

## APPENDIX. Continued.

	Mass (kg)	%
<b>Squid-eating</b>		
Wandering Albatross ( <i>Diomedea exulans</i> )	8.60	0.27
Black-browed Albatross ( <i>Diomedea melanophris</i> )	3.50	0.28
Gray-headed Albatross ( <i>Diomedea chrysostoma</i> )	3.60	0.11
Yellow-nosed Albatross ( <i>Diomedea chlororhynchos</i> )	2.00	0.07
Shy Albatross ( <i>Diomedea cauta</i> )	4.10	0.18
Sooty Albatross ( <i>Phoebastria fusca</i> )	2.50	0.22
Light-mantled Albatross ( <i>Phoebastria palpebrata</i> )	2.70	0.32
Southern Fulmar ( <i>Fulmarus glacialisoides</i> )	1.00	0.17
Cape Petrel ( <i>Daption capense</i> )	0.45	0.09
Great-winged Petrel ( <i>Pterodroma macroptera</i> )	0.58	1.23
White-headed Petrel ( <i>Pterodroma lessonii</i> )	0.75	0.72
Atlantic Petrel ( <i>Pterodroma incerta</i> )	0.52	0.01
White-chinned Petrel ( <i>Procellaria aequinoctialis</i> )	1.21	6.57
Gray Petrel ( <i>Procellaria cinerea</i> )	1.03	0.11
Greater Shearwater ( <i>Puffinus gravis</i> )	0.95	0.34
<b>Fish-eating</b>		
Cory's Shearwater ( <i>Calonectris diomedea</i> )	0.96	0.15
Sooty Shearwater ( <i>Puffinus griseus</i> )	0.79	18.46
Little Shearwater ( <i>Puffinus assimilis</i> )	0.23	0.21
Antarctic Tern ( <i>Sterna vittata</i> )	0.14	0.20
Arctic Tern ( <i>Sterna paradisaea</i> )	0.13	7.07
Common Tern ( <i>Sterna hirundo</i> )	0.12	0.17
<b>Mixed-diet</b>		
Antarctic Giant-Petrel ( <i>Macronectes giganteus</i> )	4.10	0.13
Antarctic Petrel ( <i>Thalassoica antarctica</i> )	0.70	0.54
Snow Petrel ( <i>Pagodroma nivea</i> )	0.30	0.86
Kerguelen Petrel ( <i>Pterodroma brevirostris</i> )	0.33	4.75
Soft-plumaged Petrel ( <i>Pterodroma mollis</i> )	0.31	4.10
Great Skua ( <i>Catharacta skua antarctica</i> )	1.63	0.01
Pomarine Jaeger ( <i>Stercorarius pomarinus</i> )	0.67	0.01
Parasitic Jaeger ( <i>Stercorarius parasiticus</i> )	0.53	0.01

### An Alternative Method for the Analysis of Emlen Funnel Data

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The blotter paper funnel orientation cage invented by Emlen and Emlen (1966) is widely used in studies of avian migratory behavior. From the record of the birds' footprints one can determine a central tendency in the distribution of activity (e.g. a mean direction) and a measure of dispersion of the activity (e.g. a length of the mean vector,  $r$ ) by using standard procedures of circular statistics (Batschelet 1981). We would also usually like to know whether the distribution of hopping differs significantly from random, i.e. whether  $r$  is significantly greater than 0. It is common practice to apply statistical inference tests (e.g. Rayleigh or  $V$ -test) to the distribution of footprint records on a single funnel and then to discrim-

inate between tests showing "significant" orientation and those in which the null hypothesis of randomness could not be rejected. Unfortunately, the use of such inference tests is not valid in this case, but the procedure continues to be used uncritically.

The basic problem is that a series of hops by an individual bird cannot be assumed to be independent. Thus, no matter how the sector densities are determined (by visual examination, counting, sampling sectors, or photo-optical methods), the sample size ( $n$ ) will be based on nonindependent data. Aside from various elaborate procedures to estimate when statistical independence occurs in a sequence of hops (see Hamilton 1966, Emlen 1969), there is no certain-

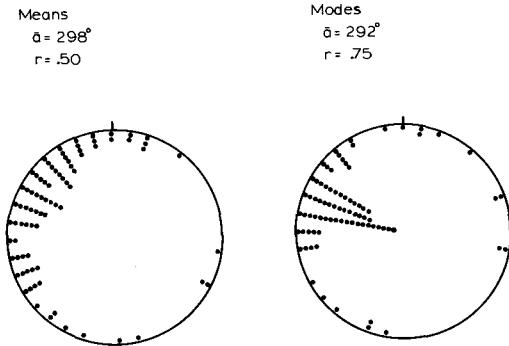


Fig. 1. Distribution of the mean directions, rounded to the nearest  $10^\circ$ , and the modal directions of 81 Emlen funnel tests of 55 American Tree Sparrows tested in spring, 1983 ( $\bar{\alpha}$  = mean angle,  $r$  = length of mean vector).

ly valid way to apply tests such as the Rayleigh to individual Emlen funnels. Similar problems confront data from multiple tests of the same bird.

It is valid to compute mean directions using sector densities and to use those means in a second-order analysis, ignoring the individual mean vector lengths (Batschelet 1978). Many recent studies have relied on this procedure (e.g. Wiltschko and Wiltschko 1972). However, the traditional method of quantifying activity in funnels (Emlen and Emlen 1966) is tedious and difficult to conduct in the absence of any potentially biasing information concerning the conditions of the test (i.e. "blind"). For cases in which a measure of central tendency in a distribution is the metric of interest and no estimate of the variance of hopping within a cage is required, we propose using modal directions. We compare the results of this method with the traditional computation of mean directions. Some workers have used modes as the basis of their analysis (Wiltschko and Schmidt 1974, Bingman and Able 1979, Bingman 1983), and Rabøl (1969, 1970) proposed using an unspecified visual estimate of "the average direction," but no systematic comparison of the methods has been made.

The procedure we used for determining modal directions is as follows. An observer is asked to select and mark the point on the funnel that has the highest density of footprints (i.e. the modal direction of activity). The funnel is presented to the observer so that no directional reference mark nor other information concerning the test is visible. If no area of the funnel has a density at least equal to the Emlens' density pattern three (Emlen and Emlen 1966), if there is uniform activity, or if there are two or more areas of equal footprint density, then the mode is not selected. If the area with the highest density is spread over a large sector of the funnel, then the center of that sector is selected as the mode. In practice we

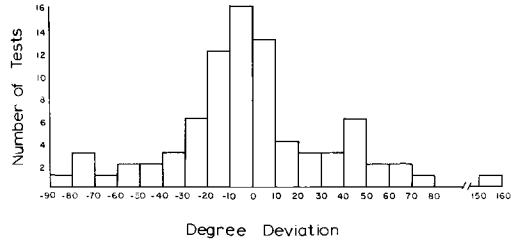


Fig. 2. Frequency distribution of the difference between the modal and mean directions (mode minus mean) of 81 Emlen funnel tests of 55 American Tree Sparrows.

have found that 10–15% of funnels are commonly rejected from the analysis as a result of the application of these criteria.

How do results from the modal method compare with the traditional method of funnel analysis? We analyzed a set of 89 Emlen funnels from tests of 55 American Tree Sparrows (*Spizella arborea*). Eight funnels were rejected because they contained too few footprints or no discernible modal direction of activity; the remaining 81 funnels were evaluated using the modal and traditional methods. The birds were tested in spring 1983 under clear skies for 2–3 h after the sun fell below the horizon (see Cherry 1984 for additional details). Modal directions were measured to the nearest  $10^\circ$  clockwise from geographic north.

The distributions of the mean and the modal directions are shown in Fig. 1. The mean of the mean directions is similar to that of the modal directions. The angular variance around the mean of the mean directions, however, was significantly greater than that around the mean of the modal directions ( $P < 0.01$ ; Mardia 1972: 161). This difference in the dispersion of the two distributions indicates that, for individual funnels, the modal direction is not always the center of mass of the distribution of activity. The modal directions of two funnels may be similar, but depending upon how the activity is spread around the mode, their means may be different, leading to a higher angular variance around the mean of the mean directions. To compare the two methods for individual funnels, we subtracted the mean direction from the modal direction for each funnel. The frequency distribution of the differences (Fig. 2) is centered close to zero ( $\bar{x} = -1.2^\circ$ ,  $SD = 37$ ) and shows that most of the modes were close to their means. These data show that the modal method yields second-order estimates of directionality similar to those of the traditional method.

The modal method has two advantages over the traditional method: it is faster, and it facilitates blind analysis. It is far easier to coerce an unbiased observer into selecting modal directions than to quantify sector densities for a large set of funnels. A possible

shortcoming of the modal method is that it estimates only the direction of activity and gives no indication of the scatter of hopping, whereas the traditional method indicates the degree of concentration of a bird's hopping (mean vector length,  $r$ ). This is not often a major problem because most recent studies have relied on second-order analyses of mean directions that ignore the mean vector lengths. Indeed, at this point the biological meaning of the dispersion of a bird's hopping activity is not clear and is in part a reflection of the idiosyncracies of individual birds (Wiltschko and Wiltschko 1978, Moore 1985).

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Notes on the Plumages of the Paramo Seedeater (*Catamenia homochroa*)

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Many species of nonpasserine birds, especially among the Ciconiiformes, Falconiformes, and Charadriiformes, exhibit three or more successive, pre-definitive, full basic plumages. Comparable sequences are little known among Passeriformes; for one example, Parkes and Humphrey (1963) described four age classes in male Yellow-backed Tanagers (*Hemithraupis flavicollis*), and I have found four age classes in male Altamira Orioles (*Icterus gularis*; Dickerman MS).

The acquisition of freshly collected and correctly aged specimens of the Paramo Seedeater (*Catamenia homochroa*) from Cerro Neblina in extreme southern Venezuela stimulated me to review the geographic variation in the species. In preliminary studies it was immediately obvious that the species is not only sex-

ually dimorphic, but that there are several plumage stages. Geographic variation could not be evaluated until the plumages were identified so that comparable age classes could be compared.

I obtained 107 specimens of *C. homochroa* on loan (see Acknowledgments) for comparison with the 65 specimens in the collection of the American Museum of Natural History (AMNH). Included in the series of *C. homochroa* were 5 specimens of *oreophila*, the subspecies from Cerro Santa Marta, Colombia. For the purposes of this study, all Andean specimens of *C. homochroa*, from Merida, Venezuela to Chuspipata, Bolivia, were combined and segregated by sex, and thence by plumage stage, regardless of date of collection. Similarly, all specimens of *C. h. duncani*, the subspecies from the Pantepui region of southern