	—	—	—	—	—	—	—	—	—	—	19	16	18	15	17	17
Cardinal—C (<i>Cardinalis cardinalis</i>)	22	19	17	18	16	15	27	21	23	21	21	20	20	20	19	17	19	18	18
Rose-breasted Grosbeak—RBG (<i>Pheucticus ludovicianus</i>)	—	17	15	14	16	16	—	19	20	17	20	21	—	17	16	17	18	13	13
Indigo Bunting—IB (<i>Passerina cyanea</i>)	—	—	17	14	20	18	—	—	—	—	—	—	—	—	—	—	—	—	—
Field Sparrow—FS (<i>Spizella pusilla</i>)	26	22	18	17	21	15	—	—	—	—	—	—	—	—	17	20	17	16	16

^a Based upon all observations. See Figure 1 for explanation of habitat and period abbreviations.
^b Abbreviation for common name.
^c Fewer than 10 distances sampled.

(2) song used to attract a mate. For a given species, song may have either one or both functions. Although woodpecker vocalizations were recorded as singing-male observations, they were not advertisement songs (characteristic of passerines) but rather location calls (Lawrence 1967:18). Location calls function to locate other conspecifics and thus are given in a different context from that of advertisement songs.

Singing frequency declines dramatically after pair formation in species in which song has evolved primarily for mate attraction (Tinbergen 1939:80; see also "Stage of the breeding cycle"). An exception to this may be polygynous species that mate sequentially (e.g., Armstrong 1963:118). In Figure 1, the Brown Thrasher is the most graphic example of song attenuation after pairing (see also Kroodsmas and Parker 1977). Colquhoun (1940b) commented that cessation of song in woodland species that keep low in the vegetation may render them so inconspicuous that conventional census procedures would be futile, the alternative being a species-by-species study of marked individuals. When song is primarily for territorial advertisement, singing may be much more consistent throughout the breeding season (e.g., Smith 1959), although there often is a gradual seasonal decline. In some species, both sexes sing, and the song frequency may be quite constant throughout the breeding season (e.g., Laskey 1944). This may account for the relatively protracted period of OD for the Cardinal (Fig. 1). Knowing the function of song in individual species would facilitate interpreting their SPDs, although information on this subject is generally lacking.

The time of first song and the duration of singing in early morning change throughout the breeding season. Song initiation is stimulated by increasing light intensity at dawn. Not only does the time of sunrise vary seasonally, but singing for many species becomes progressively earlier relative to civil twilight until the north solstice and then gradually grows later (e.g., Allard 1930, Nice 1943:109, Davis 1958, Leopold and Eynon 1961, Nolan 1978:62). Song initiation in the House Wren occurs at civil twilight throughout the breeding season (Leopold and Eynon 1961). The duration of singing also is influenced by the rise in daytime temperatures (Robbins and van Velzen 1970), which changes seasonally. Planning the time of day to make counts should take these changes into consideration.

Differences among species in their spring arrival times may influence the period and duration of frequent singing. Slagsvold (1977) reported that species arriving early begin singing earlier in the season, have a longer interval between arrival and maximum song activity, and

have a longer period of peak song activity than those arriving late.

Stage of the breeding cycle

The breeding behavior and activity level of birds may change as they progress from an unmated to mated status and then from nest building through fledging of the young. Sometimes these behavioral shifts are abrupt, particularly with respect to singing frequency. Such changes may affect census results dramatically, and Järvinen et al. (1977b) have cautioned that census results used in comparative studies should be from similar parts of the breeding season. Reported yearly fluctuations in population estimates may be purely artifactual (see Slagsvold's [1973c] comments relative to Enemar's [1966] findings) if the time when counts are taken each year varies relative to species' periods of OD.

The effects that stage of the breeding cycle can have on bird detection are illustrated by count data collected from the Field Sparrow population in Illinois. Singing observations constituted 92% of all observations made of unmated males, whereas only 13% of the observations made of pairs during other stages of the breeding cycle were singing males (Fig. 2). Dramatic declines in singing frequency of males once they have paired also have been documented in many other species (e.g., Michener and Michener 1935, Quaintance 1938, Tinbergen 1939:77, Lack 1943, Nice 1943:172, von Haartman 1956, Durango 1956, Davis 1958, Frankel and Baskett 1961, Armstrong 1963:152, Bell et al. 1968, Kroodsmas and Parker 1977, Nolan 1978:63, Samson 1978). Once the nesting cycle has begun, singing frequency in the Field Sparrow evidently is greater during incubation than the nestling stage (see also Nice 1943:119, Davis 1958, Smith 1959, Armstrong 1963:153, Verner 1965, Falls 1969, Nolan 1978:63). An opposite pattern has been reported by others (Colquhoun 1940b, Clark 1947). No male Field Sparrows were heard singing during the interim after a successful nest and before egg laying in the subsequent nest. In some species, vocalization increases noticeably after the young leave the nest (e.g., Lawrence 1967:23, Falls 1969, Slagsvold 1973b, 1977). Stage in the nesting cycle evidently has little effect on song frequency in the House Wren (Gross 1948), thus accounting for the relatively flat SPDs for this species once breeding is initiated (Fig. 1).

Likelihood of escaping detection during a count also is influenced by stage of the breeding cycle. In the Field Sparrow study, the total number of times that pairs (or unmated males) were at given stages of the breeding cycle during counts was determined and used to calculate the

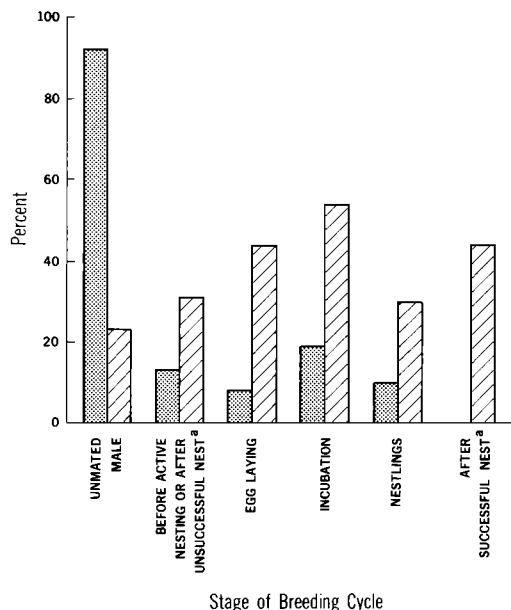


FIGURE 2. The percentage of all Field Sparrow observations during counts that were singing males (stippled bars) and the percentage of the time that pairs (or unmated males) were unsighted during counts (crosshatched bars). Categories with superscript "a" included only the interval until egg laying in a subsequent nest.

percentage of the potential observations during which birds remained unsighted (Fig. 2). Unmated males were least frequently missed during counts, whereas pairs were most likely overlooked during incubation. The undulating SPD for the Field Sparrow (Fig. 1) probably is associated with different stages of the nesting cycle that are repeated throughout the breeding season. Lows in the curves could be associated with a preponderance of pairs in the incubation stage, and the peaks may correspond with more in the nestling stage. The pattern is cyclic because this species is a persistent renester. The midseason low in the song SPD for the Blue Jay reflects its inconspicuousness during nesting (Tyler 1946).

In most species, males arrive before females in the spring (Dorst 1962:252). Thus, there is a period of frequent song during territory establishment, followed by reduced singing associated with pair formation (at least for species where song functions primarily for mate attraction). Males on territories of inferior quality often are unmated longer before acquiring mates, or in some cases, they remain unmated throughout the breeding season (see also Samson 1980). Once the main period of territory es-



FIGURE 3. Seasonal Profiles of Detection for a Field Sparrow population with extremely low nesting success (old field in Illinois) and one where nesting success presumably was considerably higher (open-canopy upland woodland in Iowa).

tablishment and pair formation has occurred, males still unmated may be represented disproportionately in counts. Also, males may be deserted by their mates during the breeding season, resulting in increased song activity. All these factors influence seasonal detection of individual territorial males, and unfortunately, males most easily observed during a count are those without mates that likely occupy inferior sites.

Although nesting chronologies have been reported for many species, changes in detectability associated with different stages of the breeding cycle are generally unknown, and, if they are known, rarely have they been quantified. Such information can be obtained only when marked populations with known nesting histories are counted regularly. This is a productive area for future research, and the results of such efforts will greatly facilitate interpreting seasonal patterns of detection.

Nesting synchrony

The degree of synchrony in arrival of males and of females on their breeding sites influences the period over which unmated males prevail in the population. The more asynchronous the arrival, the more protracted is the period of pair formation. This, in turn, can influence the seasonal pattern of singing by males (e.g., Bell et al. 1973).

If females arrive synchronously on the breeding grounds, members of a population will be at a similar stage in the nesting cycle (at least until nesting efforts are disrupted). This would maximize the effects that stage of the nesting cycle has on seasonal detection patterns. Where members of a population lack synchrony in their nesting, effects of stage of the nesting cycle are attenuated (see also Slagsvold 1977). Migrant species that arrive late may nest more synchronously than those that arrive early (Slagsvold 1977). The abbreviated nesting seasons of species that breed at higher altitudes or latitudes also may cause greater synchrony, both intra- and interspecifically. And finally, greater nesting synchrony would be expected in colonially nesting species than in solitary nesters because of social stimulation (Orians 1961). Species that

exhibit successive polygyny nest asynchronously in as much as pair bonds are formed over a time interval (von Haartman 1951).

Nesting success also may influence nesting synchrony. If predation, desertion, or other factors inducing nest failure occur regularly, then members of a population would soon be at all stages of the nesting cycle. Although the first nesting may be synchronous, renestings would not be. This is particularly true of multibrooded species later in the breeding season.

Effects of nesting success on SPDs are evident in the Field Sparrow data. Figure 3 illustrates SPDs obtained from counts of the Illinois population, where nesting success was known to be extremely low (Best 1978), and from the Iowa population, for which the form of the curves suggests that nesting success was considerably higher. Detection was low for both populations in early May, probably associated with the incubation stage of first nestings. As the breeding season progressed, nesting became asynchronous in the Illinois population. Synchrony persisted to some degree in the Iowa population, as evidenced by the cyclic pattern of detection throughout the breeding season, undoubtedly associated with second and possibly third nestings. Thus, variability in nesting success may affect the predictability of seasonal changes in detection (see also Haukioja 1968, Slagsvold 1973b).

In censusing entire avian communities, the degree of synchrony among species in their breeding seasons becomes more important than intraspecific variations in nesting chronology (see also Haukioja 1968). Although breeding seasons of some species overlap considerably, those of others are nearly mutually exclusive. In my study, the Eastern Wood Pewee and Indigo Bunting began their nesting season later than the other species, whereas the Mourning Dove, Cardinal, and Blue Jay were particularly early. Species differ, not only in the beginning of their breeding seasons, but also in the period when nesting reaches a peak. Also, the factors that influence nesting synchrony generally would not affect all species within a community equally.

Breeding season length

Length of the breeding season and propensity to renest after nest failure differ among bird species. Some species produce only one brood per season, whereas others may rear two or three broods yearly (Fig. 1). At higher altitudes or latitudes, breeding seasons generally are shorter, as well as is the period between spring arrival and start of breeding (Slagsvold 1976b). If stage of the breeding cycle significantly influences frequency of detection, then cyclic pat-

terns would be more pronounced in SPDs of multibrooded species than those of single-brooded species (see also Slagsvold 1977).

Length of the breeding season influences nesting synchrony. Nesting becomes less synchronous as the breeding season progresses and as more nesting attempts are disrupted. The SPD for the Iowa Field Sparrow population (Fig. 1) evidently illustrates this, where the amplitude of oscillation in total observations dampens as the breeding season advances.

The degree of "clumping" of count observations also may depend upon length of the breeding season. In multibrooded species, successive nests may be considerable distances apart. If pairs concentrate their activities near the nest, observations would tend to be clustered around nests active when the counts were taken. Over the season, this could result in several clumps of observations. Thus, individual territorial pairs would be more difficult to identify, and population size might be overestimated. Restricting counts to a single nesting cycle would reduce the likelihood of this bias, although it still could occur if nesting chronology within the population was asynchronous. Nesting success may influence the extent of clumping of observations about nests. If nests are frequently disrupted early in the nesting cycle, count observations will be more dispersed than when nesting attempts are successfully completed. Multiple clumpings for a pair pose the greatest problem for the Spot-mapping Method because it depends on clusters of observations to enumerate territorial males (International Bird Census Committee 1970).

The Field Sparrow data (Fig. 4) illustrate clumping of observations near active nests; a relatively large and a relatively small territory (Best 1977) are included for comparison. Clumping is quite discernible in the large territory, but less evident in the small one. In smaller territories, nests are closer together; thus, observations associated with each nest overlap more, and the likelihood of multiple clusters for a single breeding pair is less. In contrast to my findings, Enemar et al. (1976, 1979) reported no relationship between the distribution of nests and clusters of observations.

Flux in community composition

Counts conducted early in the season more likely include migrants and transients than do those made later (Enemar 1959:20). Also, early in the season, territories still are being established, and site tenacity of males may not be fully developed. As the breeding season progresses, some females will desert their mates, and males will begin abandoning their territo-

ries. A high rate of nest failure may increase the frequency and advance the date of mate desertion and territory abandonment. Territory fidelity varies among species. Males of most species usually persist on a single territory for the entire breeding season, although others (particularly males of polygynous species) often shift territories during the season (e.g., Kendeigh 1941:37, von Haartman 1951, Bell et al. 1968, Robins 1971). Species with more protracted breeding seasons, by virtue of the time span involved, probably incur greater change in population composition than those with relatively short seasons. All these factors influence composition of individual populations and, consequently, community composition.

The more extended the period for counts, the more results will be confounded by flux in community composition. Shortening the count period would reduce this confounding effect, and knowledge of species' SPDs would facilitate determining the most appropriate periods for counts.

Habitat

Foliation and growth of plants during the breeding season, at least in temperate regions, change the degree that vegetation visually screens potential bird observations. Seasonal changes in the "vegetative screen" vary among habitats and probably are less pronounced in arid habitats than in mesic ones characterized by lush plant growth during the breeding season. My counts were confined to forest habitats exposed to the same regional climate; thus, comparisons among habitats would not be expected to show differences. Within deciduous forests, the most dramatic increase in visual screening occurs in spring when leaves first emerge. (The reverse would be true at leaf fall in autumn.) The early-season reductions in mean detection distance noted for some species in Table 1 likely are attributable to plant foliation and growth.

Habitat may influence nesting chronology. Erskine (1976b) noted that nesting in artificially warmer urban environments may begin earlier than in nearby rural areas. Length of the breeding season also may differ with habitat. Forest interior species tend to produce only one brood per breeding season, whereas species associated with more open habitats may produce two or three broods yearly (Brewer and Swander 1977).

In dense habitats, such as a closed-canopy forest, greater reliance is placed on aural observations during counts than in more open habitats. Thus, species with marked seasonal variation in song frequency are more difficult to accurately census in dense cover than in open areas. Interestingly, communication by sound

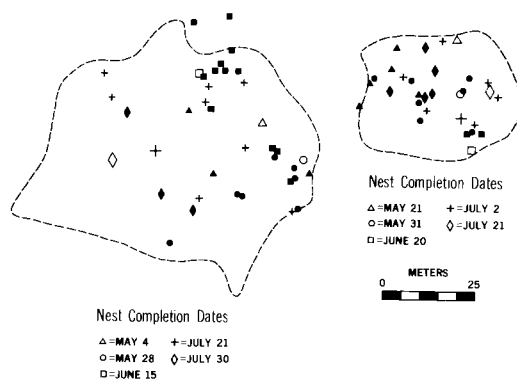


FIGURE 4. Spatial distribution of observations during counts and nests for two Field Sparrow pairs. Each open symbol represents a nest, and closed symbols of similar shape represent observations made when that particular nest was active. Only nests with observations from more than one count are included; designated locations are initial sightings (see "Study area and methods"). Dashed lines represent territory boundaries.

(versus by sight) is more widely distributed among birds of closed habitats than of open ones (Armstrong 1963:227).

Habitat may influence the function of song and, consequently, persistence of singing throughout the breeding season. Songs of species occupying open areas, where sight advertisement of territories could suffice, may serve primarily to attract mates, whereas songs of birds in dense habitats may function also to proclaim territories (e.g., Brown Towhee, *Pipilo fuscus*, vs. Rufous-sided Towhee, *P. erythrophthalmus*, Quaintance 1938; Sedge Warbler, *Acrocephalus schoenobaenus* vs. Reed Warbler, *A. scirpaceus*, Catchpole 1973). The relationship between function of song and SPDs has been discussed (see "Frequency of song").

Weather

Year-to-year variations in weather influence arrival times of migrants and may cause seasonal shifts in plant phenology and nesting chronology. In many species, particularly early-spring migrants, arrival time (Nice 1937:43, Williams 1950, Dorst 1962:237, Slagsvold 1977) and nesting chronology (Nice 1937:98, von Haartman 1963, James and Shugart 1974, Slagsvold 1976a, 1977) are advanced by warmer temperatures. Weather has relatively little effect on migrants of late spring (Dorst 1962:232). Thus, within a community, nesting chronologies of different species may not be affected equally by yearly variations in weather. Yearly variations in breeding chronology may not necessarily modify

the general form of SPDs, but they would cause temporal displacement.

Inclement weather (particularly early in the season) can modify seasonal patterns of detecting species either by checking or retarding breeding (Armstrong 1963:214) or by increasing nest failure rate, consequently disrupting nesting synchrony. Weather also may influence the length of the breeding season. Slagsvold (1977) reports that warm and wet weather may prolong the period of song activity in some species.

Extremes in weather, whether cold (Alexander 1931, Smith 1959, Garson and Hunter 1979) or hot (Robbins and van Velzen 1970), inhibit song; the former would be more likely early in the season, the latter, more likely later. These probably would have minor effects on SPDs if counts are restricted to days with moderate weather and are conducted only during early morning. Both are recommended procedures.

APPLICATION OF SEASONAL PROFILES OF DETECTION

In this study, SPDs were developed for 16 representative species that breed in deciduous forests of Iowa. Some SPDs in Figure 1 undoubtedly will require additional refinement and verification, and SPDs need to be developed for habitats and species not addressed in this report. At present, little information is available on seasonal patterns of detection (or song) of avian species during counts; the best documentation comes from European studies (Colquhoun 1940b, Cox 1944, Slagsvold 1973b, 1977; Järvinen et al. 1977b, Nilsson 1974b, 1977; O'Connor 1980c; O'Connor and Hicks 1980). Weber and Theberge (1977) presented weekly counts of common birds breeding in Canada. To my knowledge, no one has attempted to standardize information on seasonal patterns of detection into a series of profiles that could be made available for widespread use in determining the most appropriate times to count birds.

One major factor influencing the general applicability of SPDs is their consistency. That they may differ for a given species among habitats need not be an overriding concern, as long as they are consistent within each habitat. Differences among habitats would require developing a series of profiles covering the habitats occupied by the species and of interest to census takers. Where habitat does not significantly influence seasonal detection of a species, a single SPD would suffice. SPDs would have limited applicability for species whose seasonal patterns of detection are inconsistent even within the same habitat. More research is required to determine whether or not the SPDs in Figure 1 are consistent patterns for the respective species

and to make similar assessments for other species. Assuming that patterns of detection for most species prove to be relatively consistent, then it would be practical to develop a series of SPDs for the species of a given region and to use this information in planning census schedules.

Two characteristics of SPDs that should be considered in their interpretation and implementation for censusing are the time and duration of OD. Identifying the exact time period when observations reach their peak probably is not as important as demarking the interval over which observations remain relatively high. Determining the lower limits of OD is arbitrary and could be set at any percentage of the maximum. If a 75% limit were applied to the SPDs in Figure 1, considerable variation among species in both time and duration of OD is evident. Once periods of OD are defined for the species to be studied, then counts can be planned. The smaller a species' range of OD, the more precisely its census schedule must be timed to avoid underestimating population density (see also Bell et al. 1973). This is especially critical when either the period for counts is short or few counts are taken, such as the North American Breeding Bird Survey (Robbins and van Velzen 1970). Range of OD could be used to identify "sensitive species" that require special attention in planning their counts. For example, Cardinals probably could be censused during any period of the breeding season, whereas Brown Thrasher populations probably should be censused only in the brief period before pair formation (see also Haukioja 1968). Single-brooded species with a single, sharp peak in their SPDs (e.g., GCF, RBG) also would require confining counts to relatively brief intervals. The corollary of a more confined census schedule for sensitive species is a reduction in the interval between successive counts such that the period of OD is adequately sampled and not missed between counts. Thus, not only the number of counts but also their timing and spacing should be considered when planning census schedules (Bell et al. 1973).

Planning counts for populations of a single species requires determining the species' period of OD and then adjusting the census schedule accordingly. Censusing efforts are most productive when confined to the period of OD. Censusing entire avian communities presents a much more complicated situation. Both the length and the seasonal timing of the period of OD vary among species. Thus, overlap in OD is highly variable within a community. A general principle in planning community counts would seem to be: A single census schedule, unless it is both *intensive* and *extensive*, cannot do all

things for all species. To adequately sample an entire avian community, frequent counts over the entire breeding season may be necessary. Then, subsets of all the counts could be selected to estimate population sizes of individual species on the basis of their periods of OD (see also Shields 1979).

Once a general series of SPDs was developed, implementation still would require adjusting for factors such as year-to-year differences in weather and differences in altitude and latitude. Yearly variations in weather cannot be anticipated in advance, but their relationship to time of arrival and chronology of the breeding cycle is somewhat predictable (see "Weather"). According to Slagsvold (1973b, 1977), temperature, snowmelt, and plant development (specifically birch leaf emergence) are correlated with the start of song and the time of song maxima, particularly for "early" species. By using these or other predictors of yearly variation in weather, SPDs could be temporally adjusted accordingly. Such "predictors" would require field verification for different species and different geographical regions before their widespread use.

Higher altitudes or latitudes delay spring arrival and the onset of nesting (e.g., James and Shugart 1974) and shorten the season length in a predictable way. The former is more pronounced in species that arrive early than in later ones (von Haartman 1963, Slagsvold 1975, 1976b). A general series of SPDs probably could be corrected for altitude and latitude, but developing more than one SPD for species that breed over a broad altitudinal or latitudinal range might be more practical.

Other factors, such as effects of nesting success on nesting synchrony and flux in population or community composition, influence seasonal patterns of detection in more subtle ways, and adjusting for these factors is unrealistic. Their effects can be evaluated only by intensive monitoring the breeding activities of the species involved. Usually, this requires marking the birds for individual identification, and having done so, the need to census is eliminated. At the community level, such intensive study is unwieldy and impractical; thus, such factors affecting seasonal change in detection frequency are largely ignored. It would seem, then, that some sources of error in interpreting seasonal changes in counts can be remedied only by mod-

ifying the research design such that censusing is no longer necessary. For species in which these sources of error significantly influence seasonal patterns of detection, generalizable SPDs would be difficult, if not impossible, to develop.

Attempts to "standardize" the number and seasonal distribution of counts may be overly optimistic, particularly if census results are used for interspecific comparisons. Opinions vary widely relative to these two aspects of census planning (for a review, see Berthold 1976). Characteristics of seasonal detection for individual species must be considered when planning a census schedule, especially at the community level; otherwise, species populations will be sampled disproportionately (see also Slagsvold 1973a). Some species may require fewer counts than others to adequately sample their populations. Even for a single species, the number of counts necessary to estimate population size may vary throughout the season; during periods when individuals are more detectable, fewer counts would be required (see also Slagsvold 1973c, Svensson 1978b). And, as already discussed, periods of OD for individual species are highly variable within a community. Thus, neither the period in the season when counts should be conducted nor the minimum number of counts required may be standardizable, at least at the community level (see also Jensen 1974, Nilsson 1977). Standardization may be most practical in developing a series of SPDs that could be used to make enlightened decisions about the temporal spacing and number of counts required and to increase effectiveness of censusing efforts.

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