Wilson Bull., 95(3), 1983, pp. 453–459

On the relationship between breeding bird survey counts and estimates of male density in the Red-winged Blackbird.—The annual North American Breeding Bird Survey (BBS) developed in the United States in 1964 began in Canada in 1966 (Erskine, The first 10 years of the co-operative breeding bird survey in Canada, Can. Wildl. Serv., Rept. Ser. No. 42, 1978). The BBS is potentially valuable as an aid to research in population dynamics since surveys are conducted across the continent, are censused according to a standard methodology, and the same routes may be sampled annually over many years. Shortcomings of the survey, including sources of error, have been addressed by Weber and Theberge (Wilson Bull. 89:543–560, 1977) and Erskine (1978).

The BBS provides a source of data from which trends in species numbers have been derived, but Erskine (1978) has warned against using these counts as indicators of species density. Tempero-spatial changes in blackbird (Icterinae) and Eurasian Starling (*Sturnus vulgaris*) population indices derived from BBS counts have been assessed by Dolbeer and Stehn (Population trends of blackbirds and starlings in North America, 1966–76, U.S.D.I., Fish Wildl. Serv., Spec. Sci. Rept. Wildl. No. 214, 1976). BBS data have also been integrated into computer models designed to facilitate decision-making regarding the possible killing of millions of blackbirds and starlings (Dolbeer et al., Proc. Vert. Pest Conf. 7:35–45, 1976). Central to these endeavors have been the assumptions that: (1) changes in BBS counts reflected actual changes in population densities (levels), and (2) a substantial positive correlation existed between BBS counts and densities at least as they relate to the above species.

Intuitively, these assumptions seem reasonable, although neither the degree of correlation nor the form of the relationship have been substantiated. Employing data from independent studies conducted in separate years and from widely-separated regions, Dolbeer et al. (1976) derived a curvilinear association between BBS counts and estimates of male Red-winged Blackbird (*Agelaius phoeniceus*) density. The logarithmic relationship derived showed that, with increasing increments in BBS red-wing counts, there was a reduced rate of increase in estimated male density as density approached 30 males/km^2. Presumably, regions having large male density values were associated with areas of high habitat suitability (Fretwell and Lucas, Acta Biotheor. 19:16–36, 1969) which, in turn, attracted proportionately more females or sub-adult males; thus, BBS counts of all red-wings increased more rapidly than male density. A better understanding of the relationship between BBS values and estimates of breeding (male) density is necessary if BBS data are to be used effectively in population studies, not only of Red-winged Blackbirds, but ultimately for other species as well. Thus, we collected data over a broad region of southwestern Quebec that would allow comparison of BBS and estimated male density values over the complete range of red-wing densities likely to be encountered. Our aim was to determine the degree of correlation, if any, between BBS red-wing counts and male density estimates, and to identify the form of that relationship.

Methods.—Between 20 June–1 July 1980, estimates of male red-wing density were made along eight BBS routes within the agricultural zone along the St. Lawrence River Valley from Montreal to Quebec City (Weatherhead et al., Phytoprotection 61:39–47, 1980). BBS routes were 40-km transects travelled by motor vehicle and comprised 50 stops made at 0.8-km intervals (Erskine 1978). At each stop an observer recorded all birds seen or heard in 3 min. Counts were totalled after 10 stops, thus five 10-stop summary totals were obtained for each BBS route. Further details may be found in Weber and Theberge (1977) and Erskine (1978). A total of 24, 2.5-km-long, roadside censuses were conducted to estimate male density (Hewitt, J. Wildl. Manage. 31:39–47, 1967; Weatherhead et al. 1980). The roadside census technique involved estimating the total number of territorial male red-wings within 75 m of the roadside using a modified capture-mark-recapture method (Hewitt 1967). Since the area

TABLE 1

THE MEAN PERCENTAGE ($\bar{x}$), STANDARD ERROR (SE), AND RANGE OF NINE HABITATS ENCOUNTERED ON 24 CENSUS ROUTES ALONG EIGHT BBS ROUTES IN SOUTHERN QUEBEC, JUNE 1980

Habitat type	Percentage of land use	
	$\bar{x}$ ± SE	Range
Hay	22.8 ± 4.2	4.7–36.9
Cultivation (crops)	13.0 ± 4.5	3.0–36.8
Pasture	12.1 ± 3.8	0.0–25.6
Farm	5.9 ± 1.7	0.0–10.9
Old fields	3.7 ± 1.7	0.0–14.7
Forest	16.5 ± 7.4	0.9–50.0
Water (edge)	4.2 ± 1.8	0.0–13.1
Urban	14.3 ± 6.0	0.5–50.0
Miscellaneous[a]	7.1 ± 3.9	0.3–33.5

[a] Includes orchards, fallowfields, ditches, and, on one route, a sparsely wooded peat bog.

censused was a known constant, it was possible to derive an estimate of male density for each roadside census. In addition to these distinctions, a major difference between the BBS and roadside censuses was that the latter method involved continuous counts of males and repeated sampling of the same route, whereas the BBS method relied on single counts at 0.8-km intervals. Along each BBS route starting points for the roadside censuses were chosen at random from the set of BBS stops between stops 1 and 46. Since roadside censuses overlapped four BBS stops, censuses could not be initiated beyond BBS stop 46 nor extend beyond stop 50. Overlap in roadside census strips along each BBS route was not permitted. One BBS route had two roadside censuses, six routes had three censuses, and one route had four censuses. Censuses were done consistently by two observers and, to be in keeping with BBS regulations (Erskine 1978), were conducted in good weather during June. Following each census, habitats adjacent to the route were recorded at 0.16-km intervals.

TABLE 2

THE MEAN ($\bar{x}$) BBS COUNT AND MALE DENSITY, COEFFICIENTS OF VARIATION (CV) AND RANGES FOR RED-WINGED BLACKBIRDS BASED ON 24 INDEPENDENT SAMPLES AND POOLED DATA FOR EIGHT BBS ROUTES, SOUTHERN QUEBEC, 1980

Source	N	BBS counts			Male density[a]		
		$\bar{x}$	CV	Range	$\bar{x}$	CV	Range
Independent census routes[b]	24	43.5	92.9	1–170	26.6	85.9	0–103.0
Pooled per BBS route	8	206.5	76.3	25–512	26.8	63.0	2.8–54.2

[a] Males/km^2.

[b] Data are 10-stop summary totals for BBS counts.

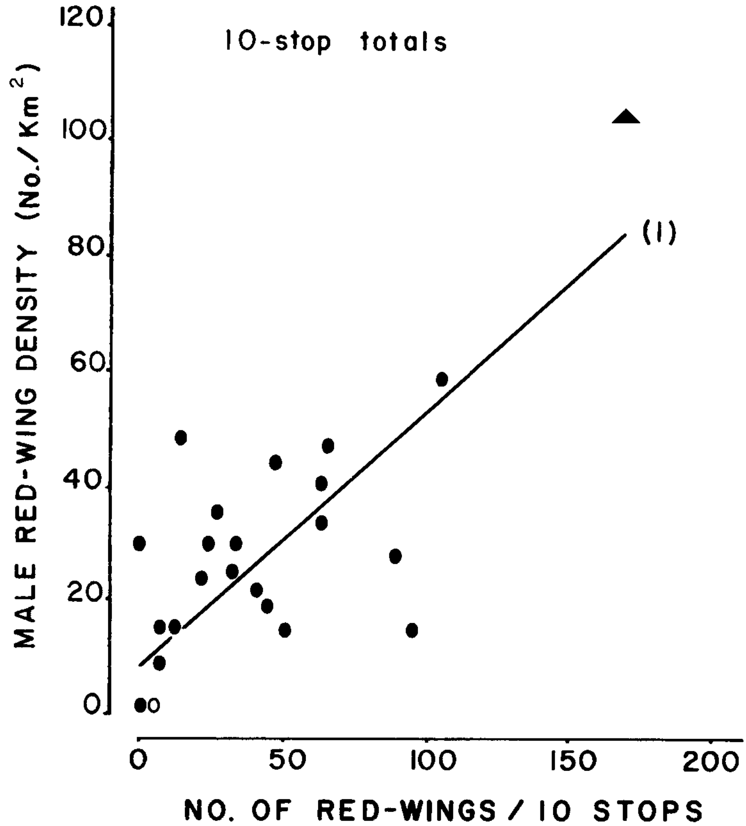

FIG. 1. Relationship between BBS 10-stop summary count of red-wings and corresponding male red-wing density. The solid line represents the significant linear regression (1) described in the text (○ denotes two observations). The triangle (▲) represents the outlying data point referred to in the text.

Two analyses were performed: (1) 10-stop summary totals were correlated with comparable roadside density estimates, and (2) total BBS counts were correlated with averaged male densities censused on that route. The 10-stop summary totals and comparable roadside density estimates referred to the summed data from the 10 BBS stops overlapping most closely with the census routes used to derive the roadside density estimate, while in the second analysis the total red-wing count for each BBS route was correlated with the mean density derived from averaging the density estimates for censuses conducted along that route. Spearman rank correlation coefficient (R_s) and both linear and curvilinear least squares regression models were computed for each analysis (Zar, Biostatistical Analysis, Prentice-Hall Inc., Englewood Cliffs, New Jersey, 1974). The linear and curvilinear models were compared with respect to coefficients of determination (R^2) in order to assess the relevance of the model proposed by Dolbeer et al. (1976) when applied to data at the regional level (i.e., southwestern Quebec).

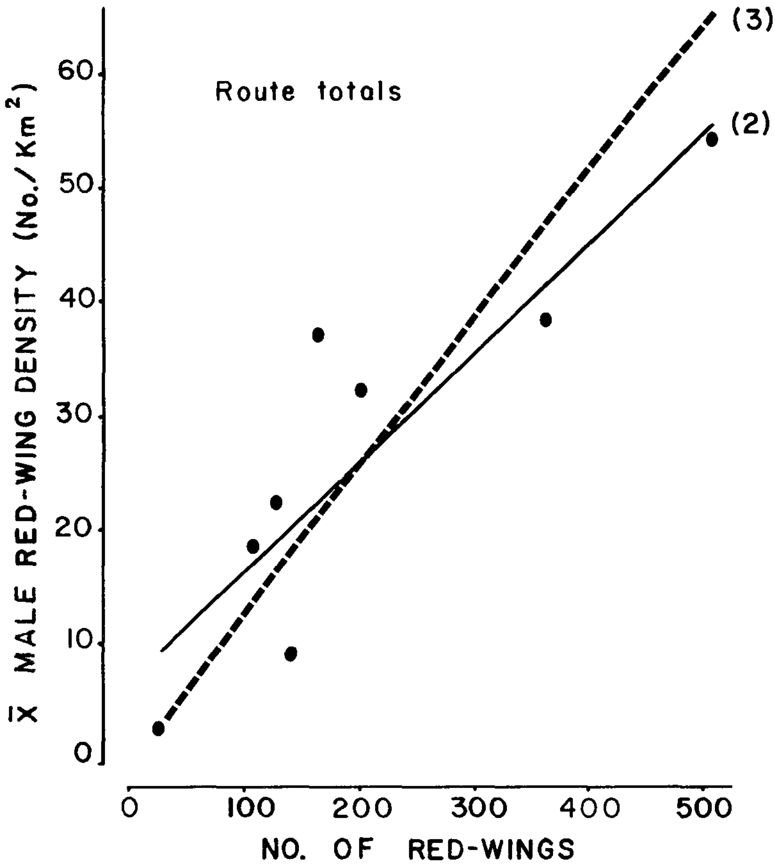

FIG. 2. Relationship between BBS total count of red-wings and corresponding mean male red-wing density. The solid line represents the linear (2) and the dotted line, the curvilinear (3), regressions described in the text.

Habitat.—Census routes traversed many habitats, but agricultural land use (hay, cultivation, pasture, farm) was predominant (Table 1). Forested and urban areas dominated (50%) the censuses on two BBS routes, while another route crossed a sparsely-wooded peat bog (33% miscellaneous). Although BBS routes were 40 km in length and census routes had a mean length of 7.5 km (about 19% of the BBS route), the values in Table 1 should be reasonably representative given that initiation points were randomly selected. Information regarding land use characteristics was considered important because the BBS count and density estimate relationships described below may be quite different from intensively cultivated to non-agricultural areas.

BBS red-wing counts and estimates of male density.—Overall, estimated density of males averaged 27 individuals per km^2 in 1980 (Table 2). Wide ranges in BBS counts and density estimates were obtained, but densities had slightly smaller coefficients of variation. It was

TABLE 3

MEAN ESTIMATED MALE RED-WING DENSITY AND VALUES PREDICTED VIA LINEAR REGRESSION MODEL 2 USING BBS COUNTS, SOUTHERN QUEBEC, 1977–1980

	Estimated density[a]		Predicted density[a]	
Year	N	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE
1980	24	26.6 ± 4.7	8	26.9 ± 5.3
	21[b]	30.0 ± 4.9	7[b]	29.3 ± 5.4
1979	23	39.0 ± 5.6	7	33.2 ± 7.3
1978	37	24.8 ± 2.7	7	32.5 ± 5.4
1977	32	33.5 ± 2.7	7	39.0 ± 8.1

[a] Males/km^2.
[b] Recalculated using only the seven routes which were run in all 4 years.

possible that the differences in methodologies alone accounted for this consistent decrease in variation.

There was a significant positive correlation (R_s = 0.654, N = 24, $P < 0.001$) between summary counts and male density (Fig. 1). A simple linear regression was also significant (F = 34.8; df = 1, 22; $P < 0.001$):

$$\text{density} = 7.33 + (0.443 \pm 0.075 \text{ SE [summary count]}),\ R^2 = 0.613 \quad \text{(model 1)}.$$

Both the rank correlation (R_s = 0.631) and the linear regression (R^2 = 0.346) remained highly significant ($P < 0.005$) even with one apparent outlying data point removed (Fig. 1). These results indicated that male density along a BBS route may be predicted from respective 10-stop summary totals with a significant level of precision. A curvilinear (power) model did not substantially improve the predictive ability (R^2 = 0.617, a difference of 0.004); therefore, the linear model was considered adequate. One major reason the degree of correlation was likely not greater was the overlap of census routes with four, rather than all 10, BBS stops. This analysis illustrated that, for the study of red-wing responses to current land use practices and/or land use change, one could employ the 10-stop summary totals to obtain five sampling units per BBS route and thereby improve the level of replication (i.e., sample size). This could be important for analyses in regions where relatively few BBS routes have been conducted annually.

The total number of red-wings per BBS route and estimates of male density were strongly positively correlated (R_s = 0.905, N = 8, $P < 0.01$; Fig. 2). A simple linear regression provided considerable precision in predicting male density from the BBS route total (F = 21.2; df = 1, 6; $P < 0.01$):

$$\text{density} = 7.24 + (0.095 \pm 0.02 \text{ SE [BBS count]}),\ R^2 = 0.780 \quad \text{(model 2)}.$$

An improvement in R^2 of 4.8% resulted from a curvilinear power function (F = 30.0; df = 1, 6; $P < 0.01$) suggesting that male density increased more slowly than BBS counts at higher values (Dolbeer et al. 1976), however the slowdown was very minimal (Fig. 2):

$$\text{density} = 0.15\ ([\text{BBS count}]^{0.971 \pm 0.18 \text{ SE}}),\ R^2 = 0.828 \quad \text{(model 3)}.$$

Because this R^2 increment was not significant (F = 1.71, $P > 0.05$, Zar 1974:271), due to the relative ease of formulating the linear model, and because of the minimal slowdown in density increase at higher BBS values, we felt justified in using the simple linear regression in the following test.

Test of model 2.—An ideal test of model 2 was to compare estimates of male density from southwestern Quebec with values predicted from the model using BBS red-wing counts as input data. To this end, we used BBS counts and roadside census data for the years 1977–1979. The roadside census data were those used by Weatherhead et al. (1980) and were thus unrelated to the census data used to generate the model. For this analysis, a subset of roadside census routes was selected each year to minimize the distance between roadside and BBS routes and thereby reduce biases associated with land use changes or other spatially variable factors. This objective was achieved by pooling male densities from roadside census routes within 30 km of BBS routes. BBS red-wing counts were used to predict male density and then these predicted values were used to compute a mean male density for the year. To avoid unknown biases due to missing data, we employed the seven BBS routes which were completed in all 4 years (Table 3).

The 1977 and 1979 predicted densities were close to the independent estimates based on actual censuses of male red-wings and differed by ca. 5.7 males/km^2, while the largest discrepancy (7.7 males/km^2) occurred in 1978 (Table 3). Note that the predicted density varied directly with estimated density during the period 1977–1980, but the magnitudes of the change were unrelated. For example, although the estimated and predicted densities declined between 1977 and 1978 and then increased from 1978–1979, the predicted density in 1979 rose above the predicted 1977 level; whereas, the estimated density in 1979 remained below the estimated 1977 level (Table 3). Finally, we calculated the mean and variation in male density for the years 1977–1979 using all census routes conducted in southwestern Quebec, and compared these with values for the subset described above and shown in Table 3. Overall, regional male red-wing density averaged 28.7 (SD = ±14.8, N = 114) in 1977; 22.6 (SD = ±16.0, N = 104) in 1978; and 36.4 (SD = ±22.3, N = 59) in 1979. The means and variances of the subset were not significantly different (t-tests and F-tests, $P > 0.05$) from respective overall values.

The estimated and predicted densities were similar given that, other than in 1980, census and BBS routes did not overlap. Thus, effects due to differences in habitat were unavoidable. In addition, the range in estimated male densities during 1977–1979 (24.8–39.0, Table 3) was slightly less than the range calculated from a further subset of 23 census routes sampled all 3 years (20.7–37.1). The latter subset of census routes varied relatively little with respect to habitat between 1978 and 1979, although significant differences in male density were evident (Clark and Weatherhead, unpubl.). Moreover, red-wing populations may undergo an annual redistribution known as the "checkerboard effect" (Rotenberry and Wiens, Oecologia 47:1–9, 1980), especially if red-wings are not habitat limited.

The degree of variation in red-wing estimates observed in this study raises serious questions about sampling precision, not only for the BBS but for the census routes as well. From the coefficients of variation in Table 2, censuses of male density were associated with more stable variances. More importantly, it was evident from the comparison of the subset of roadside censuses used in the test of model 2 with the overall regional set that variation did not change significantly with the addition of two to three times more census routes. Clearly, red-wing populations exhibited substantial tempero-spatial variability. Nevertheless, male red-wing density can be predicted from BBS counts if one applies the model(s) to data from similar landscapes. We echo Weber and Theberge's (1977) suggestion that general habitat information be collected along BBS routes. At the regional level, a linear relationship between BBS counts and male densities was appropriate; our analyses provided little support for the strongly curvilinear model of Dolbeer et al. (1976). Some caution must be exercised in interpreting population indices from BBS data. For example, if BBS indices indicated yearly increases, our results suggest that one could infer that the population had indeed increased but one could only speculate on the magnitude of the change unless additional supportive information, e.g., important habitat changes, was available. While we believe that male density can be derived from BBS counts via the statistical models presented, and subjected to the logical constraints defined above, we acknowledge that neither predictive models nor single-sample surveys can replace carefully implemented censuses of bird populations (Wiens, Am. Nat. 117:90–98, 1981). This study demonstrated that BBS counts can be extremely useful in deriving estimates of male red-wing density; further research appears warranted to determine the nature of the relationship between BBS counts and (male) densities for other species.

Acknowledgments.—R. Dolbeer, H. Greenwood, and J. Rotenberry suggested several improvements of earlier drafts of this manuscript. S. Wendt and I. Price of the Canadian Wildlife Service, Ottawa, kindly provided BBS results. It is a pleasure to thank M. McIntosh for allowing RGC to help conduct a BBS route, and M. Silverstone for field assistance in 1980. This study would not have been possible without the efforts of BBS volunteers and the technicians who conducted census routes. Financial support was provided by Agriculture Canada and the Ministere de l'Agriculture du Quebec, and by a scholarship to RGC from the Ministere d'Education du Quebec. Computing costs were paid by the Faculty of Graduate Studies and Research, McGill University.—ROBERT G. CLARK, *Dept. Renewable Resources, MacDonald Campus of McGill Univ., 21111 Lakeshore Rd., Ste. Anne de Bellevue, Quebec H9X 1C0, Canada*; PATRICK J. WEATHERHEAD, *Dept. Biology, Carleton Univ., Ottawa, Ontario K1S 5B6, Canada;* AND RODGER D. TITMAN, *Dept. Renewable Resources, MacDonald Campus of McGill Univ., 21111 Lakeshore Rd., Ste. Anne de Bellevue, Quebec H9X 1C0, Canada.* (Present address RC: *Oikos Ecological Research Associates Ltd., P.O. Box 8818, Saskatoon, Saskatchewan S7K 6S7, Canada.*) *Accepted 20 Jan. 1983.*

Wilson Bull., 95(3), 1983, pp. 459–461

Calculating incubation periods of species that sometimes neglect their last eggs: the case of the Sora.—Most investigators follow Heinroth (J. Orn. 70:172–285, 1922) and Nice (Condor 56:173–197, 1954) in determining the shortest normal incubation periods of birds by calculating the time elapsed between laying of the last egg to hatching of the last young in nests in which all eggs hatch (and preferably in which each egg is marked individually on the day of laying). Usually hatching occurs between successive visits to a nest by the observer, so any estimate of the incubation period of a clutch should be accompanied by a "margin of error" (Nolan, Ornithol. Monogr. No. 26, 1978). The Heinroth-Nice method standardizes the incubation periods of free-living birds reported in the literature, applies to most species with different hatching schedules, and minimizes the uncertainty concerning the time when attending adults begin incubating.

We describe here a modified Heinroth-Nice procedure that is recommended for determining the minimal normal incubation periods in large-brooded species which sometimes neglect the last one or two eggs in a nest causing them to hatch later than they otherwise would have (Nice 1954:173; this study). We examine this problem using the Sora (*Porzana carolina*) as an example.

The Sora has a clutch-size of 5–15 eggs (9–12 is a more typical range) and incubation and care of young is shared by the sexes (Pospichal and Marshall, Flicker 26:2–32, 1954; Tanner and Hendrickson, Iowa Bird Life 26:78–81, 1956). During the hatching period, one adult