

**Age-dependent Variability in the Migratory Orientation of the Savannah Sparrow (*Passerculus sandwichensis*)**

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Variability characterizes the orientation of migratory birds much as it does other aspects of their behavior. If one migrant behaves differently from three other migrants, the proper tactic is to find out why. What are the sources of variability? Experience, including individual responses to experience, is one obvious source of variability. Although individual differences in orientation behavior need not be a function of experience, they often are (see Graue 1965, Brown and Mewaldt 1968, Keeton and Gobert 1970, Keeton 1972, Wallraff 1972, W. Wiltschko and R. Wiltschko 1975, W. Wiltschko, R. Wiltschko, and Keeton 1976, Ralph 1978, Edrich and Keeton 1978, Williams 1978, Bingman 1981, R. Wiltschko and W. Wiltschko 1981, R. Wiltschko, Nohr, and W. Wiltschko 1981, Beacham 1982, Gauthreaux 1982). The effect of experience on orientation might manifest itself in several ways: more experienced individuals might (1) be able to select or maintain a direction based on less information (e.g. Keeton 1972, Wiltschko and Wiltschko 1975, Bingman 1981), (2) display greater flexibility in cue utilization (e.g., Wiltschko and Wiltschko 1975), (3) be able to switch more easily from one source of directional information to another (e.g. Baker and Mather 1982), or (4) be less susceptible to the distracting effect of the moon (Brown and Mewaldt 1968) or artificial horizon glows (Williams 1978, Beacham 1982, Gauthreaux 1982). In any case, inexperienced migrants are more likely to commit orientational errors (see Drury and Keith 1962; DeSante 1973, 1983; Ralph 1978, 1981; McLaren 1981).

Greater individual variability among naive migrants would not be surprising in light of their lack of migratory experience and their maturational differences. On the one hand, naive migrants might display less consistent compass orientation on a night-to-night basis, which would yield greater within-individual variability. Greater within-individual variability would be indicative of less accurate orientation (see Emlen 1969, 1972; Moore 1978, in press). On the other hand, a sample of naive migrants might display a wider array of individual preferences and greater between-individual variability. Both within- and between-individual variability were analyzed in this study to test the hypothesis that naive migratory Savannah Sparrows (*Passerculus sandwichensis*) have greater individual variability in their compass orientation than do experienced migrants.

Savannah Sparrows were mist netted in late August 1981 in eastern North Dakota near Grand Forks and transported to southcentral Mississippi, where orientation experiments were conducted. The age of

the birds, either hatching-year (HY) or adult (AD), was determined upon capture by the extent of skull pneumatization. I housed the birds individually in an outdoor aviary under natural photoperiod and the local geomagnetic field (0.53 Gauss,  $mN = 360^\circ$ ,  $64^\circ$  inclination). Both HY and AD birds deposited subcutaneous fat and displayed nocturnal locomotor activity (*Zugunruhe*) before testing. Emlen funnel cages (Emlen and Emlen 1966) were used to record the orientation of migratory activity. Angular deviations were calculated according to Zar (1974). Orientation tests were conducted under clear, starry skies on moonless nights from 15 September through 30 October 1981 in an open field adjacent to the aviary. Birds were placed in orientation cages at 1900 (CST) with a clear view of the setting sun and were removed 3 h later. A bird's position within the arrangement of orientation funnels was randomly varied from night to night. Nights when naturally occurring fluctuations in the geomagnetic field exceeded a K-index value of 3 ( $>40$  gamma) for the 3-h intervals during or preceding a test night were not included in the analysis. [See Moore (in press) for additional details.]

The mean heading from a night's cage activity is usually in a seasonally appropriate southerly direction whether or not the bird possesses migratory experience. When the nightly means are plotted for both experienced (AD) and naive (HY) birds, the means of the sample distributions are essentially the same (Figs. 1 and 2), although the HY distribution is characterized by greater scatter [compare measures of concentration for adult ( $r = 0.802$ ) and naive birds ( $r = 0.618$ )]. Differences between the two groups of migrants appear when individual behavior is examined. Night-to-night consistency in orientation is especially evident among the birds with migratory experience (Table 1, Fig. 1). The high  $r$  values and low angular deviations associated with the distribution of mean headings for each adult point to narrow within-individual variability. Yet not all experienced adult migrants are oriented in the same southerly direction. Several AD birds consistently oriented their activity to the SSW-SW (AD 03, AD 11, AD 18, AD 22), whereas others (AD 08, AD 21) were just as well oriented to the SSE. This pattern is confirmed after the variability in adult headings is partitioned into between- and within-group components by an analysis of variance. Variability among adult individuals accounts for a significant portion of the variability in headings ( $F = 2.32$ ;  $df = 7,40$ ;  $P < 0.05$ ). The problem of applying an analysis of variance procedure to cir-

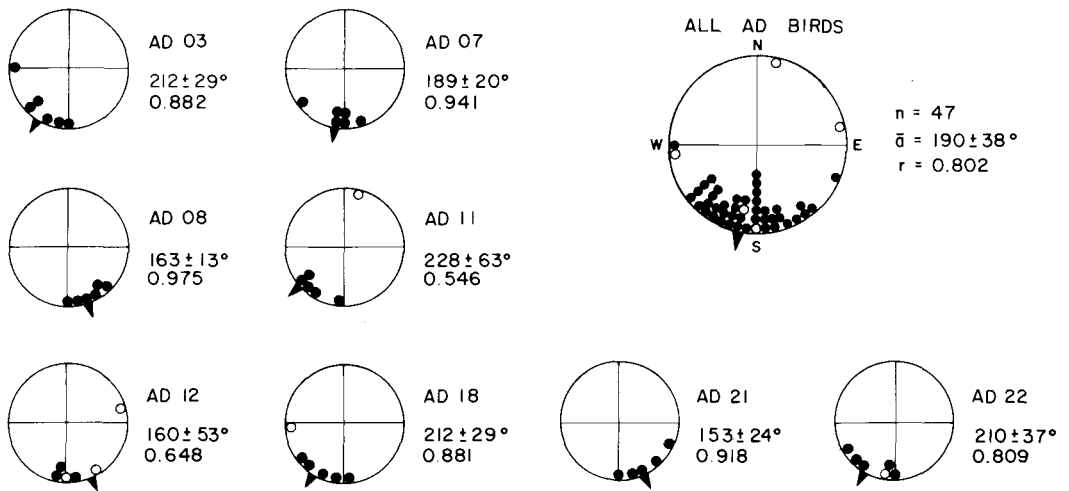


Fig. 1. Individual nightly mean headings are plotted for eight experienced (AD) Savannah Sparrows. The mean headings ( $\pm$  angular deviations) and the  $r$  values are given, and the headings are shown as arrows on the circumference. North is to the top.

cular data is circumvented by converting the headings to deviations from south, thereby linearizing the data. This is statistically acceptable, because nearly all the nightly means are in the southern half of the possible range of headings (see Batschelet 1965).

Naive birds are less consistent from night to night in their orientation (see Table 2, Fig. 2), although the means based upon the six test nights are seasonally appropriate for each individual. The angular devia-

tions associated with the HY distributions are, with two exceptions (HY 05, HY 19), comparable to the highest AD values (compare Figs. 1 and 2). When the mean headings of naive birds are subjected to an analysis of variance, the amount of within-individual variability was found to be substantially greater than the among-individual component ( $F = 0.24$ ;  $df = 7, 39$ ;  $P > 0.05$ ). Moreover, a comparison between AD and HY samples revealed that there is significantly

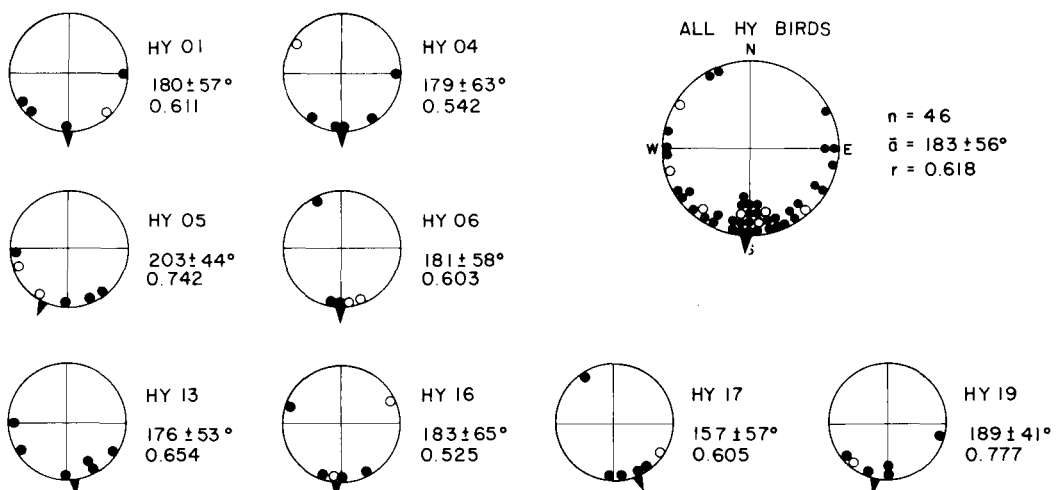


Fig. 2. Individual nightly mean headings are plotted for eight naive (HY) Savannah Sparrows. See Fig. 1 for further explanation.

TABLE 1. Compass orientation of eight experienced Savannah Sparrows tested over six nights in the fall, 1981. The mean heading ( $\bar{a}_i$ )  $\pm$  angular deviation and nightly vector length ( $r_i$ ) are given.

Bird	Night						$\bar{r} \pm 1 \text{ SD}^a$
	1	2	3	4	5	6	
AD03	$\bar{a}_i = 195 \pm 58^\circ$ $r_i = 0.596$	$220 \pm 63^\circ$ $0.542$	$201 \pm 33^\circ$ $0.846$	$179 \pm 57^\circ$ $0.607$	$270 \pm 70^\circ$ $0.474$	$218 \pm 54^\circ$ $0.639$	$0.617 \pm 0.126$
AD07	$\bar{a}_i = 166 \pm 34^\circ$ $r_i = 0.839$	$182 \pm 41^\circ$ $0.772$	$230 \pm 66^\circ$ $0.511$	$180 \pm 49^\circ$ $0.690$	$189 \pm 61^\circ$ $0.561$	$193 \pm 60^\circ$ $0.577$	$0.658 \pm 0.130$
AD08	$\bar{a}_i = 144 \pm 53^\circ$ $r_i = 0.655$	$161 \pm 38^\circ$ $0.803$	$169 \pm 40^\circ$ $0.782$	$175 \pm 36^\circ$ $0.820$	$180 \pm 25^\circ$ $0.910$	$150 \pm 50^\circ$ $0.681$	$0.775 \pm 0.094$
AD11	$\bar{a}_i = 15 \pm 79^\circ$ $r_i = 0.383 \text{ ns}^b$	$225 \pm 52^\circ$ $0.661$	$216 \pm 58^\circ$ $0.596$	$228 \pm 40^\circ$ $0.781$	$190 \pm 60^\circ$ $0.573$	$208 \pm 62^\circ$ $0.555$	$0.592 \pm 0.131$
AD12	$\bar{a}_i = 180 \pm 91^\circ$ $r_i = 0.283 \text{ ns}^b$	$148 \pm 80^\circ$ $0.377 \text{ ns}^b$	$176 \pm 56^\circ$ $0.616$	$190 \pm 48^\circ$ $0.701$	$80 \pm 100^\circ$ $0.217 \text{ ns}^b$	$185 \pm 71^\circ$ $0.462$	$0.443 \pm 0.189$
AD18	$\bar{a}_i = 215 \pm 49^\circ$ $r_i = 0.693$	$200 \pm 66^\circ$ $0.514$	$265 \pm 81^\circ$ $0.370 \text{ ns}^b$	$195 \pm 62^\circ$ $0.555$	$227 \pm 41^\circ$ $0.772$	$174 \pm 51^\circ$ $0.672$	$0.596 \pm 0.145$
AD21	$\bar{a}_i = 139 \pm 35^\circ$ $r_i = 0.826$	$160 \pm 59^\circ$ $0.585$	inactive	$182 \pm 37^\circ$ $0.810$	$115 \pm 88^\circ$ $0.305$	$168 \pm 68^\circ$ $0.493$	$0.604 \pm 0.220$
AD22	$\bar{a}_i = 196 \pm 46^\circ$ $r_i = 0.725$	$209 \pm 55^\circ$ $0.626$	$219 \pm 40^\circ$ $0.781$	$191 \pm 72^\circ$ $0.452 \text{ ns}^b$	$232 \pm 48^\circ$ $0.700$	$183 \pm 51^\circ$ $0.671$	$0.701 \pm 0.058$

<sup>a</sup> Mean of nightly vector lengths ( $r$ )  $\pm$  1 standard deviation.

<sup>b</sup> ns = nonsignificant  $r$  ( $P > 0.05$ ) according to Rayleigh Test (see Zar 1974).

more within-individual variability in naive than in AD birds ( $F_s = S^2_{HY}/S^2_{AD} = 2.47$ ;  $df = 45,46$ ;  $P < 0.05$ ). The differences between the two groups in variability among individuals are also substantial ( $F_s = S^2_{AD} / S^2_{HY} = 3.87$ ;  $df = 46,45$ ;  $P < 0.05$ ).

An examination of within-night variation also reveals differences between the AD and HY groups (Tables 1 and 2). Sometimes a bird's activity is not well concentrated in any particular direction (low  $r$  statistic and large angular deviation). This is more often the case with the orientation behavior of naive birds. Although some HY birds are as well oriented as experienced birds on a nightly basis, nightly  $r$  values are typically lower (higher angular deviation) for the former group. With the exception of AD 12, whose activity was uniformly scattered as often as it was concentrated, mean  $\bar{r}$  values are higher for experienced birds. Moreover, AD birds are more consistently well oriented regardless of direction than are HY birds, as is evidenced by the standard deviations of the  $\bar{r}$  values. Caution must be exercised, however, when interpreting certain findings associated with within-night variation, because the method of quantifying the activity records does not yield highly reliable variance estimates.

More variability in the cage orientation of Savannah Sparrows that have never undertaken a migration was not expected, although empirical support for that expectation is limited at best. The individual variability that characterizes cage-orientation studies seldom receives explicit attention other than the spe-

cial statistical effort made to reduce it. Emlen (1969) did point out that immature Indigo Buntings (*Passerina cyanea*) were less consistent from night to night in their headings when tested in orientation cages essentially identical to the ones used in this study. Both Williams (1978), working with White-crowned Sparrows (*Zonotrichia leucophrys*), and Beacham (1982), working with Indigo Buntings, also examined age-dependent aspects of migratory orientation (see also Gauthreaux 1982). Interestingly, less experienced, immature birds responded more than adults to a horizon glow present during orientation tests with both species and were well oriented with respect to this horizon glow. Quite possibly this phototactic response obscured age-related differences in individual variability. It is also worth mentioning that both studies were conducted in the spring; so the immature birds possessed some migratory experience.

The differences observed in this study between experienced and naive Savannah Sparrows presumably reflect the importance of experience gained at the time of migration. To the extent that the process of selecting a direction in an orientation cage resembles free-flight selection, individuals that consistently select seasonally appropriate headings will be at an advantage *vis-à-vis* the added energetic costs and potentially dire consequences associated with errors in orientation. Interestingly, when orientational errors are mentioned in the literature, it is usually in conjunction with the migration of first-year, less experienced migrants (see Drury and Keith 1962; DeSante

TABLE 2. Compass orientation of eight naive Savannah Sparrows tested over six nights in the fall, 1981. The mean heading ( $\bar{a}_i$ )  $\pm$  angular deviation and the nightly vector length ( $r_i$ ) are given.

Bird	Night						$\bar{r} \pm 1 \text{ SD}^a$
	1	2	3	4	5	6	
HY01	$\bar{a}_i = 220 \pm 64^\circ$ $r_i = 0.536$	$192 \pm 80^\circ$ 0.374	$140 \pm 94^\circ$ 0.259 ns <sup>b</sup>	$90 \pm 59^\circ$ 0.587	$237 \pm 75^\circ$ 0.423	inactive	$0.436 \pm 0.131$
HY04	$\bar{a}_i = 92 \pm 73^\circ$ $r_i = 0.441$	$175 \pm 78^\circ$ 0.393	$152 \pm 52^\circ$ 0.652	$183 \pm 62^\circ$ 0.310	$210 \pm 77^\circ$ 0.403	$302 \pm 106^\circ$ 0.181 ns <sup>b</sup>	$0.387 \pm 0.156$
HY05	$\bar{a}_i = 186 \pm 43^\circ$ $r_i = 0.754$	$168 \pm 55^\circ$ 0.491	$205 \pm 111^\circ$ 0.152 ns <sup>b</sup>	$263 \pm 71^\circ$ 0.563	$148 \pm 39^\circ$ 0.784	$256 \pm 80^\circ$ 0.374 ns <sup>b</sup>	$0.520 \pm 0.238$
HY06	$\bar{a}_i = 337 \pm 77^\circ$ $r_i = 0.401$	inactive	$170 \pm 92^\circ$ 0.273 ns <sup>b</sup>	$181 \pm 61^\circ$ 0.566	$165 \pm 94^\circ$ 0.259 ns <sup>b</sup>	$191 \pm 67^\circ$ 0.502	$0.400 \pm 0.136$
HY13	$\bar{a}_i = 235 \pm 60^\circ$ $r_i = 0.575$	$155 \pm 74^\circ$ 0.432	$120 \pm 73^\circ$ 0.442	$160 \pm 70^\circ$ 0.472	$185 \pm 87^\circ$ 0.314	$270 \pm 54^\circ$ 0.631	$0.478 \pm 0.112$
HY16	$\bar{a}_i = 180 \pm 81^\circ$ $r_i = 0.365$	$63 \pm 103^\circ$ 0.198 ns <sup>b</sup>	$285 \pm 94^\circ$ 0.258	$188 \pm 94^\circ$ 0.261 ns <sup>b</sup>	$157 \pm 32^\circ$ 0.854	$199 \pm 89^\circ$ 0.298	$0.372 \pm 0.242$
HY17	$\bar{a}_i = 120 \pm 93^\circ$ $r_i = 0.268 \text{ ns}^b$	$144 \pm 48^\circ$ 0.704	$158 \pm 76^\circ$ 0.412	$333 \pm 86^\circ$ 0.322	$171 \pm 78^\circ$ 0.394	$185 \pm 50^\circ$ 0.683	$0.464 \pm 0.185$
HY19	$\bar{a}_i = 178 \pm 51^\circ$ $r_i = 0.666$	$200 \pm 72^\circ$ 0.450	$229 \pm 74^\circ$ 0.432	$185 \pm 67^\circ$ 0.500	$101 \pm 80^\circ$ 0.374	$215 \pm 114^\circ$ 0.138 ns <sup>b</sup>	$0.427 \pm 0.173$

<sup>a</sup> Mean of nightly vector lengths ( $r$ )  $\pm$  1 standard deviation.

<sup>b</sup> ns = nonsignificant  $r$  ( $P > 0.05$ ) according to Rayleigh Test (see Zar 1974).

1973, 1983; Able 1977; Ralph 1978, 1981; McLaren 1981).

Furthermore, a fundamental difference is thought to exist between experienced and inexperienced migrants with respect to navigational ability (Baker 1978, R. Wiltschko and W. Wiltschko 1978, Able 1980). Current theory argues that a migrant's ability to navigate is dependent upon *en route* experience (see Baker 1978, R. Wiltschko and W. Wiltschko 1978). Although the direction (Gwinner and Wiltschko 1978, 1980) and distance (Berthold and Querner 1981) of their first autumnal migration may be endogenously determined, naive birds have no information about their route or final destinations at the time they initiate migration. The high within-individual variability and the lack of clear between-individual differences among the inexperienced Savannah Sparrows are consistent with this notion (see DeSante 1983). Only after an individual becomes familiar with an area can site-specific information be used to determine the direction towards a goal (see Wiltschko and Wiltschko 1982). Experience is likely to be important in any process whereby migrants "attach" themselves to their wintering grounds and possibly *en route* locations (see Perdeck 1958, 1967; Ralph and Mewaldt 1975; Baker 1978; Berndt and Winkel 1978). The apparent differences among *experienced* migrants in their directional preferences, although based upon small sample sizes, may reflect different wintering goals (see Moore in press). Because all the birds used in this study were probably drawn from the same

breeding population does not necessarily mean that they share a common wintering area (Quay 1957, Norris and Hight 1957, J. Rising pers. comm.).

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### Algae on Jackass Penguins (*Spheniscus demersus*)

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Algae have been recorded growing on a number of aquatic animal species (Round 1981: 238). Boersma (1975) noted that algae occurred on the ventral surfaces of some Galapagos Penguins (*Spheniscus mendiculus*) but did not identify the algae concerned.

During a 7-yr study of Jackass Penguins (*Spheniscus demersus*) at St. Croix Island (33°48'S, 25°46'E) off the southeast coast of South Africa, we noted the occasional occurrence of algae on penguins. The algae were visible even from a distance but were observed only on penguins less than 3 yr old and predominantly on those in juvenal plumage. During 1982 and 1983 we made regular counts to establish the proportion of juveniles affected by algae (Table 1). A marked seasonal occurrence of the algae on juvenile penguins did not entirely coincide with the seasonal variation in juvenile numbers. Peak numbers of individuals with algae occurred during September, when the numbers of juveniles at the island begin annually to swell rapidly. At that time the juveniles return for a few days before departing for the pre-molt fattening period; they return about 6-8 weeks later to molt into adult plumage. Algae were not observed on molting penguins.

Whenever possible, we caught penguins with algae, recorded the extent of the areas covered with algae, obtained algal samples, and banded the penguin before release. The samples were obtained by wetting the affected area and then scraping off a sample with a scalpel blade. Part of the sample was placed in seawater, and the remainder was preserved in 10% formalin in seawater. Identification was later confirmed under a light microscope. The samples in seawater were examined as soon as possible after collection to note the degree of bleaching. A few feather tips were also removed to check for damage and points of algal attachment. The dominant algae in samples

could be identified only to the generic level. Of the 26 penguins from which samples were obtained at St. Croix Island, 15 had *Enteromorpha*, 10 had *Ectocarpus*, and one had *Enteromorpha* and *Ectocarpus* in separate areas. In addition, one filament of *Porphyra capensis* was found in a sample of *Enteromorpha*, and diatoms were found in five of the *Ectocarpus* samples. Diatom growth, as described by Croll and Holmes (1982) on Common Murres (*Uria aalge*), was not observed. Fresh, unbleached, moist samples of *Ectocarpus* and *Enteromorpha* contained numerous protozoa. We have also noted algae on Jackass Penguins at other islands. For instance, on a visit to Dyer Island (34° 41'S, 19°25'E) on 29 October 1982, 0.4% (n = 708) of juveniles had algae. *Enteromorpha* was the only alga represented in the three samples obtained.

Visible algae were present only on the dorsal surfaces of the penguins (Fig. 1) and covered areas of up to 200 cm<sup>2</sup>. (Bright green patches on the ventral surfaces were due to fecal matter.) Apparently the midback area became colonized only when growth had proceeded from the upper back and when moisture retention had been sufficient to allow colonization. The greater maximum length attained by *Enteromorpha* (10 mm), as compared with *Ectocarpus* (3 mm), when growing on penguins and possibly a greater dessication tolerance, as reflected in its higher position in the intertidal zone, might account for the more widespread occurrence of *Enteromorpha* on the penguin body.

Areas of worn plumage on subadult Jackass Penguins, particularly juveniles, often occurred in positions similar to those where algae grew. Typically, algae were attached to the rachis of feathers and often caused the tip of the rachis to curl upward. In Jackass Penguins with worn plumage and in those with algae, both barbs and barbules were frequently miss-