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A COMPARISON OF TRANSECTS AND SPOT MAPPING IN OAK-PINE WOODLANDS OF CALIFORNIA[1]

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Abstract. We compared density estimates of birds using the spot-mapping and transect methods in grazed and ungrazed habitats in foothill woodlands of the western Sierra Nevada, California. As judged by the percentage error of transect estimates in relation to those from spot mapping, the exponential polynomial estimator from program TRANSECT (Laake et al. 1979) consistently gave better estimates of density than either the Fourier series or exponential power series estimators. Distance estimates grouped into bands of some specified width consistently performed better than ungrouped data, although no single band width was best in all cases. Although several alternatives tested in this study gave density estimates with errors only about half those by a variety of previous methods, even the best alternatives had mean errors of about 25% and maximum errors ranging from 37% to 109%. Errors involved both over- and underestimation of density in relation to spot-mapping estimates, even for the same species on the same site in different months or by different observers. The two habitats affected TRANSECT estimates of density differently, and observers differed significantly in the accuracy of their estimates. Because of these problems, transect methods could lead to misinterpretation of real abundance patterns by masking differences between years or sites, even to the extent of suggesting that a species was more abundant in a given year or site than another when the reverse was true. As sample sizes increased, both overestimates and underestimates of density by transect methods converged on density estimates by spot mapping, suggesting a real correspondence in density estimation by these two methods. Empirical assessment of the sample size needed to use program TRANSECT indicated that a data set should include at least 100 records per species—far more than the number normally used to estimate densities by transects.

Key words: Density estimates; transects; spot mapping; oak-pine woodlands; California.

INTRODUCTION

Several studies have compared density estimates using transect methods with those using spot mapping (e.g., Emlen 1971, 1977; Franzreb 1976, 1981; Dickson 1978; Järvinen et al. 1978a, 1978b; Tiainen et al. 1980; Hildén 1981; O'Meara 1981; Redmond et al. 1981), using mapping estimates as the standard on the general assumption that they are more accurate than transect estimates. Although the validity of that assumption is still generally unconfirmed when individual species are considered separately (see Verner 1985), we make the same assumption for this study.

Earlier studies that compared transect results with those from spot mapping did not have access to program TRANSECT (Laake et al. 1979) or to the extensive discussion and testing of that program given in Burnham et al. (1980). This program has potential advantages over previous methods of estimating bird densities from transect data. It allows analysis by a variety of estimators, and data may be analyzed with or without being grouped by sighting distances. It lacks much of the subjectivity inherent in some methods, and it computes confidence intervals for the density estimates.

On the other hand, several critical assumptions of program TRANSECT are probably violated by most or all studies that use the program to estimate true densities of birds in terrestrial communities: (1) All birds exactly on the transect line are detected; (2) no bird moves in response to the observer before being detected; (3) perpendicular distances from birds to the transect line are recorded accurately; (4) no bird is counted more than once; and (5) all detections are independent events. Although this study violated most or all of these assumptions, it is probably representative of most such studies. For that reason, its results are probably generally applicable. Although it is unrealistic to imagine that studies of birds in terrestrial communities will ever sat-

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isfy all assumptions of line-transect sampling, one might at least hope that we can show, empirically, that certain ways of analyzing the data compensate better than other ways for violations of the assumptions.

The objectives of this study were: (1) to determine whether plotting bird locations on maps as they were detected along transects would eliminate the heaping (see Hobson 1976) of records at 5- and 10-m intervals, typically seen when observers record estimated distances in the field; (2) to determine whether a single estimator from program TRANSECT and a single grouping procedure (ungrouped data, or some grouping interval based on distance) would consistently result in density estimates closest to those from spot mapping; (3) to measure the effect of sample size on the accuracy of density estimates from transect data; and (4) to determine whether significant biases in density estimates from transect data could be attributed to observers and habitats.

STUDY AREA

Two study sites were located at the San Joaquin Experimental Range in Madera County, California, an area of about 1,875 ha in oak-pine woodlands in the western foothills of the Sierra Nevada, at 215 to 520 m elevation. The "grazed site" has experienced light to moderate grazing at least since the turn of the century, and the "ungrazed site," although grazed to the same extent as the grazed site prior to 1934, has had no significant land-use activity since that time.

A spot-mapping grid of 19.8 ha (660 × 300 m) was established in each site, with grid lines carefully surveyed every 30 m in each direction and each intersection identified by a stake bearing an alpha-numeric code. Tree cover on both sites was almost entirely gray pine (*Pinus sabiniana*), interior live oak (*Quercus wislizenii*), and blue oak (*Q. douglasii*). Based on vertical projections from 5,500 points regularly spaced at 6-m intervals throughout each mapping grid, the grazed site had 32.3% tree cover, with slightly more than half in live oak. The ungrazed site had only 25.3% tree cover, nearly half of that in gray pine. Shrub cover on both plots was mainly buckbrush (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and mariposa manzanita (*Arctostaphylos mariposa*). The ungrazed site had 21.8% shrub cover and lacked a browse line; the grazed site had 6.6% shrub cover and a distinct browse line. Further details and a map of the study sites are given in Verner and Ritter (1985).

METHODS

SPOT MAPPING

We both made five visits to each site in each of 4 months during the breeding season—March, April, May, and June—of 1978. Each visit was done on a different day, beginning within 15 min of sunrise and ending after the entire grid had been sampled according to the study design. Alternate lines in the longer dimension of the grid were walked during each visit, after which a line 30 m beyond the perimeter of each grid was walked to obtain additional records of birds outside the grid to assist in delineating territories that overlapped grid boundaries. The initial line and direction walked were randomly chosen each day. As birds were detected in the field, their locations were plotted on a map of the grid (scale = 1:3,000). We combined our visits to give a total of 10 per month and jointly interpreted individual species maps to estimate a density for each species each month, following guidelines of the International Bird Census Committee (Anonymous 1970).

TRANSECTS

Density estimates by spot mapping and transects came from the same data. We used a new field map for every line walked on the mapping grids, so records were unambiguously definable by line. Lines were walked at a pace commensurate with recording all birds as they were detected, as if conducting a standard transect count (i.e., we did not deviate from the lines). Observations made along the line 30 m beyond the grid perimeter were not used for transect data, because records plotted near a corner could not be unambiguously assigned to one of the lines converging at the corner. Using all cases (species by month) with 40+ records (as recommended by Burnham et al. 1980:35) in our pooled data sets, we used vernier calipers to measure distances from the transect lines to bird records on the maps, to the nearest meter. This restricted our analysis to the most abundant species—the Ash-throated Flycatcher (*Myiarchus cinerascens*), Scrub Jay (*Aphelocoma coerulescens*), Plain Titmouse (*Parus inornatus*), Bushtit (*Psaltriparus minimus*), Bewick's Wren (*Thryomanes bewickii*), and

Brown Towhee (*Pipilo fuscus*). (We included Bewick's Wren data, $n = 38$, for May on the ungrazed site for comparison with the June case on the same site.) The mix of species dictated by sample size precluded examination of such questions as the relationship between accuracy of transect estimates of density and a species' foraging or nesting guild, its size, or its detectability. To examine the relationship between sample size and the accuracy of transect estimates of density, we used the data for these same species, unpooled across observers. This gave us sample sizes ranging from 16 to 144, the smaller samples being justified in this case because sample size was the object of the inquiry.

Because we sampled the same lines more than once, and because we may have detected the same bird from different lines, our records were not completely independent. According to K. P. Burnham (pers. comm.), this should not affect our point estimates of density but would influence estimates of variance an unknown amount. Accordingly, our emphasis in this paper is on the accuracy rather than precision of the estimates.

ANALYSES

Density estimates from transect data were based on program TRANSECT (Laake et al. 1979, Burnham et al. 1980), using three estimators: Fourier series, exponential power series, and exponential polynomial (hereafter the FOSER, POWER, and EXPOL estimators, respectively). Eight "grouping" procedures were used for analysis by each estimator: (1) ungrouped data; (2) 5-m grouping = 5-m intervals to 30 m, 10-m intervals to 60 m, 15-m intervals to 90 m, and 30-m intervals beyond 90 m (asymmetrical groupings were used with narrower band widths because observers should be able to more accurately estimate distances to birds closer to the transect); (3) 10-m grouping = 10-m intervals to 60 m, 15-m intervals to 90 m, and 30-m intervals beyond; (4) 15-m grouping =15-m intervals to 90 m and 30-m intervals beyond; (5) 20-m grouping = 20-m intervals throughout; (6) 25-m grouping = 25-m intervals throughout; (7) 30-m grouping = 30-m intervals throughout; and (8) 45-m grouping = 45-m intervals throughout. The performance of each estimator and each grouping procedure was judged by the percent error (E) of the transect estimate of density (T) in relation to the density estimate from spot mapping (M):

$$E = \frac{100(M - T)}{M}$$

Most of the analysis used the absolute value of the percent error; when otherwise, we refer to overestimation and underestimation. Our measure of error may, itself, be erroneous, because we have assumed that density estimates from spot mapping were reasonably accurate.

Transect data were analyzed separately for Observer I and Observer II. In addition, the data from both observers were pooled (referred to hereafter as Observers I + II) and rerun as though they were from a third observer, even though the data set was not independent from that of either observer singly. Because the distribution detection functions in the pooled data set were different from those of the observers separately, and the sample size was nearly double in each case, results from the pooled data were not merely means of the separate data sets.

Because skewed distributions often limited determination of statistically significant differences among sets of density estimates, we sometimes used ranks and summed ranks to help identify the best estimator or grouping procedure. Statistical tests have been identified as used, and an arbitrary alpha level of 0.05 was chosen for statistical significance.

RESULTS

FIELD TIME

The mean time taken to complete a visit to a mapping grid was 312 min, pooling across observers, sites, and months. This expands to 3,120 min (52 hr) of field time to complete the 10 visits used in this study (or 158 min per ha, a measure of effort that could be compared with other mapping studies). Observer II averaged 19 min longer per visit than Observer I ($0.05 > P > 0.02$; Wilcoxon's signed-ranks test of a pairwise comparison of observers by site and month). The average visit of 322 min on the ungrazed site was not significantly longer than that of 301 min on the grazed site (Wilcoxon's signed-ranks test; $0.10 > P > 0.05$). Finally, visits by each observer on each site were longest in April or May and shortest in June. Thirteen of 24 month-by-month comparisons were significantly different (using pairwise t-tests with the Bonferroni adjustment for multiple comparisons).

The mean time taken to complete 660-m transects on the mapping grids was 39 min, pooling

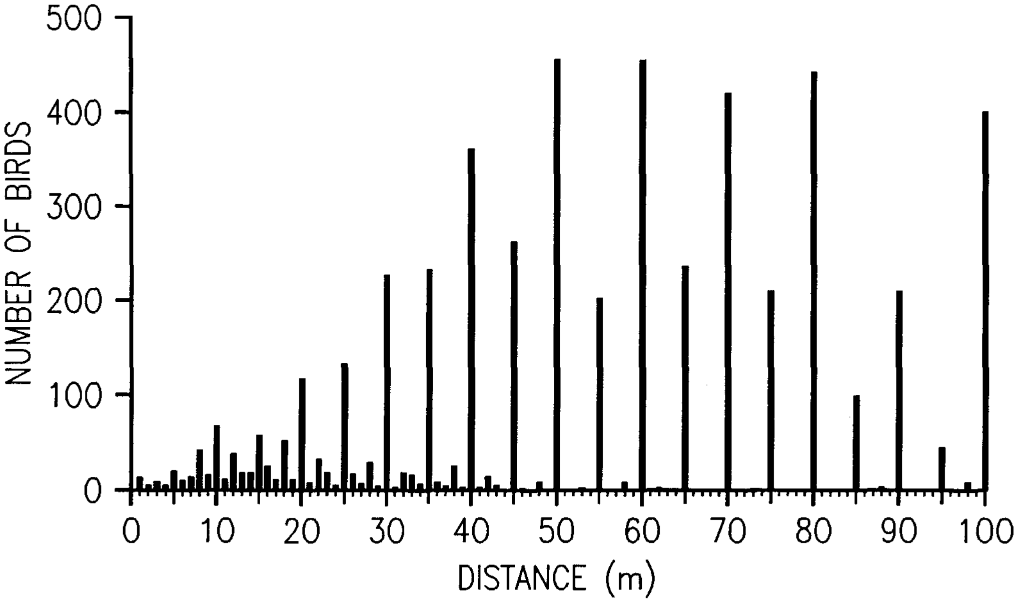


FIGURE 1. Histogram of detection distances as estimated in the field, showing typical heaping of estimates at 5- and 10-m increments (data pooled across three observers and all species, unadjusted for differences in the areas of bands at different distances from the counting point—Verner, unpubl. data). Data were taken in oak-pine woodlands at SJER during April 1985, using 5-min point counts at 210 counting stations that were sampled once each by all three observers. These data suggest that an observer's confidence in discriminating even 5-m intervals began to yield to 10-m intervals at about 40 m. The increasing height of spikes from 0 to about 50 m reflects use of the point-counting method, because the area sampled in any band of equal width increases with the square of the distance from the observer.

across observers, sites, and months. This expands to 59 min for a 1-km transect (a common standard length) in a comparable habitat, so an observer could complete 53 such transects in the time needed to complete the fieldwork for one spot-mapping effort. Although transect time did not differ significantly between observers, it did between sites (Wilcoxon's signed-ranks test; $0.05 > P > 0.02$) and between all pairwise comparisons of months except April vs. May on the ungrazed site for one observer (*t*-tests with Bonferroni adjustments). As with visits, the mean time taken to complete a transect was greatest in April or May and least in June.

DISTANCE DETECTION FUNCTION

Measuring distances to birds recorded on spot maps eliminated the usual sort of heaping characteristic of estimated distances recorded in the field (Fig. 1) but gave distance estimates characterized by a different sort of heaping (Fig. 2). The "canyons" in the plotted distance histogram corresponded to the 30-m grid intervals on maps of the plots. The plots were distinctly bimodal within each 30-m interval—peaks between 5 and 10 m on either side of the canyons, and a valley at about 15 m.

ESTIMATOR

EXPOL was consistently the best estimator. Among all combinations of observers, species, sites, and procedures, 768 comparisons were made. EXPOL was best (i.e., gave the smallest percent error) in 74% of the cases, POWER was best in 14%, and FOSER was best in 12%. Even when subsets of the data (sites, species, observers, and grouping procedures) were considered separately, EXPOL most often gave the best estimate (Table 1). Moreover, means of the percent error were best for EXPOL in 44 of 48 comparisons and standard deviations were best in 21 of 48 comparisons (Table 2).

Because each estimator depends on a different underlying distribution of detection distances, we sought reliable ways to predict which estimator would give the best density estimate for any given data set. To do this, we selected nine examples from each observer (I, II, and I + II pooled) to

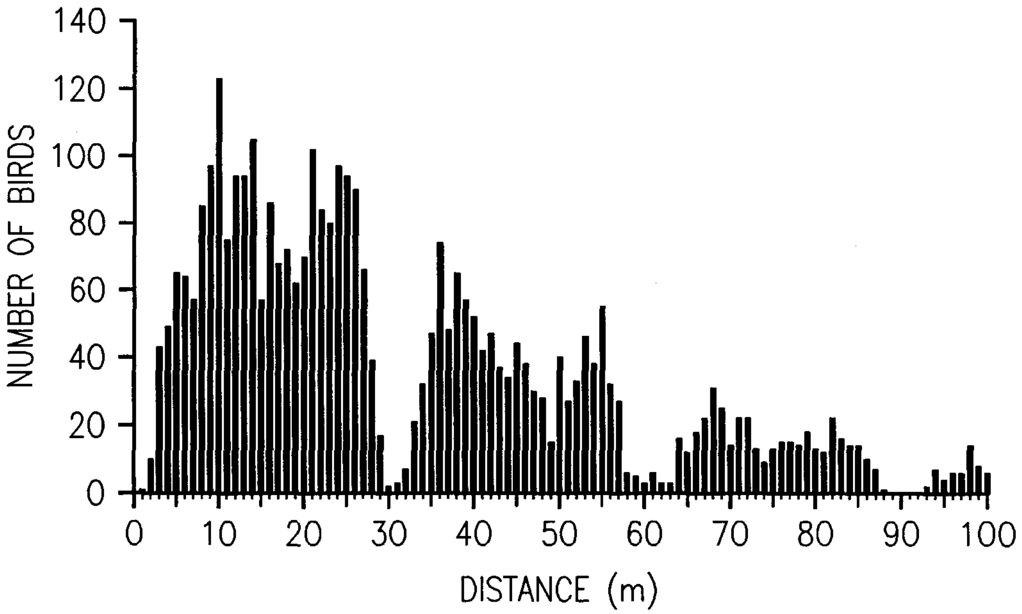


FIGURE 2. Histogram of detection distances as measured from spot maps for this study. The canyons at 30-m intervals correspond to grid lines on the maps.

demonstrate three detection functions for each estimator; the criterion for selection was that the error for the given estimator was less than half that for one of the other two estimators. When visual inspection of these examples failed to suggest reliable ways to use the distribution of detection distances for selecting an appropriate estimator, a priori, we randomly selected (stratified across observers and sites) an additional 36 examples for further study. These samples also failed to provide reliable clues for choosing an appropriate estimator. Examples were found for which each estimator performed best with distributions that peaked in the first (Fig. 3A), second (Fig. 3B), and third (Fig. 3C) grouping interval and then generally decreased with increasing distance from the observer.

EXPOL gave the smallest error for most distribution functions with a distinct peak only in the third grouping interval (Fig. 3C). Furthermore, distributions that tended to be "messy" in the sense that they lacked a generally smooth ascent to a peak, followed by a decline to zero (i.e., bimodal, trimodal, etc.), were most often fit best by EXPOL and never by FOSER (Fig. 3D). All histograms depicted in Figure 3 were sent to K. P. Burnham for recommendations on appropriate truncation and the number of terms to use for FOSER. New density estimates based on those recommendations had no measurable effect on results. Mean errors by each estimator were identical before and after we followed the recommendations, and the performance of EXPOL improved relative to FOSER, but not significantly so. Because of these results, and the fact that EXPOL gave better estimates six times more often than FOSER and five times more often than POWER, only EXPOL estimates of density have been used for the transect data in the remainder of this analysis (see Appendix).

GROUPING PROCEDURES

Although certain grouping procedures consistently proved to be poor, determination of a single "best" procedure was clouded by differences between species. Several exploratory approaches were used to investigate this question. The 45-m grouping interval was eliminated initially, because (1) it resulted in too few groups (e.g., see Burnham et al. 1980); (2) it gave the greatest overall mean error (38.6%); (3) it had the greatest (three cases) or next-to-greatest (three cases) mean error in the six combinations of site with observer, and the largest SD in all six cases; and (4) it had the largest maximum error in all six cases. Analysis of the six remaining grouping procedures, by species, revealed only one significant difference among 180 pairwise compari-

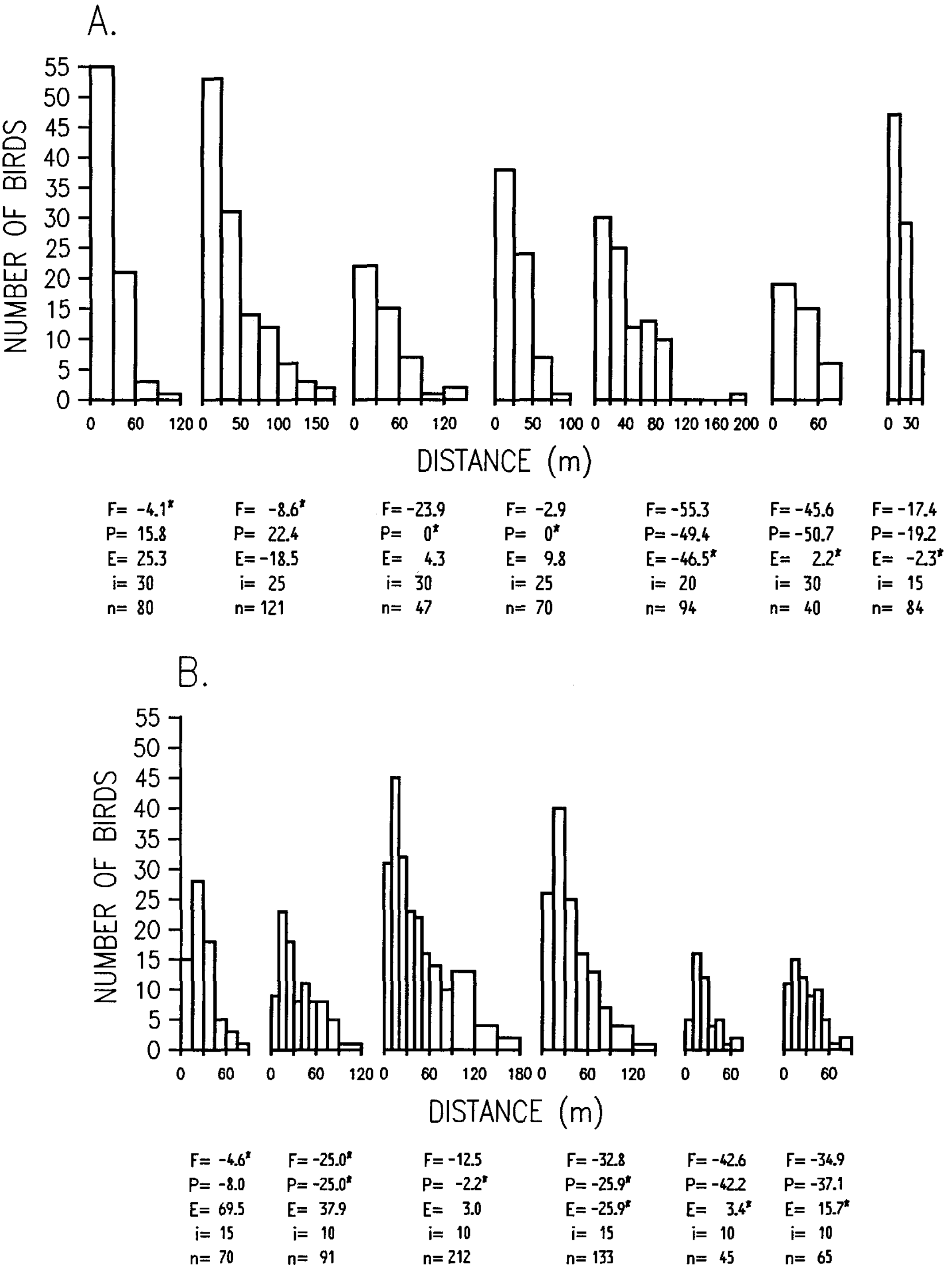
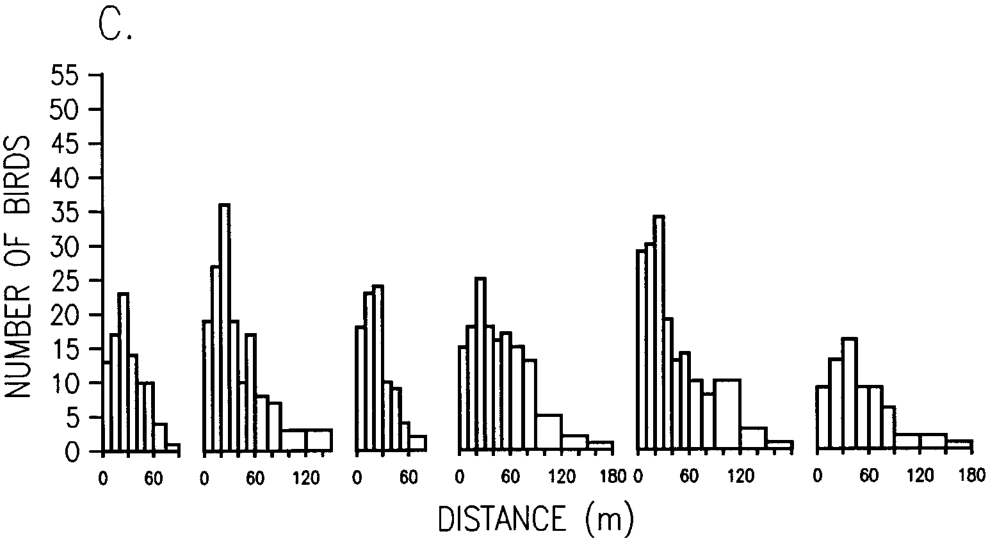
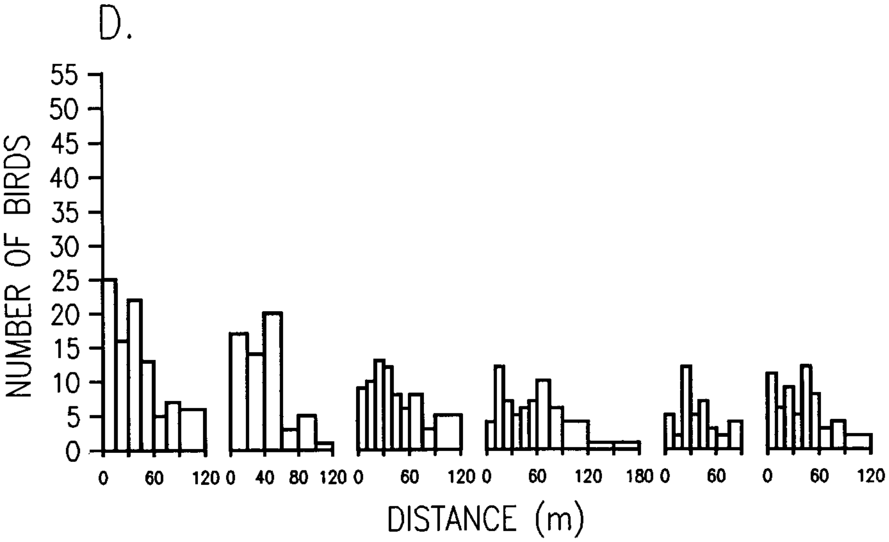


FIGURE 3. Histograms of detection distances for individual cases (A shows histograms with a distinct peak count in the first interval only; B shows those with a distinct peak in the second interval only; C shows histograms with a distinct peak in the third interval only; and D shows messy histograms—those with two or more peaks,



F= 0*	F= -20.9*	F= -13.1	F= -49.7	F= -18.4	F= -60.1
P= -10.1	P= -21.8	P= -10.9*	P= -52.8	P= -7.2	P= -60.5
E= 76.3	E= -25.5	E= 33.9	E= -17.5*	E= -1.9*	E= -33.6*
i= 10	i= 10	i= 10	i= 10	i= 10	i= 15
n= 92	n= 149	n= 90	n= 145	n= 171	n= 67



F= -2.4*	F= -65.0	F= -49.6	F= -48.3	F= -47.1	F= -64.3
P= -2.4*	P= -66.4	P= -52.7	P= -50.0	P= -50.0	P= -65.7
E= 6.2	E= -36.4*	E= -14.7*	E= -12.1*	E= -2.9*	E= -34.4*
i= 15	i= 20	i= 10	i= 10	i= 10	i= 10
n= 94	n= 60	n= 74	n= 63	n= 40	n= 60

none of which is conspicuously dominant). The percent error for each case is designated by F (FOSER estimator), P (POWER estimator), and E (EXPOL estimator); i = grouping interval in meters; n = number of birds detected. The * designates the best estimator (smallest error) in each case.

TABLE 1. Number of cases in which FOSER, POWER, and EXPOL gave the best density estimate for different subsets of the data.

Subsets of data		n	Estimators		
			FOSER	POWER	EXPOL
Site	Grazed	360	67	68	235[1]
	Ungrazed	408	28	44	347
Observer	I	256	36	37	186
	II	256	38	32	194
	I + II	256	21	43	202
Species[2]	SCJA	192	31	35	131
	PLTI	192	12	22	158
	ATFL	144	7	20	124
	BUSH	144	36	19	92
	BRTO	48	8	12	30
	BEWR	48	2	3	45
Grouping procedure	Ungrouped	96	8	18	71
	5-m bands	96	10	16	74
	10-m bands	96	14	16	69
	15-m bands	96	11	11	76
	20-m bands	96	11	12	76
	25-m bands	96	11	15	73
	30-m bands	96	9	15	73
	45-m bands	96	22	9	70

[1] Numbers in the last three columns may sum to more than the value in the n column, because occasional ties were awarded equally to each estimator involved.

[2] Species codes are: ATFL = Ash-throated Flycatcher, SCJA = Scrub Jay, PLTI = Plain Titmouse, BUSH = Bushtit, BEWR = Bewick's Wren, and BRTO = Brown Towhee.

sons of the mean error (Table 3). It also failed to show much consistency among species as to which grouping procedure was best, although the 30-m interval was best in more cases (four of 12) than any other procedure, and the ungrouped data were poorest or next poorest in eight of 12 cases (Table 3).

In the absence of significant differences among the performances of the different grouping procedures, 14 alternatives were explored as options for minimizing the mean error given by EXPOL, as follows: *Alternative 1*—ungrouped data; *Alternative 2*—5-m grouping; *Alternative 3*—10-m grouping; *Alternative 4*—15-m grouping; *Alternative 5*—20-m grouping; *Alternative 6*—25-m grouping; *Alternative 7*—30-m grouping; *Alternative 8*—means of the 5- to 30-m groups; *Alternative 9*—means of the 10- to 30-m groups; *Alternative 10*—means of the 10- to 25-m groups; *Alternative 11*—the highest density estimate from

TABLE 2. Number of cases in which FOSER, POWER, and EXPOL gave the best means and the lowest standard deviations.

Site	Observer	Parameter	Estimators		
			FOSER	POWER	EXPOL
Grazed	I	$\bar{x}$	0	1	7
		SD	1	3	4
	II	$\bar{x}$	1	0	7
		SD	6	0	2
	I + II	$\bar{x}$	1	0	7
		SD	2	0	6
Ungrazed	I	$\bar{x}$	0	0	8
		SD	5	1	2
	II	$\bar{x}$	0	0	8
		SD	3	3	2
	I + II	$\bar{x}$	0	1	7
		SD	3	0	5

TABLE 3. Mean percent errors (2 SE shown below in parentheses) between mapping estimates and EXPOL estimates of density for different species, by observer and grouping interval. Species codes are as in Table 1. Sample size (*n*) is the number of cases with at least 40 individual records for a given species.

			Ungrouped	Grouped data, by interval (m)					
Observer	Species	*n*	data	5	10	15	20	25	30
I	ATFL	4	50.0	36.0	36.5	36.2	42.9	44.3	36.5
			(10.3)	(18.4)	(18.2)	(18.4)	(4.7)	(7.2)	(18.4)
II		3	29.4	30.4	40.0	40.3	40.0	20.3	32.9
			(13.2)	(39.5)	(38.5)	(41.0)	(34.3)	(28.9)	(39.3)
I + II		6	41.7	37.3	35.5	32.4	36.8	39.7	35.7
			(14.5)	(13.1)	(13.6)	(10.5)	(12.0)	(12.7)	(9.1)
I	SCJA	8	24.7	20.7	22.5	19.7	18.2	16.5	15.0
			(12.7)	(3.9)	(7.4)	(3.5)	(3.5)	(4.7)	(3.5)
II		8	17.0	24.8	24.2	22.3	21.6	10.3	30.6
			(9.8)	(18.1)	(18.0)	(17.5)	(17.5)	(7.0)	(20.4)
I + II		8	23.9	17.3	17.4	16.8	18.4	14.9	11.7
			(11.5)	(8.2)	(8.7)	(7.6)	(8.4)	(3.7)	(5.5)
I	PLTI	7	45.7	39.5	39.5	37.2	38.7	35.9	41.9
			(6.6)	(17.3)	(17.1)	(19.1)	(16.9)	(17.7)	(14.7)
II		6	31.6	29.9	15.3	21.7	38.8	27.7	26.4
			(4.9)	(32.7)	(10.4)	(10.2)	(27.8)	(9.6)	(10.7)
I + II		8	43.4	36.1	37.9	41.1	43.4	47.2	45.2
			(10.6)	(10.6)	(13.2)	(12.3)	(12.4)	(14.7)	(12.9)
I	BUSH	4	48.0	51.0	54.0	53.2	43.0	25.8	23.8
			(39.3)	(33.4)	(27.8)	(7.8)	(21.4)	(23.0)	(14.3)
II		3	29.1	28.3	10.6	9.0	10.4	34.0	16.9
			(33.6)	(23.7)	(12.2)	(13.9)	(9.8)	(15.7)	(6.9)
I + II		6	30.1	17.5	20.0	22.0	34.1	13.8	12.4
			(25.6)	(12.8)	(8.0)	(9.9)	(8.5)	(8.8)	(7.4)

all the grouped data sets. (This criterion was based on the observation that 75% of all estimates from the grouped data sets were lower than corresponding estimates from spot mapping.) *Alternative 12* used the highest density estimate from all the grouped data sets, but when it was a conspicuous outlier compared to the remaining grouped data sets it was rejected in favor of the next-highest estimate. (A conspicuous outlier was any "highest estimate" that exceeded the mean of the five remaining estimates by 25%.) *Alternative 13* also used the highest-estimate criterion, but when it was a conspicuous outlier it was rejected in favor of the mean of the five remaining estimates. Any of the above alternatives could be applied to any data set suitable for use with program TRANSECT, without the option of comparing results with those from spot mapping.

Alternative 14 required comparison with density estimates from spot mapping. It used the "best" grouping procedure (ungrouped data or any of the grouped data sets) for each species, as determined by ranking errors among all grouping procedures. Although the ranks summed across species and sites suggested that the 25- and 30-m grouping intervals were best overall (sums of ranks in Table 4), the picture was not so clear when species were considered separately. Because within species the best grouping interval varied by month, observer, or site, ranks were summed across all samples for each species. These showed that one of the grouped-data procedures was better than ungrouped data for all species, as with mean errors (Table 3). However, the 5- and 15-m intervals tied for best for Ash-throated Flycatchers, the 25-m interval was best for Scrub Jays, the 10-m interval was best for Plain Titmice, and the 30-m interval was best for Bushtits, Bewick's Wrens, and Brown Towhees. In an alternative ranking procedure, samples for each species were scored 3 points for the best estimate, 2 points for the second best, and 1 point for the third best, and these scores were totaled for each grouping procedure. In this case, the 15-m interval was best for the Ash-throated Flycatcher, and all other species had the same best grouping

TABLE 4. Mean ranks of percent errors in EXPOL density estimates (smallest error = 1; largest = 7), as determined by various grouping procedures. Only samples with 40 or more detections were used; ties were averaged. Species codes are as in Table 1; *n* = the number of data sets available for estimating density.

Observer	Species	Site	*n*	Ungrouped data	Grouped data, by interval (m)					
					5	10	15	20	25	30
I	ATFL	Ungrazed	2	6	3	7	4.5	2	1	4.5
		Grazed	2	6	1.5	3	1.5	5	7	4
II		Ungrazed	1	3	1	6	7	4	5	2
		Grazed	2	3.5	3.5	5.5	2	5.5	1	7
I + II		Ungrazed	3	7	6	4	2	5	3	1
		Grazed	3	1	4	3	2	7	5.5	5.5
		Mean		4.4	3.1	4.8	3.1	4.8	3.8	4.0
I	SCJA	Ungrazed	4	4.5	7	6	4.5	3	2	1
		Grazed	4	7	5	4	6	3	2	1
II		Ungrazed	4	7	5	2	6	3.5	1	3.5
		Grazed	4	2	5	3	6.5	4	1	6.5
I + II		Ungrazed	4	7	4.5	6	3	4.5	1.5	1.5
		Grazed	4	6	5	2	1	3.5	7	3.5
		Mean		5.6	5.3	3.8	4.5	3.6	2.4	2.8
I	PLTI	Ungrazed	4	2	7	6	4	5	1	3
		Grazed	3	7	4	3	2	1	6	5
II		Ungrazed	2	6	2	1	4	7	3	5
		Grazed	4	3	6	1	2	5	4	7
I + II		Ungrazed	4	3	1	4	7	5	6	2
		Grazed	4	3	5	2	1	4	6	7
		Mean		4.0	4.2	2.8	3.3	4.5	4.3	4.8
I	BUSH	Ungrazed	2	3	6	5	7	4	1	2
		Grazed	2	6	5	7	3	4	2	1
II		Ungrazed	2	6	7	3	4	1	5	2
		Grazed	1	5	4	2	1	3	7	6
I + II		Ungrazed	3	7	6	3	4	5	1	2
		Grazed	3	2	1	4.5	4.5	7	6	3
		Mean		4.8	4.8	4.1	3.9	4.0	3.7	2.7
I + II	BEWR	Ungrazed	1	4	6	2	6	3	6	1
I + II	BRTO	Ungrazed	1	7	6	5	4	3	2	1
		Grazed	1	1	6	6	6	4	2.5	2.5
		Mean		4.0	6.0	5.5	5.0	3.5	2.3	1.8
Sums of ranks				125.0	122.5	106.0	105.5	111.0	95.5	90.5

interval suggested by the previous ranking. Because results of this second ranking procedure were the same as the first, except that no tie occurred for the Ash-throated Flycatcher, the grouping intervals indicated as best for each species were used in *Alternative 14*.

The five best alternatives, arranged in increasing order of overall mean error, were:

1. *Alternative 14*—Ranked first in three of the six observer-by-site combinations; mean rank = 2.9; overall mean error = 23.0%.
2. *Alternative 13*—First in one of the six observer-by-site combinations; mean rank = 4.0; overall mean error = 24.4%.
3. *Alternative 12*—Second in one of the six observer-by-site combinations; mean rank = 4.5; overall mean error = 25.5%.
4. *Alternative 6* (25-m intervals)—First in one of the six observer-by-site combinations; mean rank = 6.8; overall mean error = 26.4%.
5. *Alternative 7* (30-m intervals)—Second in two of the six observer-by-site combinations; mean rank = 6.8; overall mean error = 27.2%.

The poorest performances were by *Alternative 1* (ungrouped data—fourteenth in three of the six observer-by-site combinations; mean rank = 10.9; overall mean error = 33.4%) and *Alternative 5* (20-m grouping intervals – thirteenth in

TABLE 5. Mean percent errors (SD; *n*) of over- and underestimates of density by EXPOL.

Site		Observers		
		I	II	I + II
Grazed	Overestimates	22.5 (14.0; 4)	19.0 (22.9; 8)	11.1 (4.9; 6)*
	Underestimates	21.6 (13.5; 7)	15.8 (13.4; 3)	23.4 (12.9; 9)*
Ungrazed	Overestimates	3.2 (0; 1)	11.2 (8.4; 3)	12.5 (12.3; 2)
	Underestimates	36.7 (19.5; 11)	18.8 (18.9; 6)	32.9 (17.3; 14)

* Significantly different: $t = 2.21$; $0.05 > P > 0.02$.

three of the six observer-by-site combinations; mean rank = 11.5; overall mean error = 31.0%). Because *Alternative 14* gave the best results both by ranking and mean error criteria, all further analyses reported here used this alternative.

AGREEMENT BETWEEN TRANSECT AND MAPPING ESTIMATES

The transect data more often underestimated than overestimated density relative to the spot-mapping data. Observer I had 18 underestimates and only five overestimates ($P = 0.011$, two-tailed binomial test—Siegel 1956), Observer II had nine underestimates and 11 overestimates ($P = 0.824$), and Observers I + II pooled had 23 underestimates and eight overestimates ($P = 0.011$). The mean error of all underestimates combined for Observers I, II, and I + II pooled was 27.9% ($n = 50$; SD = 17.3) and that of all overestimates was 15.4% ($n = 24$; SD = 15.2). The difference was significant ($t = 2.952$; $0.01 > P > 0.001$). The mean of overestimates ranged from 3.2% for Observer I on the ungrazed site to 22.5% for Observer I on the grazed site, and the mean of underestimates ranged from 15.8% for Observer II on the grazed site to 36.7% for Observer I on the ungrazed site (Table 5).

OBSERVER VARIABILITY

Observer I detected more birds (1,910) than Observer II (1,744), but fewer were near birds. Within 25 m and 50 m, respectively, Observer I detected 896 (47.1%) and 1,371 (72.1%) birds, and Observer II detected 938 (53.6%) and 1,438 (82.5%). Observer I detected 107 birds beyond 100 m, but Observer II detected only 13 beyond that distance. The mean absolute error of EXPOL estimates for Observer I was 28.2% (SD = 18.24; range = 2.3% to 67.9%; $n = 23$); for Observer II it was 17.3% (SD = 17.91; range = 0.7% to 69.5%; $n = 20$); and for Observers I + II pooled it was 24.6% (SD = 16.18; range = 0.9% to 70.8%; $n = 31$). None of these means was significantly different from another, although the difference between Observer I and Observer II had a low probability ($t = 1.97$, $P = 0.056$). Similarly, Observer II had better density estimates than Observer I in 14 of 19 cases ($P = 0.063$; binomial test) and better than Observers I + II pooled in 14 of 20 cases ($P = 0.115$). Observer I + II pooled had better estimates than Observer I in 15 of 23 cases ($P = 0.210$).

HABITAT EFFECTS

The general tendency for transect results to underestimate densities relative to mapping estimates was more pronounced for the ungrazed than the grazed site. Pairwise comparisons of transect estimates were made by matching values between sites for the same observer, species, and month. Observer I had 10 estimates on the ungrazed site that were relatively lower than the matching estimates on the grazed site and only one on the grazed site that was relatively lower than its matching estimate on the ungrazed site; Observer II had eight lower on the ungrazed and none lower on the grazed site; and Observers I + II pooled had 12 lower on the ungrazed and two on the grazed site. The respective probabilities of these ratios were 0.012, 0.008, and 0.013 (binomial test).

SAMPLE SIZE NEEDED

Both the overestimates and underestimates showed trends toward smaller errors with increasing sample size (Fig. 4) for the combined data from Observers I and II. A regression of the absolute values of these errors on the number of observations was significant ($y = 73.1 - 0.582x$; $0.01 > P > 0.001$; $r = 0.39$). Some data sets with 40 or fewer records produced density estimates with relatively small errors, say <20%, but this was usually not true. Even in cases with 60 records, errors sometimes exceeded 50%. On the other hand, the largest error for any sample with

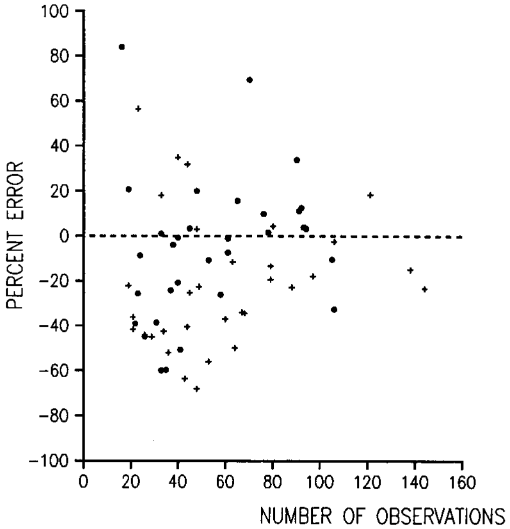


FIGURE 4. Scatter plot of percent error in EXPOL estimates of density as a function of the number of birds detected in each case by Observer I (plus signs) and Observer II (dots). The hiatus from zero to 16 detections resulted from our elimination of samples in that size range (see text for explanation).

80 or more records was 23.2% ($n = 144$) for Observer I and 33.9% ($n = 90$) for Observer II.

EXPOL density estimates using the pooled data from both observers did not give a significant regression between sample size and the absolute values of the percentage errors (Fig. 5), in spite of the fact that sample sizes for each species were much larger for the pooled data set than for either observer singly. In the case of the pooled data, in fact, bias was greater for a given sample size than it was for the separate data sets of Observers I and II.

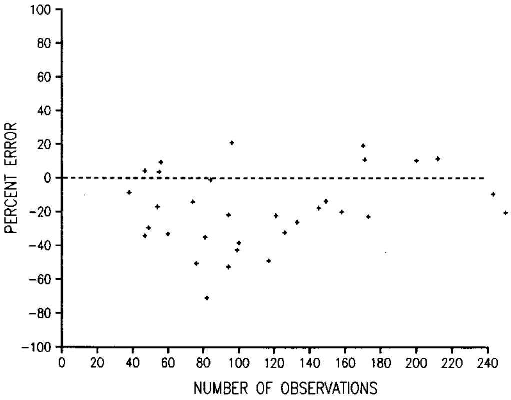


FIGURE 5. Scatter plot of percent error in EXPOL estimates of density as a function of the number of birds detected in each case for the pooled results of Observers I and II. The hiatus from zero to 38 detections resulted from our elimination of samples in that size range (see text for explanation).

DISCUSSION

DISTANCE DETECTION FUNCTION

Although distances measured from mapped locations of birds avoided the "heaping" of distances at 5- and 10-m increments typically seen when observers estimate distances in the field, the mapping approach may not be an improvement. To be legible on field maps, records of birds could not be written on map lines representing grid lines. They had to be displaced to one side of the line or the other, even if the bird was on or very near the line. If a bird record was circled to indicate a singing male (a standard symbol for spot mapping, Anon. 1970), this further displaced the mapped location from its correct place. (This effect appears to be shown in Figure 2 by the bimodal tendency of the data within each 30-m interval.) The result was a series of canyons in the distance detection function at intervals corresponding to those separating grid lines on the map. The sides of these canyons appeared to extend to about 5 m on either side of the grid line (a neatly written, lower-case letter was about 5 m wide in our map units).

Mapped distances, as used in this study, were probably no better than distances estimated in the field. Indeed they may have been worse. However, we believe an approach similar to this is worth further study. For example, one could use unmarked acetate or similar overlays on field maps, so birds' locations could be indicated directly on grid lines, when appropriate. Alternatively, one could use a colored pencil to locate a bird precisely on the map with a small dot, placing explanatory symbols to the side.

ESTIMATOR

The demonstration here that EXPOL was the best estimator supports our choice of it, in lieu of others available in program TRANSECT, for an earlier study (Verner and Ritter 1985). Our choice was based on two factors: (1) EXPOL is the most robust to movement (Burnham et al. 1980); and (2) because our EXPOL estimates were higher than those by all other estimators compared, they were probably closer to spot-mapping estimates than the others.

We failed to discern many patterns in the distance detection functions of individual data sets that could be used to choose estimators, on an ad hoc basis, to reduce error. Furthermore, fine tuning of the analyses suggested by K. P. Burnham for data shown in Figure 3 failed to change the actual or relative performance of any estimator. This is empirical confirmation of the conclusion of Burnham et al. (1980:177): "Even with sample sizes of 100, one has difficulty in inferring the true underlying detection function. . . . The numbers and sizes of the groups can make the data appear markedly different. . . . Even movement away from the line may be suspected . . . when, in fact, no movement occurred. Those results support the need for robust estimation methods that are not dependent on subjective examination of the data."

Because several studies have found a majority of transect estimates of density to be lower than mapping estimates (see review by Verner 1985: 280–282), and the latter are generally regarded as more accurate (although themselves probably negatively biased, e.g., see Jensen 1974), a reasonable alternative for users of program TRANSECT would be to apply more than one estimator (at least FOSER and EXPOL) and use results from the one giving the highest density estimate in most cases. Such an approach would probably reduce overall bias, but it may not be preferable if the objective is to improve precision, as opposed to accuracy. On the basis of our results, and the robustness of EXPOL to movement (Burnham et al. 1980), we suspect that EXPOL will prove to be the best estimator for most community-level studies. Users should also be mindful, however, of the conclusion by Burnham et al. (1980:21) that "if the subject of the study is a highly mobile animal (such as a passerine bird), serious problems due to movement can arise, often to the extent of rendering line transect sampling useless for such species."

GROUPING PROCEDURES

The generally poor performance of the ungrouped data compared with data grouped by some interval was probably related to the canyon effect in the distribution of distances as measured from field maps, and to observer errors in assigning map locations to birds detected in the field (see Burnham et al. 1980:49, 66, 103, 132–133). Although the use of ungrouped data is normally the method of choice, instances occur when analyses of grouped data are more appropriate (Burnham et al., 1980:103). In fact, in our opinion, grouping will probably give better results in most or all cases involving song birds, because (1) it can overcome some of the effects of bird movement in response to an observer, before detection, and (2) it can mask many errors in distance estimation, especially those resulting when observers heap distance estimates at increments of 5 or 10 m (see Hobson, 1976).

The 45-m grouping interval probably performed poorly because it gave too few intervals for model sensitivity—93% of Observer I's observations and 99% of Observer II's were within 90 m, or two 45-m intervals. As Burnham et al. (1980:103) point out, the grouping of data is an arbitrary matter, with results depending to an extent on the number of groups and the counts within them. This is especially true with small samples (e.g., $n = 25$ to 40 individual records) or when only two or three groups are used. In our case, even with 30-m grouping intervals, most records were included in the first three intervals, so the better performance of the 30-m groups in so many cases was unexpected. We suspect that it related to the fact that grid lines were 30 m apart, so the canyons in the distance distribution were exactly 30 m apart. The relatively good performance of the 15-m grouping interval was probably also related to its being in phase with the 30-m separation between canyons. Intervals of 10 m might perform well too, for the same reason, although across each plateau they would have two intervals including one side of a canyon and one without any canyon influence. In our case, however, the 10-m grouping interval was not a uniform one (10-m intervals to 60 m, 15-m intervals from 60 to 90 m, and 30-m intervals beyond that). The effect of this asymmetry relative to uniform intervals (in this study, all intervals of 20 m and larger) was not ascertained.

Because the 20- and 25-m grouping intervals were out of phase with respect to the canyons, they might be expected to perform less well than other grouping intervals. Although this was true for the 20-m interval, the 25-m interval was among the best procedures tried. We believe the 20-m grouping interval would perform better with field-recorded distance estimates than it did in this study, because it would accommodate estimates heaped at 5- and 10-m distances and because it should give counts in at least five intervals for most data sets. Reasons for the good performance of the 25-m interval are not clear. However, it was enough in phase with the 30-m intervals between canyons that each 25-m interval included one canyon out to the point at which too few birds were detected to have any influence on the density estimate. The 25-m interval was also large enough to mask many bird movements and many observer errors in distance estimation, but it was small enough to give five or more groups for most species.

The choice of a "best" grouping interval did not clearly emerge from our analysis. Indeed, when using the best as defined for each species for some of our analyses (*Alternative 14*), we verged on committing a Type III statistical error—selecting a model because it fit the data best, as opposed to *a priori* selection of a model and evaluating how well the data fit that. Although our approach gave us certain insights about EXPOL and its application to line transect data for birds (e.g., the best interval differed among species), it did not lead to a supportable recommendation of an appropriate grouping interval for future studies in habitats like those we studied. Nor can our results be used to recommend an appropriate grouping procedure for all habitats. Although this may be an unattainable goal, we believe it is worth further study along lines similar to those taken here. In lieu of mapping data for comparative purposes, *Alternatives 12* and *13* are worth considering. Both take advantage of the fact that most transect estimates are low relative to mapping estimates of density, and both adjust for occasional high outliers. Even with these, however, mean error rates exceeded 25%, and maximum errors were 83.2% and 102.3%, respectively.

Errors of this magnitude are sufficient to mask substantial changes in abundance from year to year in the same area, or differences in abundance between areas in the same year. If the errors were consistent in direction and magnitude, this might not be a problem for comparative studies. The unsettling fact is, however, that one cannot know without some standard for comparison, such as mapping estimates, which estimate of any given species is in error, or by how much, or in which direction. This situation severely challenges our ability to measure real differences in bird abundances by estimating densities from transects or point counts (estimation of density from point counts depends on many of the same assumptions as transects, especially that no bias is introduced by movement of birds).

SAMPLE SIZE NEEDED

Without providing a clear empirical or theoretical basis for their recommendations, Burnham et al. (1980:35) stated that "as a practical minimum, studies should be designed to assure that at least 40 total objects ($n \geq 40$) are detected; it might be preferable, if the total length (L) of the survey were sufficient, to allow the location of at least 60–80 objects." In relation to analysis of grouped data, which tends to be less efficient than analysis of ungrouped data, they stated that "there may be little, if any, loss of efficiency when analyzing grouped data if the number of groups is at least six and the sample size is large (say, greater than 60)" (Burnham et al. 1980:79).

Because precision (Verner and Ritter 1985) and accuracy (this study) both showed continued improvement even with samples of 80 and more records per species, use of program TRANSECT to estimate densities of birds with smaller samples from the habitats we studied would be imprudent. A sample of fewer than 80 detections might be safe for studies that satisfy assumptions of the models, but such studies involving birds are not typical. Indeed, this is an indictment of this study, because we based many of our observations on samples with as few as 40 detections. We justify this decision on the grounds that most studies of birds that have used transect methods to estimate densities have done so with even fewer records. Our results, then, are probably representative of most such studies. A striking exception is the transect system used to monitor changes in bird populations in Finland (e.g., Järvinen and Väisänen 1981), a system involving hundreds of transects and very large numbers of records of many species.

Our efforts to find empirical guidelines for the minimum sample size needed (Verner and Ritter 1985; this study) gave no reason to be satisfied with samples of 40 detections and little reason to be satisfied with samples of 80. We believe a minimum sample of 100 detections is a more appropriate standard. This is not an unexpected result, however. The recommendations of Burnham et al. (1980) were intended for data sets that meet the assumptions of their models, which was not true in our study. For example, we did not detect all birds exactly on the transect line; many birds undoubtedly moved away from us before they were detected; we probably counted some birds more than once; we did not accurately determine all perpendicular distances from the line to birds detected; and not all detections were independent events. Probably most studies using transects to estimate the abundance of birds fail to meet these same assumptions.

Achieving a sample of 100 records is likely to be unattainable in most studies that attempt to estimate densities of birds, because the effort needed for uncommon species is prohibitive. In our case, even with more than 34 km of transect records, a sample of at least 100 was obtained in only 5.4% of the cases involving probable breeding species on the ungrazed site and in only 9.8% of those on the grazed site. Had our transect data included records obtained during the final walk around the perimeters of the grids, at the end of each visit, the transect effort would have been equivalent to 53 km. In that case, only species that averaged at least two records per kilometer would have met the criterion of at least 100 records. Simple pilot studies could easily be done to determine whether or not species of interest will give records at this rate, and, if not, spot mapping should be considered as a more economical way to obtain density estimates. Furthermore, any comparison of effort between transects and spot mapping should assume a mapping grid of sufficient size to give negligible bias from interpretation of territories that overlap grid boundaries (see Marchant 1981; Scherner 1981; Verner 1981, 1985).

OBSERVER VARIABILITY

Although comparisons of density estimates between Observers I and II were not significantly different, probability values for the two comparisons were low (0.056 and 0.063). We believe these differences were biologically significant, i.e., that Observer II generally estimated densities by transects more accurately than Observer I. This may have resulted from the facts that (1) a higher proportion of Observer II's detections were within 50 m of the transect line, and (2) Observer II estimated near distances more accurately than Observer I (unpubl. observ.). As Burnham et al. (1980:105) pointed out, accurate distance values near the line are more critical for density estimation than accurate values near the outer limit of detection.

Presumably differences in the distance detection functions of the two observers were responsible for the general lack of improvement in the pooled data set over that of either observer individually (e.g., compare Figs. 4 and 5), although why this might be true was not clear from visual inspection of distance histograms (Fig. 3). This problem needs further study, because an attractive way to increase sample size is by pooling results from two or more observers.

HABITAT EFFECTS

Most observers acknowledge that the detectability of birds is affected by vegetation structure. Gill (1980), for example, believed that some measured differences in the abundances of birds in a New Zealand forest may have resulted from seasonal differences in their visual and vocal conspicuousness. However, because (1) most detections are aural, and (2) methods of analysis are thought to compensate adequately for differences in detectability (e.g., see review by Shields 1979), the potential effects of habitat differences on estimates of bird density have apparently been largely ignored.

We believe the generally poorer performance of the transect method on the ungrazed plot in our study, compared with the grazed plot, was related to differences in the density and structure of shrubs on the two plots. The grazed plot had less than a third as much shrub cover as the ungrazed plot, although it had 16.8% cover by interior live oak, as opposed to only 7.2% on the ungrazed site (this tree commonly grows in a shrub-like form). The combined cover of shrubs and interior live oak was 22.4% on the grazed site compared with 29.0% on the ungrazed one. However, all shrubs and many of the interior live oaks had a conspicuous browse line only on the grazed site, enhancing visibility for an observer there. The ungrazed site was chosen because it was the only one known to us in the vicinity that had a long history of nondisturbance. The grazed site was selected from aerial photographs to have comparable canopy cover. Based on the general similarities in appearance of the two sites, we did not expect to find a consistently poorer performance of the transect method on the ungrazed site. Because observers generally tend to neglect the possibility of habitat-related bias in measures of bird abundance between sample areas, or between seasons on the

TABLE 6. Comparison of the mean percentages of over- and underestimated densities by line transect methods compared to spot-mapping estimates. In all cases, line transect estimates were based on total detections, not twice the number of singing males. The EMLEN estimator was based on Emlen (1971); the LINEAR, EXPONENTIAL, and NORMAL estimators were based on Järvinen and Väisänen (1975); and the EXPOL estimator used program TRANSECT (Laake et al. 1979). Values shown are $\bar{x}$ (SD; *n*).

Estimator	Overestimate	Underestimate	Source
EMLEN	16.0 (18.9; 6)	43.1 (34.7; 10)	Emlen 1971
EMLEN	none	83.7 (24.9; 21)	Emlen 1971
EMLEN	25.7 (24.9; 3)	42.0 (20.0; 23)	Emlen 1977
EMLEN	36.3 (37.3; 5)	52.0 (31.2; 24)	Franzreb 1976
EMLEN	44.8 (40.0; 11)	48.8 (27.6; 27)	Franzreb 1981
EMLEN	41.7 (–; 1)	48.4 (18.3; 11)	Dickson 1978
EMLEN	9.4 (–; 1)	41.6 (25.8; 6)	O'Meara 1981
EMLEN	13.9 (–; 1)	47.2 (25.4; 8)	O'Meara 1981
EMLEN	48.0 (–; 1)	43.4 (18.4; 10)	O'Meara 1981
LINEAR	21.4 (–; 1)	51.7 (25.2; 6)	O'Meara 1981
LINEAR	12.4 (6.8; 2)	48.1 (17.6; 7)	O'Meara 1981
LINEAR	none	46.5 (24.4; 11)	O'Meara 1981
LINEAR	90.7 (41.2; 18)	52.1 (27.8; 16)	Järvinen et al. 1978a
LINEAR	54.2 (47.3; 17)	63.6 (36.4; 23)	Järvinen et al. 1978b
LINEAR	none	46.7 (30.2; 8)	Hildén 1981
LINEAR	none	55.0 (17.9; 10)	Hildén 1981
EXPONENTIAL	15.6 (–; 1)	50.4 (31.2; 6)	O'Meara 1981
EXPONENTIAL	26.7 (4.5; 2)	40.9 (19.9; 7)	O'Meara 1981
EXPONENTIAL	29.3 (–; 1)	44.6 (25.5; 10)	O'Meara 1981
NORMAL	12.7 (–; 1)	54.9 (24.4; 6)	O'Meara 1981
NORMAL	9.9 (–; 1)	45.3 (23.3; 8)	O'Meara 1981
NORMAL	none	53.3 (22.5; 11)	O'Meara 1981
EXPOL (Observ. I)	18.6 (14.8; 5)	30.8 (18.6; 18)	This study
EXPOL (Observ. II)	16.8 (19.8; 11)	17.8 (16.4; 9)	This study
EXPOL (Observ. I + II)	11.4 (6.3; 8)	29.2 (16.1; 23)	This study

same area, this is a fruitful area for some careful research.

AGREEMENT BETWEEN TRANSECT AND MAPPING ESTIMATES

By comparison with published studies giving density estimates from spot-mapping and transect methods using all birds detected, results obtained with the EXPOL estimator in this study were markedly better. In general, transect methods have underestimated densities relative to spot mapping for most species (Table 6). Based on previously published studies reported in Table 6, mean underestimates ranged from 40.9% to 83.7% ($\bar{x}$ = 50.2%; *n* = 22) and mean overestimates ranged from 9.4% to 90.7% ($\bar{x}$ = 29.9%; *n* = 17). For each observer separately and both observers pooled, EXPOL results of this study (using *Alternative 14*) were better than the means of previous studies. In the case of the mean underestimates, all EXPOL results from this study were from 63% (Observer I) to 182% (Observer II) better than the means of previous studies (see Table 6). Indeed, the means of this study were from 33% (Observer I) to 130% (Observer II) better than the *best* result previously reported. In fact, all alternatives tried in this study gave better results than previous studies.

Among the most interesting (and promising) results of this study was the fact that EXPOL estimates converged on the spot-mapping estimates with increasing numbers of observations, both for underestimates and overestimates (Figs. 4 and 5). We believe this suggests a real coincidence between density estimates by these two methods. However, the percent error in EXPOL estimates did not get better than about 20%, even with 120 observations or more. This might mean (1) that EXPOL estimates in the bird community we studied may never get much better, (2) that the spot-mapping estimates are not so accurate as they have generally been considered to be by practitioners, or (3) a combination of these problems. We believe the last alternative is the correct one.

We are not optimistic about transect methods for estimating densities of most bird species in community-level investigations, because most studies produce too few observations of most species to allow the use of transect models. Without such estimates, one cannot compare abundances of all species—part of the bird community is ignored. As recommended by Emlen (1971), some observers have "borrowed" distance detection functions from common species judged to be "equally as detectable" as the uncommon ones, using the borrowed data to estimate densities of the uncommon species in their data sets. Others have used distance information from the same species recorded in different habitats where they were more common (e.g., Ralph 1985). When we tried the latter procedure, using only those species with counts large enough to independently estimate densities in both habitats, the borrowed estimates both overestimated ($\bar{x} =$ 115.7%) and underestimated ($\bar{x} =$ 79.1%) densities as calculated directly (Verner and Ritter 1985).

Other measures of abundance, e.g., total counts or frequencies, have their problems too, but at least one can obtain a value for all species. Spot mapping is an option if density estimates are required, but it can be prohibitively time consuming, it gives density estimates only for territorial species, and it is also subject to interpretational problems. Hopefully, most questions about avian communities that have heretofore used density estimates of questionable value can be addressed satisfactorily with standardized measures of relative abundance (Verner 1985).

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APPENDIX. Density estimates (birds/40 ha) by spot mapping and by the EXPOL estimator of Program TRANSECT (Laake et al. 1979), using data from ungrouped distance estimates and the same data grouped into distance intervals by 5-m increments (see text). Species codes are as for Table 1; sites are ungrazed (UN) and grazed (GR). The number of individual records of a species in a monthly transect sample is designated by *n*.

Observer	Species	Site	Month	Mapping data	Ungrouped data	*n*	Grouped data, by interval (m)						
							5	10	15	20	25	30	45
I	ATFL	UN	April	8.2	5.7	26	5.0	5.2	4.6	5.3	4.6	4.6	4.1
			May	17.8	6.8	44	10.7	10.5	10.6	10.6	10.9	10.6	10.2
			June	17.0	7.6	53	7.5	7.5	7.5	8.7	7.8	7.5	8.3
		GR	April	12.9	6.6	36	9.8	9.8	6.2	10.1	10.0	9.6	9.7
			May	17.4	9.9	63	15.4	15.3	15.4	9.7	9.5	15.4	14.9
			June	13.6	8.2	60	8.6	8.6	8.6	8.4	8.3	8.4	8.8
II		UN	April	8.2	6.0	23	6.0	6.0	6.1	5.8	6.0	5.8	6.9
			May	17.8	9.0	37	13.4	13.5	13.5	13.1	13.6	14.0	13.5
			June	17.0	9.1	41	13.5	8.5	8.4	9.0	8.7	12.4	13.3
		GR	April	12.9	8.2	38	12.3	12.2	12.4	12.0	7.7	12.2	8.5
			May	17.4	18.0	70	29.3	29.1	29.5	28.8	19.1	29.5	20.7
			June	13.6	8.4	40	13.3	13.2	13.5	12.6	13.3	13.9	15.1
I + II		UN	April	8.2	3.8	49	3.6	3.7	5.8	3.6	3.6	5.7	3.8
			May	17.8	7.9	81	11.5	11.5	11.6	11.4	11.9	11.7	11.2
			June	17.0	7.5	94	8.0	8.3	8.1	9.1	8.6	9.3	9.2
		GR	April	12.9	7.3	74	11.0	11.0	11.1	11.0	6.9	6.8	7.0
			May	17.4	15.4	133	13.1	14.3	12.9	12.8	15.3	14.4	15.6
			June	13.6	9.5	100	8.2	8.3	8.4	8.0	8.0	8.2	10.1
I	SCJA	UN	March	22.0	19.3	88	16.2	16.2	17.0	16.9	17.0	20.5	17.6
			April	29.7	9.8	97	22.8	23.2	22.8	25.4	24.4	23.8	27.4
			May	33.1	27.1	138	29.4	29.4	28.9	27.2	28.2	28.8	25.1
			June	39.6	32.9	144	28.9	57.7	29.4	30.5	30.4	32.1	28.5
		GR	March	21.1	15.9	79	16.6	17.3	17.6	19.0	18.3	18.2	16.4
			April	25.8	19.0	106	21.0	20.8	22.0	21.6	25.2	22.6	23.5
			May	20.7	15.6	79	16.0	16.1	15.6	15.7	16.7	16.1	13.5
			June	23.2	25.5	121	26.7	26.7	27.2	27.1	27.5	26.2	26.2
II		UN	March	22.0	18.8	61	30.7	30.4	30.6	30.2	20.4	19.1	20.3
			April	29.7	17.5	61	27.7	27.6	27.5	26.7	29.4	26.7	19.0
			May	33.1	27.7	105	26.5	27.1	26.8	27.9	29.6	28.0	39.0
			June	39.6	27.0	106	38.2	37.8	38.1	36.9	26.7	24.9	36.6
		GR	March	21.1	22.7	94	21.7	21.7	22.4	22.0	21.8	35.4	22.5
			April	25.8	26.4	93	23.1	23.6	22.4	23.3	26.8	23.0	33.1
			May	20.7	22.8	92	36.6	36.5	36.6	36.7	23.3	37.6	34.2
			June	23.2	20.3	91	32.1	32.0	20.3	20.5	20.6	21.2	31.6
I + II		UN	March	22.0	33.3	149	16.9	16.4	17.3	15.2	19.0	21.7	19.6
			April	29.7	19.3	158	20.0	20.6	20.1	21.4	23.8	21.8	26.1
			May	33.1	25.1	243	27.3	27.1	26.8	26.4	30.0	29.7	24.3
			June	39.6	24.9	250	26.7	25.7	27.8	27.9	31.6	32.5	27.5
		GR	March	21.1	23.2	173	18.6	18.7	19.3	16.0	16.3	19.2	19.3
			April	25.8	21.0	200	22.1	22.4	23.6	24.0	28.5	24.7	22.7
			May	20.7	23.2	171	20.0	20.3	20.3	20.3	23.0	23.1	19.8
			June	23.2	22.6	212	23.9	23.9	26.2	24.4	25.9	26.1	25.2
I	PLTI	UN	March	24.6	10.7	43	8.9	9.0	8.8	9.7	10.4	9.3	14.5
			April	31.2	11.1	48	10.1	10.0	10.2	10.6	12.2	10.7	13.1
			May	21.5	11.1	64	10.8	10.8	10.9	10.4	16.9	16.8	11.3
			June	20.4	15.0	49	15.5	15.8	18.4	15.6	18.1	25.7	16.2

APPENDIX. Continued.

				Map-ping data	Un-grouped data		Grouped data, by interval (m)						
Observer	Species	Site	Month			*n*	5	10	15	20	25	30	45
		GR	March	28.6	13.2	67	18.8	18.9	19.0	19.0	18.7	18.9	20.0
			April	25.3	11.7	68	16.6	16.6	16.5	16.8	10.5	10.5	16.9
			May	22.9	12.0	34	12.9	13.2	12.3	13.7	13.9	12.4	11.2
			June	22.1	25.7	80	22.7	23.1	22.4	21.6	20.6	27.7	35.5
II		UN	March	24.6	6.6	33	9.9	9.9	9.9	10.4	9.9	10.1	10.3
			April	31.2	8.2	35	12.6	12.6	12.6	12.6	13.7	12.2	9.9
			May	21.5	13.0	53	19.1	19.2	18.8	12.2	14.1	12.8	18.6
			June	20.4	13.4	45	21.3	21.1	13.9	13.7	22.0	16.5	14.3
		GR	March	28.6	18.2	78	29.2	29.1	29.3	28.9	17.8	30.2	28.0
			April	25.3	18.7	58	18.8	18.7	19.3	18.4	19.7	18.3	12.9
			May	22.9	17.2	65	16.7	26.5	17.5	17.0	17.0	17.0	25.0
			June	22.1	28.3	90	46.1	29.6	30.1	44.7	30.6	30.8	29.8
I + II		UN	March	24.6	13.5	76	12.2	12.2	12.2	7.3	7.0	12.4	12.5
			April	31.2	9.5	82	14.5	9.1	9.0	9.3	9.5	9.5	11.6
			May	21.5	11.7	117	11.4	11.0	11.0	11.4	10.9	11.2	11.4
			June	20.4	14.5	94	17.4	16.0	15.1	14.9	15.6	21.9	15.0
		GR	March	28.6	15.6	145	23.6	23.6	15.1	19.8	12.4	14.9	23.8
			April	25.3	11.1	126	17.2	17.2	17.4	17.2	11.0	10.4	11.3
			May	22.9	15.2	99	12.6	13.2	13.9	14.3	14.8	13.0	12.6
			June	22.1	27.2	170	28.5	26.4	25.3	29.2	25.4	30.2	37.6
I	BUSH	UN	March	38.1	30.2	45	20.9	29.3	20.3	30.5	31.9	28.5	61.0
			April	27.8	24.8	48	25.9	38.6	41.5	36.1	25.9	28.7	64.4
			June	15.9	11.8	33	11.3	12.1	17.4	11.4	16.6	18.8	10.4
		GR	March	18.9	16.8	21	16.8	16.1	17.8	10.5	14.5	12.1	32.9
			April	21.3	35.3	44	36.0	36.4	35.0	35.0	25.8	28.1	44.2
			June	13.7	26.7	40	25.1	25.1	20.9	21.6	21.8	18.5	12.9
II		UN	March	38.1	56.8	76	57.3	37.0	39.5	37.2	56.5	41.9	38.2
			April	27.8	34.5	48	34.6	34.1	34.1	33.2	33.7	33.4	56.9
			June	15.9	14.4	22	10.4	14.9	14.6	15.4	11.6	9.7	26.0
		GR	March	18.9	19.2	33	19.6	20.1	20.8	19.9	30.4	19.1	50.2
			April	21.3	18.3	40	19.2	22.6	21.2	19.3	28.2	16.9	54.9
			June	13.7	13.1	16	13.8	14.4	14.2	14.6	9.0	25.2	23.1
I + II		UN	March	38.1	71.5	121	27.9	29.1	29.2	24.9	29.9	29.7	29.9
			April	27.8	36.4	96	37.1	36.1	37.5	34.7	29.3	33.7	57.7
			June	15.9	10.3	55	10.5	11.3	10.6	10.3	16.8	16.5	9.8
		GR	March	18.9	22.9	54	18.6	16.0	16.0	12.5	14.2	15.7	42.7
			April	21.3	21.1	84	21.1	22.1	20.8	32.5	21.6	21.1	40.2
			June	13.7	13.1	56	14.8	16.2	16.8	16.9	17.0	15.0	40.2
I	BEWR	UN	May	8.2	4.2	19	4.1	6.3	4.4	4.0	6.2	6.4	6.7
			June	14.3	7.9	29	8.3	11.6	8.9	7.6	9.4	7.9	8.0
II			May	8.2	5.1	19	5.5	7.7	5.7	6.2	8.6	9.9	12.5
			June	14.3	8.6	31	8.5	8.5	8.5	8.4	8.7	8.8	8.1
I + II			May	8.2	4.2	38	5.0	4.3	6.8	4.9	5.8	7.5	6.7
			June	14.3	6.1	60	5.9	9.4	5.9	9.1	5.9	9.6	9.0
I	BRTO	UN	June	15.9	12.8	21	13.2	8.4	12.9	8.8	13.4	9.3	29.3
		GR	April	4.6	5.6	23	4.7	4.7	4.8	4.7	6.9	7.2	7.7
II		UN	June	15.9	6.0	26	5.8	5.8	7.3	7.8	8.4	8.8	5.2
		GR	April	4.6	4.1	24	4.1	5.8	5.9	5.9	6.0	4.2	5.8
I + II		UN	June	15.9	6.4	47	6.6	6.7	7.4	8.4	10.0	10.5	6.6
		GR	April	4.6	4.6	47	4.1	4.1	4.1	4.2	4.8	4.8	4.3