

Singing Rate and Detection Probability: An Example from the Least Bell's Vireo (*Vireo belli pusillus*)¹

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Abstract

We used 4-hr tape recordings to assess singing activity of a Least Bell's Vireo (*Vireo belli pusillus*) on 7 d distributed throughout the breeding season of 2001. We logged 9873 songs, for a mean singing rate of 5.84 min⁻¹, but despite this level of activity, the bird was silent during 33% of the 1691 minutes of the study. Availability, the proportion of minutes in which singing activity occurred (and hence the probability of at least one song occurring in any randomly selected minute) varied from 0.36 to 0.96. As availability is a major component of detection probability, we tested several ways of estimating availability from data that can be obtained during a brief point count. Singing rate (songs/min), estimated in 10 or more 1-min samples randomly distributed through the morning provided a good ($r^2 = 0.8$) estimate of availability for the entire morning. Measures based on a comparison of singing activity (presence/absence) in contiguous 1-min samples yielded poor estimates of availability, regardless of sample size, presumably because of the highly clumped bout structure (i.e., serial auto-correlation of singing and silence).

Keywords: detection probability, singing rate, bird survey, bioacoustics, *Vireo belli*, Least Bell's Vireo, endangered species.

Introduction

Accurate and precise estimates of numbers of migratory birds are vitally needed both to assess population status and to evaluate management decisions. This is especially true for threatened and endangered taxa. Various methods exist for counting birds, but most

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yield only indices, not true population estimates (Thompson 2002). The need to improve these index methods with estimates of detection probability is now widely appreciated, and several techniques have been suggested for obtaining such estimates (e.g., Nichols et al. 2000, Bart and Earnst 2002, Rosenstock et al. 2002, Farnsworth et al. 2002, Farnsworth et al. this volume).

Three of the four "new" methods rely on brief surveys, typically aural point counts, to obtain counts of individuals. Count data are subdivided in various ways (e.g., distance) that permit estimation of detection probabilities. A question of interest for aural surveys is the effect of singing rate on detection probability. While a high singing rate would seem to make detection likely, songs often come in bouts of intense singing, followed by periods of silence. The effect of this "bout structure" on detection has not been addressed, theoretically or empirically. Here we document the bout structure, throughout the breeding season, of a Least Bell's Vireo (*Vireo belli pusillus*), an endangered subspecies. We use these data to elucidate the relationships among singing rate, bout structure, and detectability.

One of the objectives of the larger study of which this is a small part was to estimate the optimal date and time of day for conducting point counts in the riparian areas of southern California. Here we illustrate the procedure with data on diel and seasonal variation in singing rate.

A Heuristic Model of Detection Probability

McCallum (this volume) elaborates the conceptual framework we use here. Briefly, the true number of resident individuals in a population, N , is estimated with a sample count, C , that must be adjusted by a correction factor or detection probability, p , for individuals present but not detected (Thompson 2002), such that $p = C/N$ (Nichols et al. 2000). Detection probability is subdivided into two independent components (Farnsworth et al. 2002): (1) *availability*, the probability that an average bird performs a detectable act or *cue*, and (2) *detectability*, the probability that it is detected if it gives a cue. Heuristically,

$$p = p_s (1 - (1 - p_{1d})^s) \quad (1)$$

where p_s is cue availability and the expression to its right is detectability. Detectability is a function of cue conspicuousness, p_{1d} , and cue abundance, s , i.e., the number of songs produced during a count period. Note that detectability = 1 if conspicuousness = 1, regardless of cue abundance ($s > 0$). Detectability approaches 1 as cue abundance increases, regardless of conspicuousness. See McCallum (this volume) for elaboration of these points.

This model does not provide a means of estimating parameters. It is a conceptual model that was devised in an attempt to account for all the relevant biological contributions to detection probability. McCallum (this volume) used this model to evaluate the conceptual adequacy of the four recently-published methods for estimating p in studies of bird populations. In this study we investigated the relationship between a component of detectability (s , cue abundance) and availability with direct counts (i.e., not estimates based on sampling procedures) obtained during the diel period in which point counts are typically taken, throughout the breeding season.

Methods

Study Areas

We studied singing rates of upland birds at four riparian sites in southern California in the breeding season of 2001. The four sites were Big Morongo, Riverside County; Lake Skinner, Riverside County; Hidden Valley, Riverside County; and Whiting Ranch, Orange County. Each site was surveyed once per week

(with a few interruptions caused by inclement weather), from late March through late June. The data reported here were collected exclusively at Hidden Valley (HV).

Data Collection

During exploration in February, 2001, a central recording location was chosen at each site. A Sennheiser ME-62 omni-directional microphone with K-6 power supply and a Sony TCD-D8 digital audio tape recorder were used to make a continuous 4-hr recording at the recording site on each survey date. The microphone was positioned approximately 3 m above ground level to enhance detection of distant birds. The "long-play" setting on the Sony TCD-D8 was used, sampling at a rate of 22050 points sec^{-1} . The automatic input level was set to "manual," i.e., off, to produce an accurate record of relative amplitude of ambient sounds.

After starting the long-play recording, the observer departed to allow equilibration of the local bird community and conducted point counts elsewhere on the study site. Approximately 0.5 hr later, and subsequently at 1-hr intervals, the observer returned to the recording site and conducted a standard 5-min point count from that location. In keeping with standard protocol, the observer approached as unobtrusively as possible. The approach of the observer had no detectable effect on the production of Bell's Vireo song. Additionally, the observer recorded point counts away from the long-play site with a Sony Walkman Professional (WM-D6C) cassette-recorder.

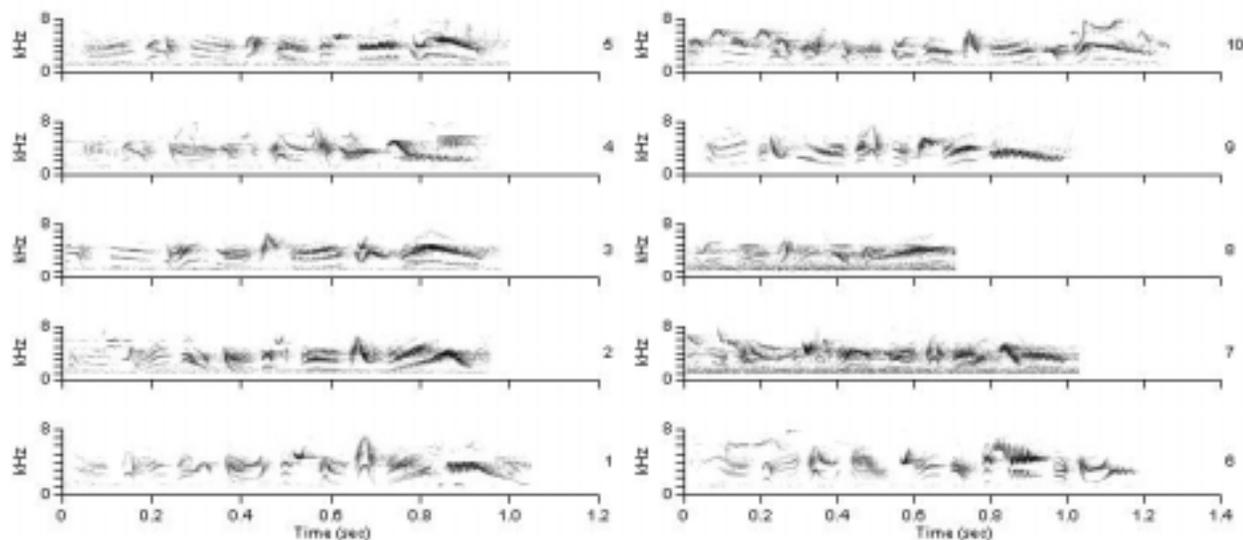


Figure 1—Sound spectrograms of the ten song-types recorded in the Hidden Valley study area, with type numbers to the right of each spectrogram. Individual songs were easily scored because of extremely high stereotypy among and within recording sessions. Despite different durations and note-type composition, all types ended in a note-type exhibiting periodic frequency modulation (FM), as indicated by the zigzag traces on the spectrograms. This is typically the most conspicuous part of the song, and we listened and looked for these sounds in logging tapes.

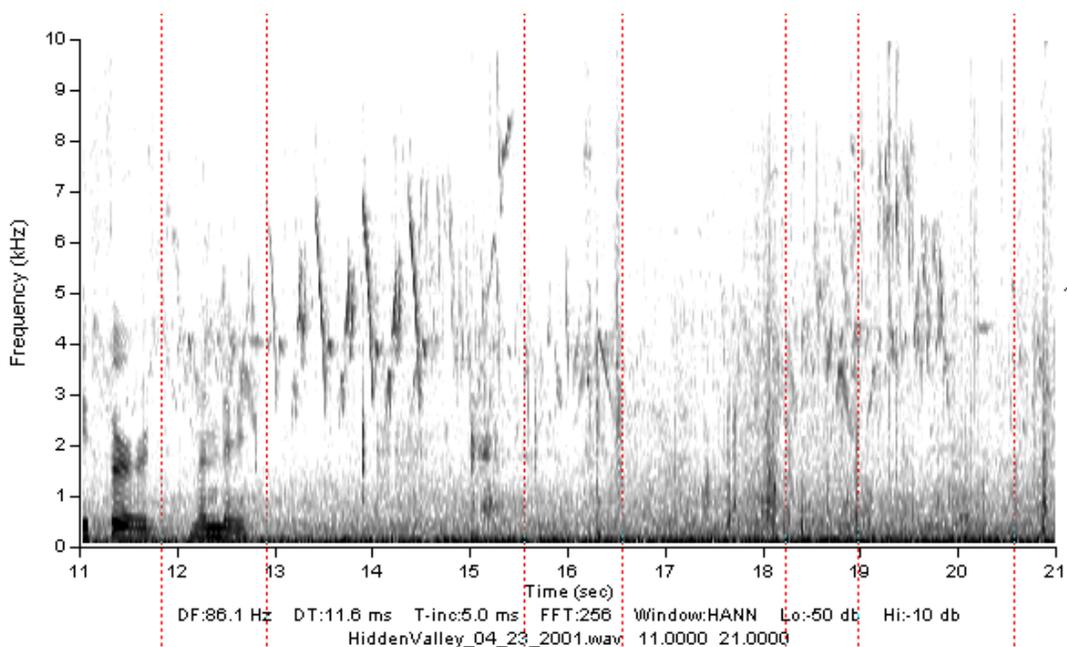


Figure 2—Spectrogram of a typical 10-s segment of recorded sounds analyzed in this study. Beginning and end of the three Least Bell's Vireo songs are marked with vertical broken lines; beginning of a fourth is near the end of the segment. Both acoustic and visual inspection were used to log all 9873 songs in this way. All analyses were performed on the beginning and ending times so derived.

Data Processing

Digital data were downloaded directly to a Windows computer, with Sony optical cables, Sony Digital I/O adaptor (RMR-D100), and Creative Recorder 1.01 software. Each day's recording was saved as a single file (approximately 0.65 GB) in 16-bit Windows (.wav) format. These were archived on compact disc, and the digital audio tape was erased for re-use. Digitized acoustic data were analyzed with Signal (Engineering Design, Belmont, MA) versions 3.1 and 4.0 software. Each tape was viewed spectrographically in its entirety, in 10 sec segments. When necessary, the sound was listened to, and/or a larger-scale spectrogram was viewed. The beginning and ending times of each LBVI song (*Fig. 1*) detected in this way (*Fig. 2*) were written to an ASCII text file for further analysis.

Data Analysis

The beginning and ending times of the vireo songs were converted to clock times in SAS, version 6.02. SAS commands were used to count the number of songs ending in each minute of the tapes. These counts were converted to 0/1 binary data for presence or absence of at least one song in the 1-min period.

The output of these basic data-handling procedures were (1) seven "s-functions," which gave the number of songs produced per minute, as a function of time of day, and (2) seven sets of "availability functions,"

which gave presence/absence of song as a function of time of day. To test for randomness of these time series, we performed runs tests (Sokal and Rohlf 1995:797).

We assessed the relationship between availability and parameters that can be estimated during point counts of a few minutes' duration. First, we compared the correlation of the daily value of availability with two measures of overall singing rate, (1) songs per active minute, calculated as total songs divided by the number of minutes containing at least one song, and (2) songs per minute, calculated as total songs divided by total minutes. We then produced random samples of 1, 2, 5, 10, 25, and 50 1-min segments from each day's data. We did this by reordering the minutes randomly and then selecting the first 1, 2, ... 50 data entries for each date. (An advantage of this nested approach to randomization is that the differences among sample sizes are wholly attributable to sample size, without a stochastic effect due to separate random draws.) We counted the number of songs in each of these randomly drawn time segments for brief estimates of singing rate. We also calculated two direct estimates of availability by comparing the presence/absence of song in the randomly drawn minute with the presence/absence of song in the minute following it chronologically (i.e., not randomized): Continuation probability was the proportion of minutes with songs followed by a minute with songs. Recapture probability was the proportion of subsequent

(second) minutes with song preceded by a minute with song.

To assess seasonal trends in availability and singing rate, we plotted these parameters against julian date, and conducted regression analysis where appropriate.

Throughout the range of the species, songs have terminal notes that are frequency-modulated (zigzag frequency contours in *Fig. 1*) and either falling or rising. Songs ending with falling notes are said to be up to 15 times more frequent early in the season, but from incubation onward the two types are delivered in couplets, with the first song ending on a rising note and the second on a falling note (Barlow 1962, cited in Brown 1993). To test for such a pattern in our data, we examined four sequences of 100 songs from each tape (beginning at 600, 4200, 7800, and 10400 seconds from the beginning of the tape), and scored the terminal note "up" or "down." Because we encountered a high degree of stereotypy during this analysis, we classified each song into one of ten song-types (*Fig. 1*).

Results

Descriptive Statistics

The Least Bell's Vireo was found at only one site, Hidden Valley (HV), where we obtained samples on 8 d (*Table 1*). Recordings ranged in duration from 191 to 254 minutes (*Table 1*). We did not detect a Bell's Vireo by any means on 30 March. Thereafter, song production exceeded 3 songs/min for each recording. The

maximum number of songs in a minute, 23, accords with the results of Barlow (1962, cited in Brown 1993). This result, and the fact that none of the 9873 songs we logged overlapped another, suggest that only one male was in our study area at any one time.

Bout Structure

The distribution of s , the number of songs counted each minute, was extremely skewed to the right. The overall mode was 0, with silent minutes ranging from 4% to 74% of the daily samples. The converse of these percentages is the realized availability (p_s) of these samples (*Table 1*). If the 558 min with no songs are omitted, the remaining data display an apparent truncated normal (i.e., lognormal) distribution, with a mode at 7-9 songs (*Fig. 3*). Songs per active minute (i.e., total songs divided by the number of taped minutes in which at least one song occurred) varied from 6.6 to 12.5 (*Table 1*).

Songs were clumped in time, as were periods of silence (*Fig. 4, Fig. 5*). The average duration of a bout of singing (defined as an interval in which at least one song occurs in every minute) was 11.71 (SD = 6.55), while a bout of silence averaged 5.96 min (SD = 5.45). (*Table 2*). All seven runs tests were significantly non-random, with negative t-values (*Table 2*), which indicates significant clumping of active and/or inactive minutes. In other words, once singing or silence had begun, the bias was to continue rather than to change to the other state.

Table 1—Recording and singing data for eight survey dates distributed approximately evenly through the Least Bell's Vireo breeding season of 2001 at Hidden Valley, Riverside County, California. Continuous recordings, beginning within 20 min of dawn, were made with a Sony TCD-D8 digital tape recorder and a Sennheiser ME62 omni-directional microphone with K6 power supply. Mean and standard deviations summarize the seven recordings in which target songs were found. Availability is the proportion of 1-min time segments in which at least one song was detected. Songs per active minute is the singing rate when the bird is singing, i.e., total songs/(total minutes*availability). Detectability is the likelihood of detecting the bird in 1 min, given an arbitrary but low conspicuousness value of 0.1, when it sings \bar{s} songs per min.

Date	Minutes recorded	Total songs	Availability ($p_{s(1min)}$)	Songs/active min (\bar{s})	Detectability ($p_{ds/p=1}$)	Detection probability (p)
3/30/01	246	0	0.000	0.00	0.000	0.000
4/16/01	253	1124	0.356	12.49	0.732	0.260
4/23/01	242	1249	0.690	7.48	0.545	0.376
4/30/01	243	1990	0.885	9.26	0.623	0.551
5/8/01	254	1746	0.787	8.73	0.601	0.474
5/14/01	254	643	0.366	6.91	0.517	0.189
5/21/01	191	813	0.649	6.56	0.499	0.324
6/4/01	254	2308	0.961	9.46	0.631	0.606
Mean	241.6	1410.4	0.671	8.70	0.593	0.397
Std. Dev.	22.9	620.2	0.237	2.02	0.080	0.153

Least Bell's Vireo Detection Probability - Scott et al.

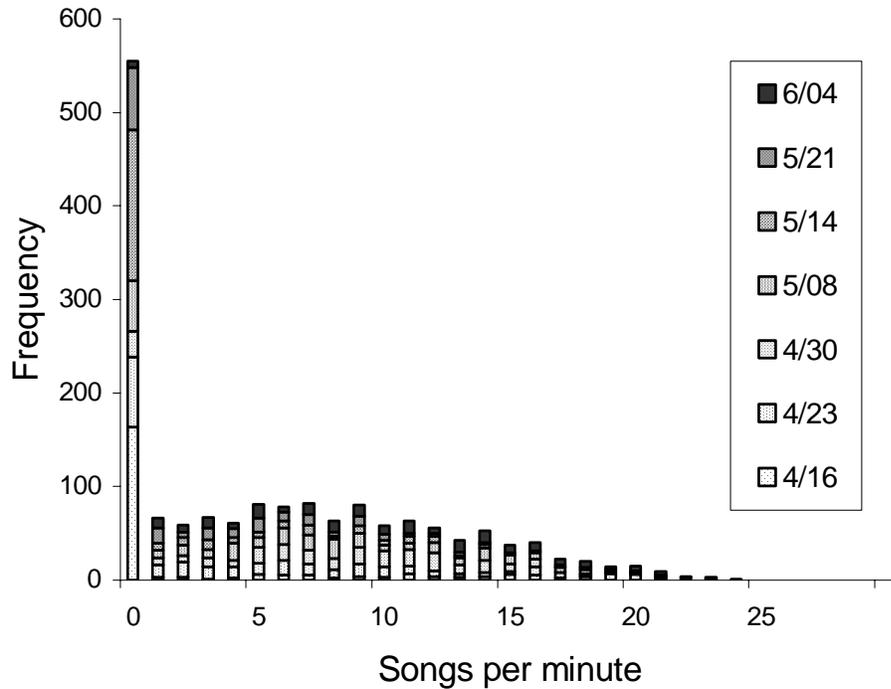


Figure 3—Frequency distributions of s , the number of songs produced in each clock minute during the morning survey period, on 7 days distributed throughout the breeding season. These results are based on actual counts of songs in each of the 1945 min in the study. Note the approximately lognormal distribution of nonzero values.

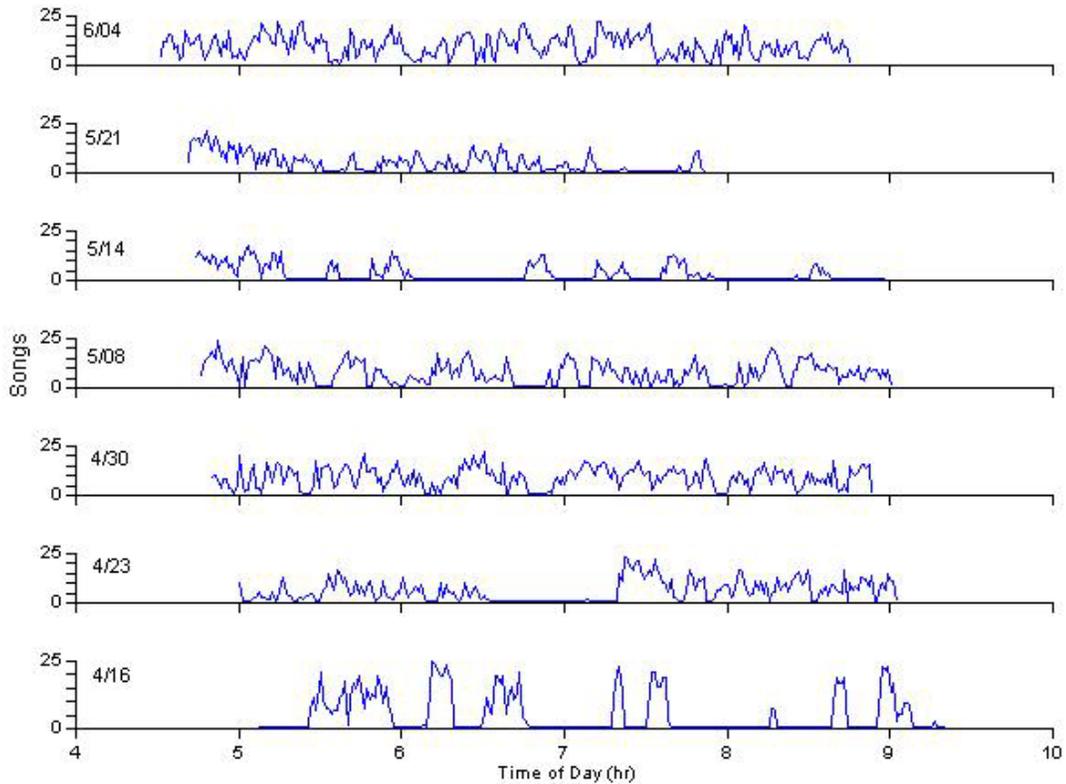


Figure 4—Song production, s , of a Least Bell's Vireo during the first 4 hr of 7 days in the breeding season of 2001.

Least Bell's Vireo Detection Probability - Scott et al.

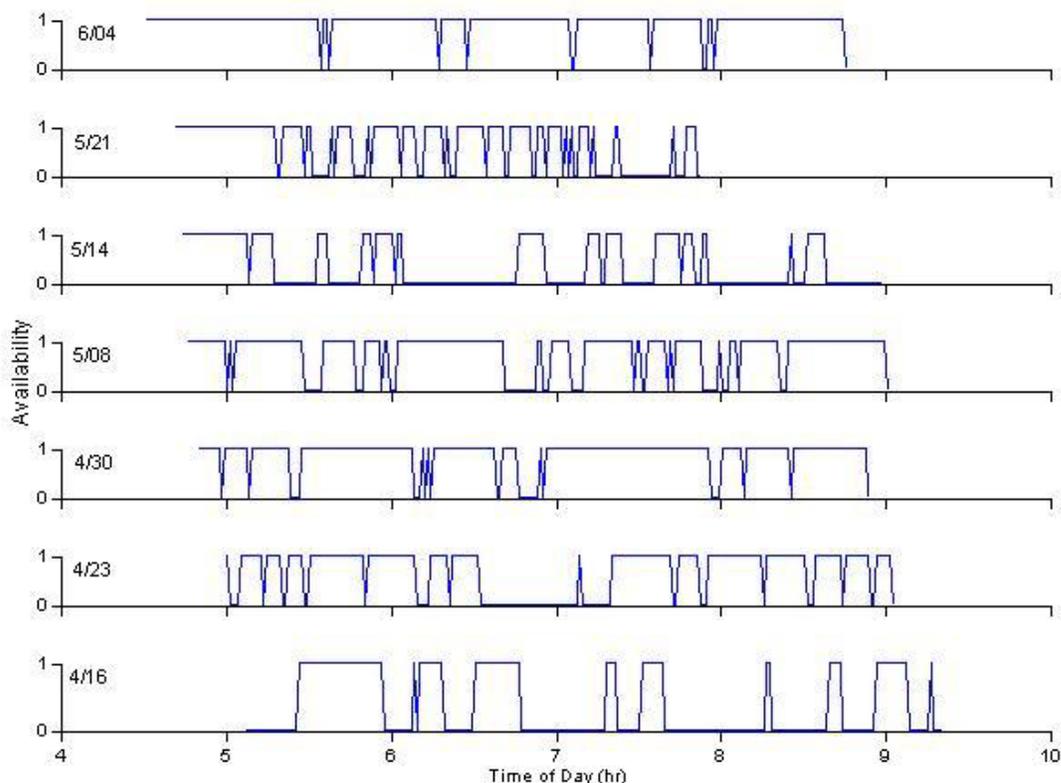


Figure 5—Availability of a Least Bell's Vireo for detection, calculated by converting all nonzero values in *Figure 4* to ones. Availability is 1 for each 1-min period in which at least one song is delivered, 0 otherwise.

Table 2—Bout-structure statistics for a Least Bell's Vireo at Hidden Valley, Riverside County, California. A run is a time segment in which a binary classification (in this case, singing vs. non-singing) does not change. The negative *t*-values indicate under-representation of runs in all samples, the very low *p*-values indicate that this under-representation is highly significant. In other words, once the bird began to sing, he continued singing much longer than expected by chance, and likewise for silence.

Date	Minutes	Mean bout duration (min)		Runs	<i>t</i> -value	<i>p</i> -value	Runs/hr
		Song	Silence				
4/16/01	253	9.00	16.00	21	-13.1938	0.001	4.98
4/23/01	242	10.73	5.00	31	-11.0786	0.001	7.69
4/30/01	243	15.67	2.33	25	-8.1033	0.001	6.17
5/08/01	254	9.65	3.18	35	-9.6032	0.001	8.27
5/14/01	254	6.64	10.85	28	-12.3157	0.001	6.61
5/21/01	191	5.64	3.14	44	-7.0112	0.001	13.82
6/04/01	254	24.63	1.25	17	-2.7317	0.01	4.02
Mean	241.6	11.71	5.96	28.7			7.366
Std. Dev.	22.9	6.55	5.43	9.0			3.202

Detection Probability

Despite the lack of serial independence in singing behavior (see above), availability increased as a roughly linear function of songs per total minute (*Fig. 6*). The short-term estimator of singing rate was also a good (although not perfect) predictor of availability

(*Fig. 7*). A sample size of approximately 10 1-min samples was optimal, with greater effort yielding little increase in the coefficient of determination (r^2), while smaller sample sizes performed poorly. The direct estimates of availability performed very poorly, regardless of sample size.

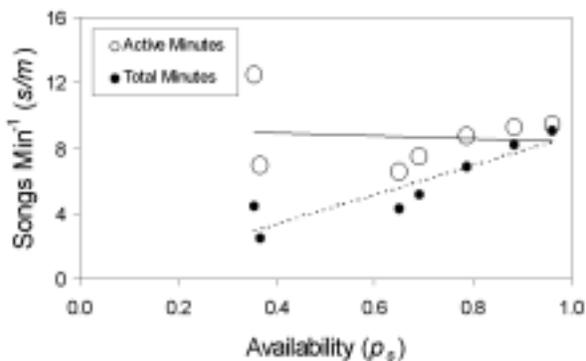


Figure 6—The relationship between mean cue abundance and availability for the seven dates on which some singing occurred. Mean cue abundance (\bar{s}) was calculated as total songs in the sample divided by (1) total minutes in the sample (closed circles) and (2) the number of minutes in the sample containing at least one song (open circles), i.e., active minutes, see equation 3 of McCallum (this volume). In this data set, availability is highly correlated with songs per total minute, but not with songs per active minute. Ordinarily availability would be estimated from cue abundance; cue abundance is plotted on the vertical axis here to facilitate comparison.

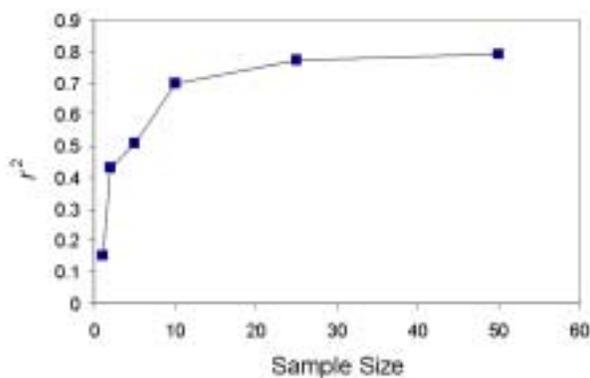


Figure 7—Improvement in predictability of availability from 1-min samples of singing rate with increasing sample size. One, 2, 5, 10, 25, and 50 1-min samples were randomly drawn from each day's data, and the per-minute singing rate was averaged across the daily samples. Availability was regressed on average singing rate for each sample size. The measure of predictability is the coefficient of determination (r^2) for each regression. The random samples were nested, that is, any sample that was in a smaller sample size was also in a larger sample size. Two other potential estimators of availability were not correlated with availability (see text).

To assess the overall detection probability of this bird, we substituted daily estimates of conspicuousness (p_{ds}), cue abundance (\bar{s}), and availability (p_s) in equation 1. As mentioned above, this is a heuristic formula; a method for estimating conspicuousness has not been devised. We set conspicuousness at 0.1, which we judge to be a low value (see McCallum this volume for

the components of conspicuousness). Calculated in this way, conspicuousness ($p_{ds|p1} = 0.1$) was surprisingly consistent at ($\bar{p}_{ds} = 0.593 \pm 0.080$ SD). Mean detection probability (p) was 0.397 (SD = 0.153) (see Table 1).

Diel Variation and Phenology

Somewhat surprisingly, song production showed no obvious hourly trend during the morning hours when most surveys are conducted (Fig. 4). Binary plots of inactivity/activity (i.e., "availability functions," Fig. 5) similarly reveal that periods of inactivity (nonavailability) were distributed throughout the recordings.

Although availability did not exhibit an hourly trend, a seasonal trend was apparent (Fig. 8). Availability climbed to 0.88 by the end of April, dropped precipitously to 0.27 by the middle of May, then climbed again to nearly 1.0 by early June (Fig. 8).

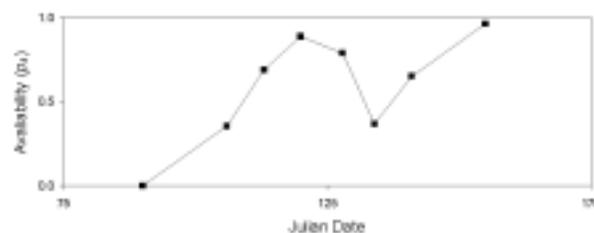


Figure 8—The phenology of availability. Availability increased seasonally, then dipped, then recovered, perhaps as a function of time invested in nesting activities.

Contrary to expectation, we did not find that the terminal notes of songs sorted readily into "rising" and "falling" categories. These terminal notes were, however, highly stereotyped, and were easily sorted visually into 10 types (Fig. 1). Moreover, this stereotypy extended to the entire song. The bird's repertoire was limited to 10 distinctive song-types (Fig. 1), which were rendered with great fidelity.

A preliminary analysis of the probability of transition from one song-type to another revealed that all song-types except type 6 repeated roughly 10% of the time. Type 6 did not repeat. Three pairs of song-types (1-2, 3-4, 7-8) tended to alternate (reciprocal transition probabilities >0.5). The remaining four song-types were inter-related, but seldom transitioned to the other six. Further analysis of this unexpectedly complex data set is beyond the scope of this paper, but will be reported elsewhere.

Discussion

Although these results from a single bird should not be generalized to other Least Bell's Vireos, the nearly 10,000 songs distributed among 8 days of recording should be adequate for describing this bird's singing

behavior. Because records this intensive are laborious to produce and thereby rare, these results are therefore of general interest.

Bout Structure

Songs per minute, calculated over the entire duration of each tape, varied from 2.5 to 9.0, suggesting that sufficient activity was occurring for the bird to be detectable at any time during the first 4 hr of the day, throughout the breeding season. Drawing this conclusion from average singing rate would, however, lead to serious error. This bird was inactive from 4-61% of the time (reckoned in minutes), depending upon the date. These periods of inactivity were, moreover, clumped, rather than being distributed randomly through the morning. Although alternation of singing and other activities is probably adaptive from the standpoint of the bird's time budget, it exacerbates the problem of detection for surveyors. Clearly, estimates of availability would be needed to correct counts of birds exemplified by our subject.

Detection Probability

Detection probability is the product of availability and detectability. In this study we focused on the former, because it is a new concept that has not been studied extensively. Given that availability was both <1 and variable from day to day, a robust means of estimating it is needed. We first determined the correlation of availability with overall singing rate, and then explored ways of estimating availability from the sort of short samples that can be taken concurrent with point counts.

Singing Rate

Availability was correlated with songs per total minute, but not with songs per active minute. This was true with or without inclusion of the data point for March 30, when the bird was effectively (and possibly physically) absent (*Fig. 6*). Accordingly, 1-minute estimates of songs per minute, averaged over at least 10 samples, also provided a good estimate of availability.

Although it seems intuitively clear that availability and singing rate should be correlated if each song is an independent event, songs were highly clumped in this study. A simulation study (McCallum, unpubl. data) shows that, under such circumstances, fairly good correlations between singing rate and availability can be expected when songs are not too frequent (<15 song per min). Note that despite the tight correlation between availability and singing rate, averaged over the entire recording (*Fig. 6*), only 80% of the variation in availability could be explained by 1-min estimates of singing rate, even when a large number of such samples were averaged (*Fig. 7*).

Presence/absence of Song

Another simple way of estimating availability, conceptually similar to the removal method of Farnsworth et al. (2002) is to calculate the proportion of time segments containing a song that are preceded by a segment containing a song. This is equivalent to the recapture rate in a mark-recapture design. A second estimator, also based on the presence/absence of song in 1-min periods, is the proportion of minutes containing a song followed by a minute containing song. Note that these are contingent probabilities, i.e., given that the bird sings, what is the probability that it will sing (or will have sung) in the next or preceding minute? Estimating availability requires knowing that the bird is present, and singing is the only way it can demonstrate its presence. Estimating availability from raw presence/absence of song would confound presence of the bird with presence of song, which is contingent upon the presence of the bird.

These estimates of availability apparently performed poorly because of the serial correlation in song production (*Table 2*). Even using the entire data set did not improve this situation. Although the estimates for six of seven days did stabilize at high sample sizes, the resulting values were all above 0.9, not in line with the true values of availability (*Table 1*). Estimators such as these have been successful with other data sets (Farnsworth et al. 2002; McCallum, unpubl. data); the present results simply indicate that under certain circumstances, apparently resulting from clumping of on- and off-duty minutes, such estimators are not dependable.

Diel Variation and Phenology

We expected singing rate and availability to decline over the course of the morning, but such a trend was not discovered. If such a trend does exist, the decline must begin later in the morning. Even when availability was low, there was no diel trend (*Fig. 4, Fig. 5*). This is good news for surveyors, because it indicates that a wide time window is available in which to conduct surveys, if this individual is typical.

Largely unexploited by biologists monitoring bird populations is the information on breeding phenology and/or pairing status encoded in the singing behavior of males (B. Walker, pers. comm.). In many species, males sing much less after pairing. We did see a decrease in time devoted to singing, following an initial increase (*Fig. 8*), but singing increased again after the mid-May low. Unfortunately, we lack independent behavioral data that might shed light on this interesting pattern. In some species males use one song-type before pairing and another after pairing. Bell's Vireos are reported to alternate songs that end with rising

notes with songs ending with falling notes from the incubation period onward (Barlow 1962, cited in Brown 1993). Our subject alternated song-types (i.e., sang with immediate variety) throughout the breeding season, which seems unlikely to have been correlated with incubation. Both the seasonal changes in availability and the alternation of song-types suggest that studies of the singing behavior of individually recognizable Least Bell's Vireos could provide useful information on phenology.

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