ANALYSIS OF AGGRESSION IN WHITE-THROATED SPARROW TYPES OF DIFFERENT PROPORTIONS

By Jack P. Hailman

Harrington (*Bird-Banding*, **44**: 314-5, 1973) presented interesting data which are interpreted as demonstrating that winter resident White-throated Sparrows (*Zonotrichia albicollis*) are initially dominant over spring migrants but become less so as migration proceeds. However, the analysis used in the statistical tests of significance does not take into account that the two sets of birds were present in quite different proportions in each day watched. The purposes of this communication are to show how these proportions can be taken into account, to illustrate the method of analysis using Harrington's data, and to re-examine the conclusions about aggression in White-throated Sparrows.

THE METHOD BASED ON PROPORTIONS OF BIRDS PRESENT

Table 1 shows the symbolism to be employed for the observed data, in which AB means A chases B (A>B in Harrington's paper), BA means B chases A, and so on. The cells (AA, AB, BA, and BB) are the actual frequencies of chase, not percentages. The row sums D_A and D_B are the frequencies of birds chasing, and column sums S_A and S_B frequencies of being chased. N is the total number of chases observed. In Table 1, A and B could represent any distinguishable types of animals participating in an interaction; in the specific example, A symbolizes the winter residents and B the migrants, following Harrington's designations.

Table 1.
Format and symbolism for analyzing aggressive interactions (see text).

(chaser) dominant bird	(chasee) subordinate bird A	B	Totals
A	AA (aa)	AB (ab)	D_A (D_a)
B	BA (ba)	BB (bb)	D_B (D_b)
Totals	S_A (S_a)	S_B (S_b)	N

The task is then to create an analogous table for the *expected* frequencies of interactions based on the proportions of birds present (lower case letters in parentheses in Table 1). For example, on 22 April there were 14 A-type birds and about 30 B-types (Harrington had to estimate the number of B-types on all three dates).

We can thus define the proportion of A-types as $\alpha = 14/(14+30)$ and B-types as $\beta = 30/(14+30)$. From these proportions of birds present we then construct a table of expected interactions, if the interactions are at "random"—that is, are according to the relative proportions of birds present regardless of status. These expectations are:

$$aa = \alpha^2 N, \quad (1a)$$

$$ab = \alpha\beta N, \quad (1b)$$

$$ba = \beta\alpha N, \quad (1c)$$

$$bb = \beta^2 N, \quad (1d)$$

$$S_a = D_a = \alpha N, \text{ and} \quad (2a)$$

$$S_b = D_b = \beta N. \quad (2b)$$

There are now at least three kinds of principal analyses that can be made to see if A and B birds differ in aggressive behavior. First, one can ask if the types differ in overall frequency of being the chaser (or dominant bird) by calculating the following Chi-square with one degree-of-freedom:

$$\chi^2 = \frac{(D_A - D_a)^2}{D_a} + \frac{(D_B - D_b)^2}{D_b}. \quad (3)$$

Then the analogous test for being the chased (subordinate bird) may be made with the same equation (3), substituting S where D occurs. Finally, interactions in the cells of the table as a whole can be calculated using:

$$\chi^2 = \frac{(AA-aa)^2}{aa} + \frac{(AB-ab)^2}{ab} + \frac{(BA-ba)^2}{ba} + \frac{(BB-bb)^2}{bb}, \quad (4)$$

with one degree-of-freedom.

The Chi-square analysis of the total tables reveals only whether or not the four data cells are filled according to the relative proportions of the birds present—not which specific cells are the greatest contributors to non-randomness when it occurs, although that can be judged by inspection. In order to determine whether one type of bird is dominant over the other, one must examine the direction of difference in cells AB and BA.

ANALYSIS OF THE DATA AND CONCLUSIONS ON AGGRESSIVENESS

Tables 2, 3, and 4 show the data and the expectations computed by the above methods for 22, 23-24 and 25-27 April, respectively. The upper figure in each cell is the observed datum, the lower figure in parentheses the expected value based on the proportions of birds present (see Table 1 for format).

TABLE 2.
Data and expectations for 22 April (format as TABLE 1).

	A	B	Totals
A	11 (5.36)	27 (11.49)	38 (16.86)
B	0 (11.49)	15 (24.64)	15 (36.14)
Totals	11 (16.86)	42 (36.14)	53

A comparison of the outcomes of statistical tests is shown in Table 5, which summarizes the results. First, there is a difference in dominance between the two kinds of birds on every date (dominance column of Table 5). Winter residents (A-birds) are more often dominant than expected on the proportions of birds present, and migrants (B-birds) are less often dominant than expected by

TABLE 3.
Data and expectations for 23-24 April (format as TABLE 1).

	A	B	Totals
A	4 (0.67)	13 (4.16)	17 (4.83)
B	2 (4.16)	16 (26.00)	18 (30.17)
Totals	6 (4.83)	29 (30.17)	35

their abundance; that is, $D_A > D_a$ and therefore $D_B < D_b$. Second, A- and B-birds are recipients of aggression according to their proportions in the groups studied (subordinance column of Table 5); that is, none of the comparisons is statistically significant. Third, as expected from the dominance results, each of the three tables as a whole shows a significant departure from expectation (interaction column of Table 5). In all three cases (Tables 2, 3 and 4) this result is due to A's relatively greater aggressiveness because in every table AA > aa, AB > ab, ba > AB and bb > BB.

Harrington's conclusions relate primarily to which type of bird is dominant. He states that ". . . on 22 April the winter resident White-throats were dominant over the newly arrived migrants . . .," a conclusion supported by Tables 2 and 5. He then states "After 22 April the pattern of dominance appeared to change. . .," but there is no evidence of change from the analysis based on the proportions of birds present. The problem is that on 22 April only 68% of the birds were migrants, whereas by 23-24 April this figure had risen to 86%. Since there were more B-type birds, the absolute

TABLE 4.
Data and expectations for 25-27 April (format as TABLE 1).

	A	B	Totals
A	4 (3.63)	19 (10.85)	23 (14.5)
B	7 (10.88)	28 (32.63)	35 (43.5)
Totals	11 (14.5)	47 (43.5)	58

number of B-dominant chases rose, but it did so only in accordance with the proportions of birds present. Harrington finally concludes that "the winter residents still dominated the spring migrants, but

TABLE 5.
Comparisons of statistical tests for the three periods.

	Dominance		Subordinance		Interaction
Date	Result	P[1]	Result	P[1]	P[1]
22 April	$D_A > D_a$	$< .001$	$S_A < S_a$	$> .05$	$< .001$
23-24 April	$D_A > D_a$	$< .001$	$S_A > S_a$	$> .5$	$< .001$
25-27 April	$D_A > D_a$	.01	$S_A < S_a$	$> .2$	$< .01$

[1]Chi-square with df = 1; see equations (3) and (4).

not with statistically greater frequency. . . ." It is not clear from this sentence *what* the frequency was not greater *than*. The relative dominance of the A-type winter residents remains equally high throughout the period, and this result is statistically significant (Table 5) in each case. It appears, therefore, that failing to take into account the relative number of birds present led to certain incorrect statistical conclusions.

A NOTE ON AGGRESSIVENESS OF MORPHS

Harrington also presented data on the aggressiveness of different color-morphs of the White-throated Sparrow. Lowther and Falls (Bent, 1968, *U. S. Natl. Mus., Bull. 237*: 1364-1391) classify the morphs as having tan or white median stripes. Harrington further distinguished between white morphs that had crisp white median stripes lined with black and those having dull or dirty white stripes lined with black. Harrington's data suggest that crisp white morphs are most aggressive and tan morphs least, with dirty white morphs in between. However, he did not know the proportions of morphs present when his chases were recorded among the migrants so the data cannot be analyzed. R. W. and M. S. Ficken have also collected data (unpubl. Ms) on relative aggressiveness among

White-throated Sparrows of different color-morphs. Their extensive data show that white morphs are the aggressors in hostile interactions much more frequently than expected by chance. These data thus support Harrington's conclusions with regard to the aggressiveness of morphs.

SUMMARY

One cannot tell whether winter resident White-throated Sparrows or newly-arrived spring migrants are more aggressive by merely comparing their absolute frequencies as chaser and chasee in interactions. A method is presented for taking into account the relative proportions of the two types of birds that are present during interactions. Analysis of Harrington's data shows that winter residents are more frequently the chaser than expected by chance, and this is true throughout the observation period. Winter residents and migrants are equal recipients of aggression. The data suggesting that white morphs are more aggressive than tan morphs cannot be evaluated because the relative proportions of morphs present are not known.

ACKNOWLEDGMENTS

I thank B. A. Harrington, R. W. Ficken, and M. S. Ficken for criticizing the manuscript.

Department of Zoology, University of Wisconsin—Madison, Madison, Wisconsin 53706. Received 2 February 1975, accepted 22 April 1975.