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Estimating relative abundance of forest birds: simple versus adjusted counts.—In applied studies of avian ecology, one of the more commonly encountered problems is the estimation of a species' abundance across a gradient of habitat types. Recently, much attention has focused on transect or point counts incorporating detection functions derived from the distribution of distances to each detected bird (Verner 1985). Detection functions are used to calculate a "basal region" (Emlen 1971), which is that area sampled over which all individuals are believed to be detected. The count is adjusted by dividing by the basal region for any particular habitat, and this adjusted count is an estimate of the species' density in that habitat. Assuming equal sampling effort, variation of density estimates among these habitats is thus a function of two variables: (1) variation in the number of birds counted in each habitat, and (2) variation in size of basal region. If, for any particular species, basal region does not vary in size among habitats, then any variation in estimated density among these habitats can be attributed to variation in the number of birds counted. In this case, simple counts might provide as good an estimate of relative abundance across habitats as the more sophisticated adjusted counts. The purpose of this paper is to investigate how well simple counts compare to more complex methods of estimating relative abundance.

Study area and methods.—As part of a larger study on habitat associations of forest vertebrates (Raphael 1984), I established 136 study plots in forests dominated by Douglas-fir (*Pseudotsuga menziesii*) in association with tanoak (*Lithocarpus densiflora*), Pacific madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), and black oak (*Q. kelloggii*). All plots were in the Trinity and Klamath river drainages of northwestern California, at elevations between 427 and 1220 m. Plots were defined by the boundaries of timber stands delineated on U.S. Forest Service timber-type maps.

To characterize the structure and composition of vegetation on each plot, I randomly selected three 0.04-ha circular subplots within a 90-m radius of the plot center (a total of 408 subplots). Within each subplot, I recorded species, height, diameter, and crown dimensions of each shrub or tree > 2 m tall. These measurements yielded an estimate of the canopy volume of each tree; volumes of trees were summed to estimate total canopy volume on each plot (Table 1) using a modified version of the program HTVOL (Mawson et al. 1976).

An index of stand age was calculated for each plot using a basal-area-weighted average of the ages of all conifers on the 3 subplots (Raphael 1984). I estimated the age of a tree from its diameter using a regression analysis of an extensive sample of known-aged trees previously measured within the study area (Table 1). I also calculated an index of the yearly solar radiation (Frank and Lee 1966) to which each site was exposed. This index was based on slope, aspect, and latitude. Values were largest on south-facing, moderate slopes and smallest on north-facing slopes (Table 1).

Birds were counted from a point marked with plastic flagging at the approximate center of each of the 136 plots. All points were at least 360 m apart. Each plot was visited shortly after sunrise on 4 days each year during May and June 1981–1983. On each visit, an observer recorded the estimated distance to each bird seen or (more often) heard during three successive 10-min periods (for a total of 36 10-min counts per plot). Special care was taken to record a bird only once during each period, and to record observations independently among the three successive periods.

The data were analyzed in three ways. First, I simply counted the total number of detections of each bird species recorded during the 36 10-min counts at each plot over all three years. Birds detected at distances > 180 m (one-half of the minimum distance between adjacent plot centers) were excluded.

TABLE 1
CHARACTERISTICS OF DOUGLAS-FIR STANDS IN RELATION TO STAND AGE CLASS IN NORTHWESTERN CALIFORNIA

Characteristic	Stand age class (year)					Signifi- cance
	50-150	150-200	200-250	250-300	>300	
Average age	124 (55-146) ^a	178 (155-199)	229 (203-248)	272 (254-300)	329 (302-369)	N.T. ^b
Coniferous canopy volume ^c	56.1 (0.7-91.7)	52.5 (3.9-141.5)	50.4 (10.5-133.0)	42.3 (5.9-106.2)	43.3 (5.4-85.3)	>0.05
Hardwood canopy volume ^c	15.6 (0.5-34.3)	16.2 (0.0-41.8)	29.2 (1.0-91.2)	28.9 (5.2-49.0)	33.4 (12.4-83.9)	<0.001
Density (N/ha) of stems <53 cm dbh	1050 (400-2650)	964 (250-1842)	1097 (425-2600)	1416 (292-2833)	1517 (417-3075)	<0.001
Density (N/ha) of stems ≥53 cm dbh	47 (0-83)	63 (8-183)	60 (17-117)	56 (8-142)	52 (17-108)	<0.001
Elevation (m)	660 (366-1129)	819 (475-1220)	843 (442-1159)	882 (549-1280)	937 (610-1159)	<0.001
Solar radiation index ^d	0.49 (0.25-0.60)	0.51 (0.38-0.59)	0.47 (0.25-0.6)	0.47 (0.24-0.60)	0.38 (0.24-0.59)	<0.001
Number of sites	27	25	31	32	21	N.T.

^a Mean (range).

^b N.T. = not tested.

^c Expressed as thousands of m³/ha.

^d Index of potential yearly solar radiation. Larger values indicate warmer, drier sites.

TABLE 2
SPEARMAN RANK CORRELATION BETWEEN THREE ESTIMATES OF RELATIVE ABUNDANCE OF BREEDING BIRDS AND THREE ENVIRONMENTAL GRADIENTS IN DOUGLAS-FIR FORESTS OF NORTHWESTERN CALIFORNIA, 1981-83

Bird species and environmental gradient	Correlation of gradient with:		
	Total count	Fourier density	Emlen density
Black-headed Grosbeak			
Stand age	-0.04	-0.02	0.00
Solar radiation	0.06	0.06	0.04
Elevation	-0.36 ^c	-0.39 ^c	-0.37 ^c
N ^d	136	130	128
Hermit Warbler			
Stand age	0.23 ^b	0.18 ^a	0.20 ^a
Solar radiation	-0.28 ^c	-0.31 ^c	-0.35 ^c
Elevation	0.48 ^c	0.43 ^c	0.42 ^c
N	136	132	128
Western Flycatcher			
Stand age	0.18 ^a	0.16	0.10
Solar radiation	-0.13	-0.11	-0.15
Elevation	-0.24 ^b	-0.25 ^b	-0.25 ^b
N	136	136	128
Western Tanager			
Stand age	-0.43 ^c	-0.35 ^c	-0.34 ^c
Solar radiation	0.18 ^a	0.22 ^a	0.16
Elevation	-0.40 ^c	-0.35 ^c	-0.35 ^c
N	136	122	128

^a $P < 0.05$.

^b $P < 0.01$.

^c $P < 0.001$.

^d Number of sites sampled for which an abundance estimate could be calculated.

Second, I used the distance estimate to each of these birds to calculate a density estimate for each species with sufficient sample size ($N > 30$) at each plot, using the computer program TRANSECT (Laake et al. 1979). Because this program is designed to analyze transect data, several modifications were necessary to apply it to point data. All distances were transformed to area by treating each distance estimate as a radius. That is, I squared each distance and multiplied by π , and these new values were substituted for the original raw distances. The number of censuses (36) per plot was equivalent to transect line length in the program. The value actually entered into the program was one-half of the number of censuses (18) to adjust for the constant (2) in the computer algorithm that doubles line width. All data were truncated to an equivalent distance of 180 m (10.2 ha after transformation). Density estimates were calculated using the Fourier series estimator (Burnham et al. 1981).

The third analysis was a calculation of density modified from Emlen's original (1971) method. For this analysis, distances were grouped by 5-m intervals out to 20 m, and thereafter into 10-m intervals. The cumulative number of birds detected out to each interval was then calculated, and a density was estimated for each additional interval by dividing the count

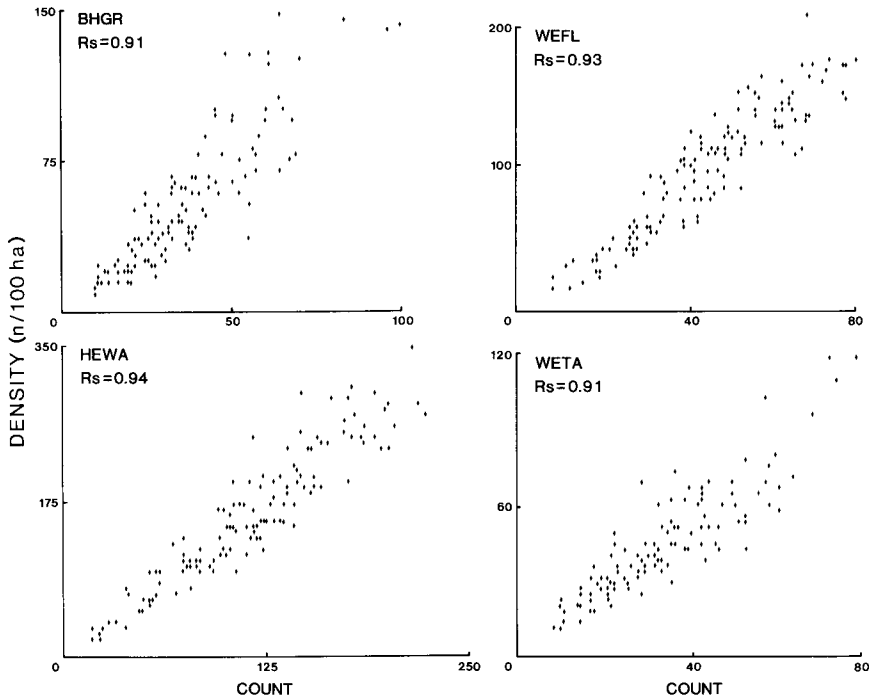


FIG. 1. Relationship of simple counts to density estimates calculated using the Fourier series estimator of program TRANSECT for four breeding bird species in Douglas-fir forests of northwestern California, 1981–83. BHGR = Black-headed Grosbeak, HEWA = Hermit Warbler, WEFL = Western Flycatcher, WETA = Western Tanager. Spearman rank correlation coefficients are listed below each bird-species code.

by the area represented by each interval. The maximum density calculated from this series of successively larger intervals was taken as the best estimate.

To evaluate how the two density estimates and the total count ranked the abundance of species across habitats (within Douglas-fir forests), I computed the Spearman rank correlation between the abundance estimates and each of three major environmental gradients (stand age, solar radiation index, elevation). I also compared the mean number of birds counted and the mean density for the two estimators among 5 stand age-classes using one-way analysis of variance.

To calculate the contributions of variation in numbers counted and basal region on variation in density among habitats, I computed the squared coefficient of variation (CV^2) for the count and for the basal region for each species among all plots for which a density estimate was derived. Burnham et al. (1980:51) showed the CV^2 of a density estimate is equal to the sum of the CV^2 for the count and effective area. Therefore, the percentage of the CV^2 of density attributed to the count or basal region was easily calculated and was used to assess the relative contribution of each source of variation.

Results. — Four species were sufficiently abundant to calculate population density estimates

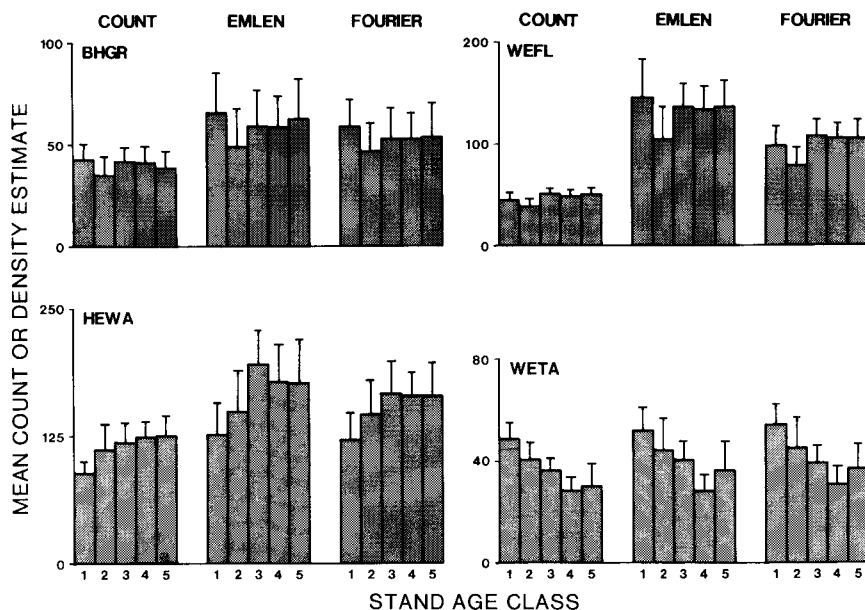


FIG. 2. Comparison of mean abundance derived from counts, and 2 density estimators for 4 species of breeding birds among 5 stand age classes of Douglas-fir forests of northwestern California, 1981–83. Vertical lines indicate 95% confidence intervals. Stand age classes are described in Table 1. See Fig. 1 for species abbreviations.

for nearly all sites: Hermit Warbler (*Dendroica occidentalis*) ($N = 15,352$), Western Flycatcher (*Empidonax difficilis*) ($N = 6265$), Black-headed Grosbeak (*Pheucticus melanocephalus*) ($N = 5445$), and Western Tanager (*Piranga ludoviciana*) ($N = 5036$). The three estimators yielded similar correlations with each of the three environmental gradients for each bird species (Table 2). All estimators suggested, for example, that the Hermit Warbler was most abundant in older, cooler, high elevation sites, whereas the Western Tanager was more abundant in younger, warmer, low elevation sites. The similarity of these habitat correlations resulted from the strong correlations among the estimators themselves, illustrated for the simple counts vs Fourier estimator (Fig. 1).

The similarity of results using the three estimators also is apparent from comparisons of mean abundance among the 5 stand-age classes (Fig. 2). Whereas the absolute magnitude of the abundance estimates varied, the relative magnitudes among the age classes were quite similar. For nearly all comparisons, the rank order of abundance among age classes was consistent among estimators. The one exception was that, for Hermit Warbler, the mean count was highest in age class 5 (> 300 yr). None of the differences, however, was statistically significant, considering the breadth of the confidence interval about each mean (Fig. 2).

The analysis of the sources of variance in the density estimates of these 4 species showed that variation in count contributed from 73 to 84% (Table 3). For any of these species, then, variation in basal region among plots was only a minor component of variation in density.

Discussion.—My results show that for the habitats I studied variation in the density estimates of bird species along habitat gradients is much more strongly influenced by vari-

TABLE 3
SQUARED COEFFICIENTS OF VARIATION OF THE SIMPLE COUNT, BASAL REGION^a, AND DENSITY ESTIMATE AMONG DOUGLAS-FIR FOREST SITES, NORTHWESTERN CALIFORNIA, 1981-83

Bird species	Squared coefficient of variation			Percent contribution of count $C/(C + BA)$
	Simple count (C)	Basal region (BA)	Density estimate (C + BA)	
Western Flycatcher	0.150	0.036	0.186	80.6
Western Tanager	0.194	0.060	0.254	76.4
Hermit Warbler	0.205	0.041	0.246	83.5
Black-headed Grosbeak	0.260	0.095	0.355	73.3

^a Basal region is approximately the inverse of $f(0)$, calculated using the Fourier series estimator in program TRANSECT (Burnham et al. 1980).

ation in the simple count than by variation in basal region. This result is shown explicitly in Table 3, and is implicit in Table 2 and Figs. 1 and 2. That the count is correlated with density (Fig. 1) is certainly expected because the count is itself the numerator in the calculation of density. Also important, however, are the strength of the correlation and the fact that little additional information is contained in the basal region component. The surprising result is that an unadjusted count was apparently as good an index of abundance as either of the more sophisticated density estimates I evaluated.

These results do not imply that investigators should abandon density estimation in favor of simple counts. Clearly this is undesirable on a number of grounds, particularly because simple counts cannot account for between-species differences in basal region size, which are probably much stronger than the within-species, between-habitat differences I report here. Rather, these results suggest that investigations on the sources of count-variation should receive greater emphasis. Many studies (see papers in Ralph and Scott 1981) have addressed the need to adjust for basal regions of birds in different seasons, times-of-day, habitats, etc., but few have discussed variation in numbers of detections. Results of this study, although limited to only a few species in one forest type, suggest the need to focus more clearly on this important component of density. In addition, this study provides evidence that if relative abundance is what one wants to estimate, simple counts can be as good an estimator as more complex estimators adjusted by basal region.

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A synthetic diet for fruit-eating birds.—Long-term maintenance of fruit-eating birds has been a major barrier to their study in captivity. Recently captured birds lose weight rapidly, even when feeding on fruits ad libitum. Birds under 50 g may lose weight so rapidly that flight muscles are seriously weakened; death may occur within a few days of capture (Moermond, Denslow, and Levey, pers. obs.). Studies using recently captured birds in poor physiological condition are unlikely to yield consistent or interpretable results. It is therefore important that experimental animals be maintained at good nutritional and energetic levels before behavioral experiments are initiated.

In this paper we describe a synthetic diet for maintaining captive fruit-eating birds, with notes on its use. We have been able to keep 25 species of tropical and temperate fruit-eating birds on this diet at steady weight and in good plumage for periods of up to 12 months. Some of these birds were recaptured in good condition months after their release.

We have used captive fruit-eating birds maintained on this diet for a variety of behavioral studies (Moermond and Denslow 1983, 1985; Levey et al. 1984). The diet is not only useful for maintaining experimental birds but can be manipulated as an experimental tool.

The diet.—The synthetic diet consists primarily of a mixture of mashed ripe bananas, soy protein isolate, and a supplement of vitamins and minerals in an agar-based gel (Appendix 1).

A protein gelatin (i.e., Knox®) may be an acceptable substitute for agar where the latter is either too expensive or unavailable. An agar or gelatin base makes the diet easy to handle, insures a uniform composition of the mixture, and precludes selection of only the more palatable components of the mixture by the birds. At warm temperatures (>25°C) under which our birds were held, the food ferments quickly; we replaced it twice daily, at sunrise and at noon. A mold retardant such as ascorbic acid could be added to retard rapid deterioration, although we have not done so.

Habituation techniques.—The yellow-brown mash bears little resemblance to brightly-colored fruits frugivores normally eat, and is thus often not recognized as food by naive birds. Newly caught birds therefore must be habituated to the mixture after capture.