Anim. Behav., 1980, **28**, 684–704

SOLAR CUES IN THE MIGRATORY ORIENTATION OF THE SAVANNAH SPARROW, *PASSERCULUS SANDWICHENSIS*

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Abstract. Results clearly implicate the setting sun as a critical source of directional information in the migratory orientation of the savannah sparrow, *Passerculus sandwichensis*. Savannah sparrows allowed a view of both sunset and stars displayed oriented behaviour in biologically meaningful directions during spring and fall seasons. When the same individuals were denied a view of sunset, and tested under the stars alone, disorientation characterized their behaviour. Furthermore, birds allowed a view of sunset, but tested under 'overcast' night skies (no stars visible), displayed well-oriented behaviour indicating the sufficiency of sunset. Experiments in which the migrant's internal chronometer was shifted suggested a fixed-angle (menotactic) response to the sunset cue rather than a time-compensating compass mechanism. I believe stars are valuable to this migrant as celestial reference points. Orientational information gained at the time of sunset is transferred to stars on a nightly basis. The relationship between solar and stellar cues is apparently hierarchical in the savannah sparrow. Information necessary to select the appropriate migratory direction is gained from the primary cue, the setting sun, while maintenance of that heading is dependent on a secondary cue, probably the stars.

Introduction

Animals are fundamentally teleonomic, performing oriented or goal-directed activities in response to nearly all environmental contingencies. Although movements may be random, animals for the most part actively regulate their behaviours in spatial and temporal relationship with their environment. Prey-catching movements are directed toward prey, male courtship oriented with respect to the female, spring migration guided toward the proper goal, and so on. Migratory orientation is goal-directed behaviour associated with migration, the 'when' and 'where' of migration (see Jander 1975).

Oriented migrations require a periodic, if not continuous, input of directional information. Environmental sources of this information are called 'cues' and enable a migrant to select or to maintain a bearing on its migratory journey. Orientation cues are by definition, then, directionally related to the goal of the migrant. I focus my attention here on the role of the setting sun in the compass orientation of a nocturnal migrant, the savannah sparrow (*Passerculus sandwichensis*).

Experimental work in the field of avian migratory orientation began in earnest with the studies of the late Gustav Kramer. His early studies (e.g. 1949, 1950) concentrated on the orientation of nocturnal migrants and hinted at the importance of the sun as an orientation cue. The sun has always been regarded as an important cue in the diurnal orientation of birds (see Kramer 1953), and so the use of directional information at sunset by nocturnal migrants might be regarded as a logical extension (see Vleugel 1954; Lowery & Newman 1955). Early workers tended to accept the importance of the sun in the orientation of night migrants, feeling that the birds either went with the wind or perhaps relied on the moon's position or star patterns once the sun disappeared (see Matthews 1968). The importance attached to the sun was primarily grounded in intuition and lacked hard experimental evidence. Some 20 years later, the speculation proved well founded (see Moore 1978a; Emlen & Demong 1978; Bingman & Able in press); but in the meantime, other cue systems, particularly those based on stars and geomagnetic cues (see Emlen 1975), ascended in relative importance and the sunset was all but discarded.

Without disputing the evidence for the significance of stars or, probably, geomagnetism in the orientation of night migrants, I believe the directional information gained from the sun at sunset to be valuable and worthy of serious reconsideration. Fragmentary and largely circumstantial evidence currently exists suggesting that solar information may be of value to nocturnal migrants. Let me outline some of this evidence.

(i) The existence of a sun compass has been documented in several night migrants (v. St. Paul 1953; Bellrose 1958, 1963, 1967; Matthews 1961, 1963; Hamilton 1962a & 1962b; Shumakov in

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Emlen 1975; Able & Dillon 1977). Whether or not night migrants make use of this compass capability is the question.

(ii) Passerine nocturnal migrants are known to make sea crossings that necessitate flying beyond darkness during daylight hours. For example, Nearctic–Neotropic migrants commence trans-Gulf flights at night, experience sunrise while flying over the Gulf of Mexico, and do not make land on the northern Gulf Coast in spring until well into daylight hours (Lowery 1945, 1946; Gauthreaux 1971, 1972). Migrants have also been observed to exhibit oriented migratory behaviour in the morning hours, possibly as a corrective measure for displacements experienced during a night's flight (Baird & Nisbet 1960; Myres 1964; Able 1977; Gauthreaux 1978).

(iii) The peak of migratory activity occurs at night among nocturnal passerine migrants, but the actual night's migration usually commences prior to the end of twilight within the first hour after sunset (Drury & Keith 1962; Swinebroad 1964; Parslow 1969; Gauthreaux 1971, 1972; Hebrard 1972; Richardson 1974; Lindgren & Nilsson 1975; Alerstam 1976), and has been observed to occur prior to sunset long before stellar cues are available (Alerstam 1976; Gauthreaux pers. comm.).

(iv) Radar tracking observations of Emlen & Demong (1978) indicate that artificially released white-throated sparrows (*Zonotrichia albicollis*) assumed appropriate migratory directions during twilight after the sun disc fell below the horizon but before stars were visible.

(v) Other studies have pointed out that migrants displayed appropriate orientation under overcast night skies if the sun had been visible prior to the nightly departure. For example, Cochran et al. (1967) observed that migrating thrushes (family Turdidae) were able to maintain their direction at night under overcast only if clear to partly cloudy skies were available during the day or evening before departure. Shumakov (1965 in Emlen 1975) reported that chaffinches (*Fringilla coelebs*) and warblers (*Sylvia nisoria*) could maintain a direction for several hours after the onset of heavy clouds if, when the sun was out, landmarks were also visible, implying that the birds transferred directional information from the sun to geographical referents. Opportunities to study migration and associated orientation over the course of prolonged overcast are few, but observations on two such occasions established a role for the sun in the orientation of night migrants and further suggested that the longer a migrant is prevented from making a 'compass reading', the more disoriented it becomes (Hebrard 1972; Emlen in press).

(vi) Finally, Kramer (1949, 1951) found that his caged nocturnal migrants assumed proper directions at night only when exposed to the sun at or before sunset. Otherwise the birds apparently mistook the glow from city lights for the setting sun and exhibited 'false' orientation.

The circumstantial evidence encouraged me to pursue experimentally the role of the setting sun in the orientation behaviour of night migrants. Initially, I felt that a view of the setting sun might improve orientation inasmuch as additional information would be available to the migrant, or at best that sunset might prove to be a sufficient cue for seasonally appropriate orientation. I address the following questions in this report. (i) Is directional information available at sunset necessary for seasonally appropriate migratory orientation? (ii) Is directional information available at sunset sufficient for seasonally appropriate migratory orientation? (iii) What is the role of stellar information? (iv) If the sun does play a role in migratory orientation, what is the specific nature of the mechanism? Is a time-compensating sun compass involved or is direction finding a simple, constant-angle response to the setting sun?

Methods

Subjects

I conducted all orientation experiments reported on here with a short-distance North American nocturnal migrant, the savannah sparrow (*Passerculus sandwichensis*). The breeding range is extensive, stretching across the northern portion of the United States and Canada. Savannah sparrows are found wintering widely across southern United States and Mexico.

Savannah sparrows are abundant winter residents in the Piedmont region of South Carolina, inhabiting weedy fields and the like. Birds used in spring orientation experiments were mist-netted during March prior to the onset of spring migration on several sites within Pickens County, South Carolina, all within 30 km of the experimental location. I travelled to Grand Forks, North Dakota, located within the breeding range of the species, to obtain fall migrants. Orientation experiments were conducted in North Dakota in early September at the onset of fall migration in the area, and the sparrows were then transported to South Carolina for additional fall work.

The fall migrants from North Dakota and the spring birds from South Carolina may well represent different subspecies. The possibility of population-related orientation differences is worthy of future attention.

The migrants were caged individually in a small aviary facility exposed to natural photoperiod and the local magnetic field. Although covered, the facility was open on two sides, and the birds were exposed to ambient conditions including sunset and a portion of the starry sky. Layena chicken feed was available ad libitum. Grit was supplied. Similar facilities were used in North Dakota.

Orientation Cage

The 'Emlen' orientation cage was used to measure migratory orientation behaviour (Emlen & Emlen 1966). Their method takes advantage of the fact that many nocturnal migrants exhibit heightened locomotor activity at night during the migration season (see Berthold 1975). This nocturnal restlessness or 'Zugunruhe' is expressed in a cage situation. In effect, the Zugunruhe observed in a cage corresponds to migratory activity under natural conditions. The critical point for orientation research is that the restlessness is usually oriented in a seasonally appropriate direction when the requisite cues are available. The bird hops or flutters preferentially in its migratory direction (Fig. 1).

In 1977, I conducted experiments in which I artificially prevented birds from seeing stars during a test (sunset/no stars situation, abbreviated as SS/NO ST). I modified the orientation cage only slightly by placing a circular board elevated approximately 6 cm over the hardware cloth cover. The edge of the board extended beyond the cone. The subject could observe the setting sun, but not the stars during the course of a test.

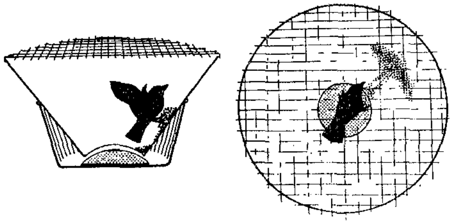

Fig. 1. Schematic of the Emlen orientation cage. The bird stands on the ink pad situated on the bottom of the pan, and each time it hops onto the sloping funnel wall it leaves footprints. Left: cross-section. Right: top view.

Experimental Procedure

All orientation experiments were conducted outdoors at two sites in South Carolina and a single site in North Dakota. Tests were first carried out in spring 1976, approximately 1 km from the city of Clemson, South Carolina, and the Clemson University campus. No landscape features were visible on the horizon, but a single prominent horizon glow from the campus was clearly visible to the ENE (east-northeast). Artificial horizon glows represent a potential problem for orientation field experiments. I moved my operation the following spring to a site located approximately 11 km from the nearest horizon glow.

Savannah sparrows put on subcutaneous fat reserves in preparation for migration and exhibit nocturnal locomotor activity (Zugunruhe), as is characteristic of other nocturnal passerine migrants (see Berthold 1975). With the appearance of this restlessness a sparrow was considered ready for testing. Birds were transported to the test site in covered holding cages and placed individually in the orientation cages before or after the sunset depending on whether or not the test called for sunset exposure. Cages were elevated above terrestrial features. I examined the orientation behaviour of 13 savannah sparrows in the spring of 1976, 23 in the spring of 1977, and 18 in the fall of 1977.

Data Analysis

Quantification of the orientation records closely followed Emlen & Emlen (1966). A scale of activity ranging from 1 to 30 units was created from actual footprint records and used to quantify activity numerically. One unit of activity was equivalent to approximately three hops by a caged migrant. I pooled the activity under a given test situation for each bird and presented the result in the form of a vector diagram. The diagrams are drawn such that the radius equals the greatest number of activity units in any one 22.5° sector. The lengths of the other vectors are proportional to the radius.

From the amount of activity per sector, I calculated by vector analysis the mean direction or heading of activity ($\bar{a}$) and the length of the mean vector (r), which represents the concentration of activity, for each occasion the bird was tested (bird-night) as well as for the pooled activity (see Batschelet 1965, 1972; Zar 1974).

Several methods were employed in treating the orientation data. (i) Bird-night: for a bird, each test's mean direction constituted a datum as did the associated r values. (ii) Mean of means: the mean of the nightly mean directions for an individual (or for a test situation) is calculated along with the r values associated with the distribution of points. (iii) Sum of total activity: the activity units in each compass sector are summed over all nights for an individual under a particular experimental situation or summed over all individuals tested on a particular night (see Wiltschko 1968), and the associated statistics computed.

Single tests with a bird in which the level of activity was not equal to or greater than 15 activity units were excluded from vector analysis, and the bird deemed migratorily 'inactive'. An N of 15 corresponds roughly to 40 hops. It is not uncommon for a bird to hop and flutter about when placed into and removed from a test cage, activity that is clearly unrelated to migratory orientation. Also, extremely low levels of cage activity do not reflect a very highly motivated migrant.

Results

Sunset: Is It Necessary?

Savannah sparrows exhibit a definite northerly directional tendency in their spring orientation behaviour, based on the sample of individuals examined in this study. Figure 2 plots the mean vectors of individual birds (bird-nights) tested under the control sunset plus stars situation (SS/ST). The two spring distributions (1976 and 1977) are not significantly different from one another according to a Watson–Williams two-sample F-test ($P > 0.05$). An equally pronounced directional tendency to the SSW ($\bar{a} = 203°$) characterizes the sample of fall birds. I draw attention to these plots so that a general impression of the migratory preferences of the savannah sparrow might be gained for both seasons.

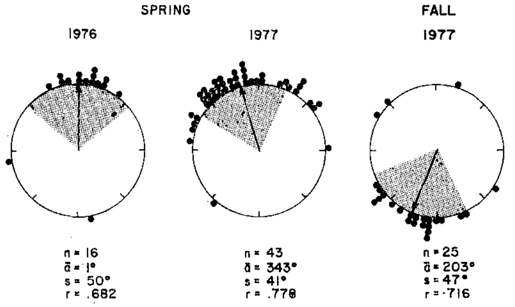

Fig. 2. Directional preferences of individual savannah sparrows tested during two springs and a fall under the sunset plus stars (SS/ST) situation. Each black dot represents the mean heading of an individual bird-night. Only headings of immature birds tested in Clemson, South Carolina are plotted for fall 1977. N = the sample size of bird-nights; a = mean direction of distribution of headings (arrow in circle); s = angular analogue of standard deviation (shaded area is ± s); r = measure of the strength of orientation varying from 0 to 1.00. In this and all other orientation diagrams, north is 0° or 360° and is toward the top of the figure.

Now examine the orientation behaviour of individual sparrows tested with a view of both sunset and stars (SS/ST) and when the same birds were tested without exposure to sunset (ST). A comparison of the results from the two test situations addresses the question of the necessity of viewing sunset. If not strictly necessary, does a view of sunset improve or in some other way affect orientation behaviour? Vector diagrams of 13 savannah sparrows tested under both situations in spring 1976 are presented in Fig. 3. Focusing on the behaviour under SS/ST, only 2 of 13 sparrows failed to orient their activity in a seasonally appropriate northward direction, though one bird (P27) failed to show statistically significant orientation (see Table I). Twenty tests among the 13 individuals were conducted exposing birds to both sunset and stars, and 14 (70%) resulted in statistically significant ($P < 0.05$) seasonally appropriate orientation.

What is surprising is the behaviour of these same individuals when deprived of solar input (ST condition) during a test. Only one sparrow (P19) displayed activity that can be regarded as directionally appropriate, and even then in only one of two tests under this situation (Fig. 3). Otherwise, the sparrows were disoriented, displaying statistically uniform distributions of activity; or when a preference was discernible (P03, P06, P10, P26, P28, and P29), it was clearly inappropriate for spring migration. Furthermore, three savannah sparrows (P03, P25, and P28) when tested under the stars-only situation a second time (Fig. 3) failed to exhibit sufficient ($N > 15$) migratory activity, while such low levels of activity were never recorded under the SS/ST situation.

During this spring a horizon glow to the ENE was present on most nights of testing. Despite the northerly headings characteristic of the birds under the SS/ST situation, some indication exists that the horizon glow may be influencing activity. Bird P27, for example, seemed to be affected whether or not sunset was available. Note also that the activity pattern of P26 under the SS/ST situation is somewhat bimodal: the more pronounced mode to the NNW and the lesser mode to the NE–ENE. Under the ST situation, orientation directed toward the ENE sky glow seems a parsimonious explanation for several birds, namely P06, P10, and P28, and probably also P27. Finally, note the striking response of P03 when tested in the presence of a moon under the stars alone. Normally, I excluded tests under a moon visible to the birds, but I show P03 because the only other ST situation test with this

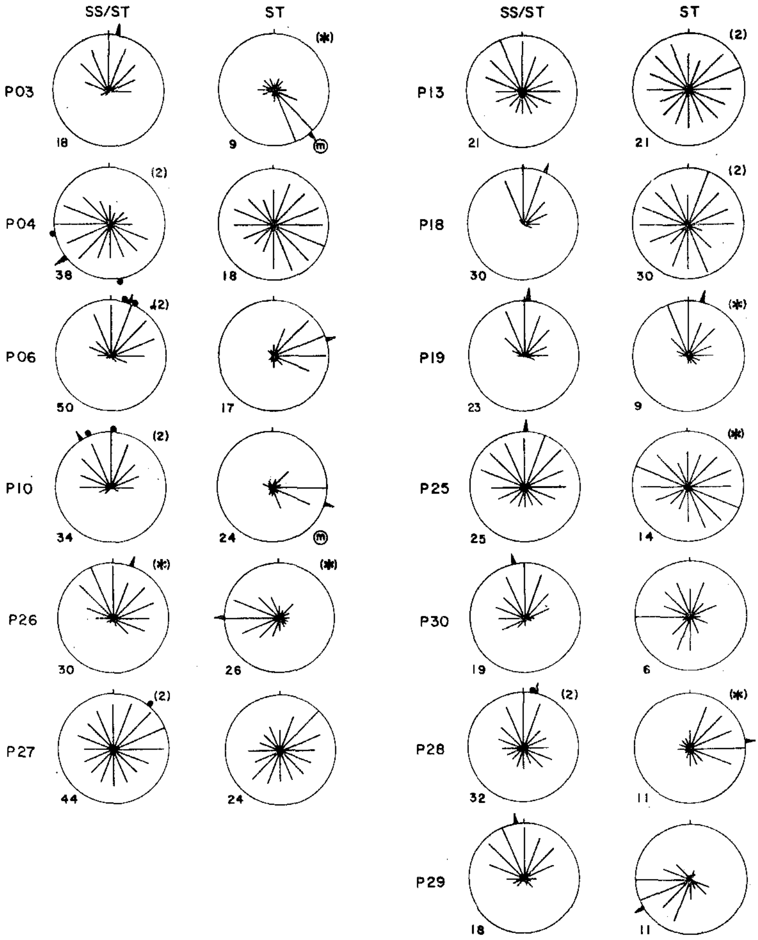

Fig. 3. Orientation behaviour of 13 savannah sparrows tested in the spring of 1976 and allowed to view sunset plus stars (SS/ST column) and stars only (ST column). Replicate tests (shown parenthetically upper right) under a test situation were pooled for an individual and analysed accordingly. Vector diagrams are drawn such that the radius equals the greatest number of activity units in any one 22.5° sector (lower left of each circle). The arrow on the circumference indicates the mean direction of orientation when the distribution is statistically significant ($P < 0.05$). The dots on the circumference of some diagrams represent the mean headings of statistically significant individual tests (bird-nights) when the activity of more than one bird-night was pooled to yield the vector diagrams shown. Unless otherwise indicated by a moon symbol (encircled *m*), all tests were conducted on moonless nights. Additional tests under a given situation but not shown either because $N < 15$ (P03, P25, P26) or because of the moon's presence (P26, P19) are identified by an asterisk. See Table I for statistics.

bird failed to meet the activity criterion ($N > 15$). The moon azimuth on that night passed from 130° to 142° over the course of the test period (the moon symbol only coincidentally is located in that direction). A treatment of lunar influences is in preparation.

Comparable results from a second spring (1977) of study are revealed in Fig. 4. Fifteen of 17 savannah sparrows, some of which were tested repeatedly, displayed well-oriented migratory activity to the north (NNE to NW) under the control situation (see Table II). A total of 46 SS/ST tests were conducted on moonless nights with these birds, and 33 (72 %) were not only statistically significant, but also meaningfully oriented. Reasonable arguments could be made that two additional birds (S06 and S19) be included among the well-oriented. Clearly, the mean heading of S19 ($\bar{a} = 48°$) deviates only somewhat from the norm, and one of the four SS/ST tests with S06 is directionally appropriate and statistically significant. Only savannahs S01 and S08 display unquestionably poor cage orientation.

Table I. Statistical Results of Spring 1976 Experiments Comparing the Orientation Behaviour of 13 Savannah Sparrows Allowed a View of Sunset and Stars (SS/ST) and Stars Only (ST). Figure 3 Presents Circular Diagrams

Bird	Test	*N*	$\bar{a}$	*r*
P03	SS/ST	38	12°	0.599*
	ST	17	140	0.332*
P04	SS/ST	126(2)	234	0.225*
	ST	80	99	0.111
P06	SS/ST	132(2)	19	0.560*
	ST	36	73	0.567*
P10	SS/ST	85(2)	328	0.394*
	ST	39	106	0.442
P13	SS/ST	93	348	0.175*
	ST	92(2)	29	0.045
P18	SS/ST	48	23	0.750*
	ST	135	315	0.046
P19	SS/ST	41	6	0.763*
	ST	19	15	0.591*
P25	SS/ST	102	3	0.226*
	ST	63	42	0.061
P26	SS/ST	90	18	0.450*
	ST	62	274	0.414*
P27	SS/ST	192(2)	47	0.122
	ST	87	99	0.093
P28	SS/ST	99(2)	14	0.204*
	ST	27	79	0.497*
P29	SS/ST	49	354	0.502*
	ST	26	238	0.524*
P30	SS/ST	47	348	0.500*
	ST	17	290	0.199

$\bar{a}$, mean direction of activity; *r*, Rayleigh's measure of concentration (length of mean vector). When a bird was tested more than once under a particular situation, I noted it parenthetically.
*Indicates statistical significance at the 0.05 level.

When these same 17 individuals were tested without sunset exposure (ST situation), orientation activity decreased (Table II), and for the most part the birds were disoriented (Fig. 4). More critically, only one bird (S07) behaved in a manner that might be construed as seasonally appropriate, and even then the northerly trend lacked statistical significance ($P > 0.05$). The directionality of S17, S30, and S26 is apparently biased by the presence of the moon. Lunar influence often dominated the behaviour of birds tested under the ST situation, while bimodal patterns of activity were not unusual when sunset was coupled with a view of the stars (see Moore 1978b).

The reduced levels of Zugunruhe alluded to in the spring 1976 data set are clearly evident in the spring of 1977. Of 19 tests with stars alone and no moon present, 12 (63 %) failed to meet the activity criterion; only seven of these instances are actually shown in Fig. 4 (one of which is a test with the moon present), because when a bird was tested more than once it often was sufficiently active, and that record was plotted.

The results of my fall experiments are equally convincing. Vector diagrams are presented (Fig. 5) for 14 savannah sparrows tested in South Carolina. SS/ST and ST tests conducted on moonlit nights are excluded from this analysis. When the moon was a factor during the fall its azimuth varied from 105° to 205°. As a result, differentiating between well-oriented Zugunruhe and a locomotor response to the moon was not always easy. Eight of 14 sparrows are statistically well oriented in a southerly to SSW direction, and another (F33) is equally well oriented to the SW. Three other savannah sparrows (F02, F04, and F39) showed preferential activity to the SW and S, though neither distribution was deemed significant. I must comment briefly on the orientation behaviour of F11, F24, and F30 in light of the fact that all three are adult migrants as are F06, F12, and F39, and are being tested in South Carolina following a substantial eastward displacement from North Dakota. The westerly preference of the former three adults may not be inappropriate under the circumstances (see Moore 1978b).

When the fall birds were tested after the sun had set, but allowed access to stars (ST situation), disorientation or seasonally inappropriate orientation behaviour was typical of the active birds. Activity levels declined under this test situation (Table III) as fully half of the sparrows were 'inactive' ($N < 15$). In two instances, however, southerly preferences were recorded under the

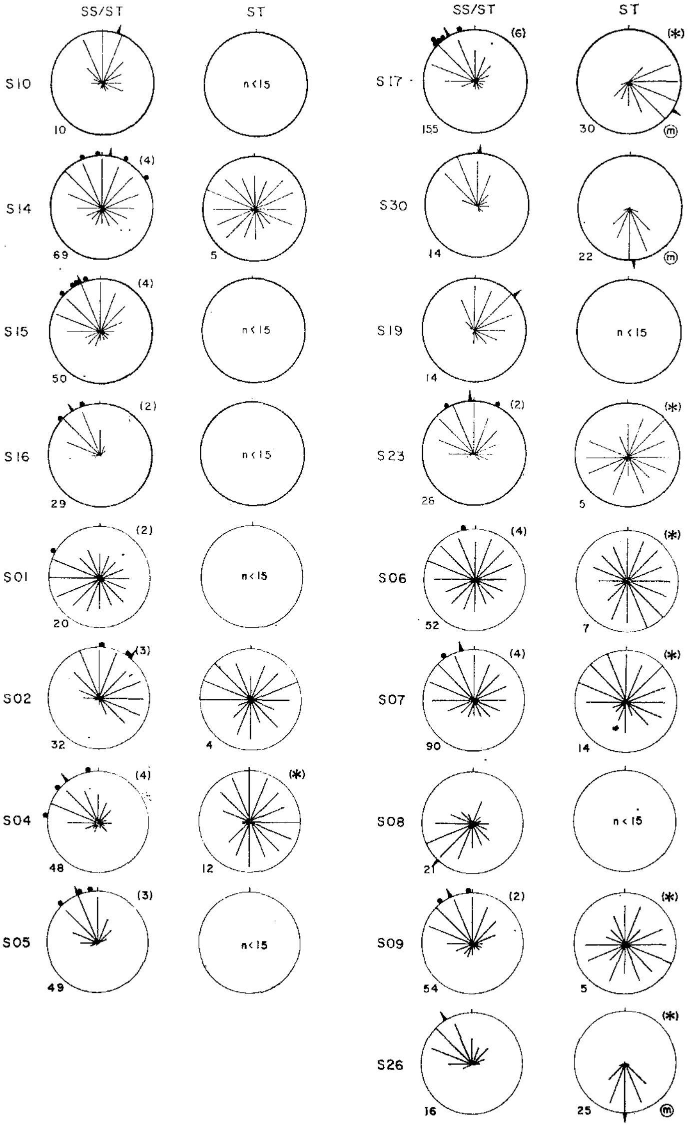

Fig. 4. Orientation behaviour of 17 savannah sparrows tested in the spring of 1977 and allowed to view sunset plus stars (SS/ST column) and stars only (ST column). Unless otherwise indicated by a moon symbol (encircled *m*), all tests were conducted on moonless nights. Asterisks identify additional tests not shown because $N < 15$ (S06, S09, S17, S26) or because the moon was present (S04, S07, S23). See Fig. 3 for figure details, and Table II for statistics.

stars alone: F13 ($\bar{a} = 180^\circ$) and one of two ST tests of sparrow F23 ($\bar{a} = 186^\circ$). The pooled activity of the latter bird yielded non-significant uniform orientation.

Table II. Statistical Results of Spring 1977 Experiments Comparing the Orientation Behaviour of 17 Savannah Sparrows Allowed a View of the Sunset and Stars (SS/ST) and Stars Only (ST). Figure 4 Presents Circular Diagrams

Bird	Test	N	$\bar{a}$	r
S01	SS/ST	79(2)	249°	0.148
	ST	< 15		
S02	SS/ST	109(3)	37	0.406*
	ST	17	352	0.071
S15	SS/ST	161(4)	337	0.389*
	ST	< 15		
S04	SS/ST	110(4)	323	0.430*
	ST	54	70	0.166
S05	SS/ST	94(3)	337	0.703*
	ST	< 15		
S06	SS/ST	230(4)	330	0.114*
	ST	32	97	0.109
S07	SS/ST	351(4)	346	0.236*
	ST	60	11	0.207
S08	SS/ST	61	222	0.310*
	ST	< 15		
S09	SS/ST	165(2)	336	0.412*
	ST	21	130	0.090
S10	SS/ST	23	19	0.508*
	ST	< 15		
S14	SS/ST	257(4)	9	0.276*
	ST	21	306	0.084
S16	SS/ST	41(2)	328	0.838*
	ST	< 15		
S17	SS/ST	353(5)	328	0.483*
	ST	71	123	0.617*
S19	SS/ST	34	48	0.561*
	ST	< 15		
S23	SS/ST	75(2)	356	0.529*
	ST	30	89	0.310
S26	SS/ST	32	330	0.637*
	ST	37	180	0.858*
S30	SS/ST	27	2	0.566*
	ST	32	176	0.823*

See Table I for symbol explanation.
*Indicates statistical significance at the 0.05 level.

Ink Cover Tests

Let me anticipate a criticism traceable in part to the methodology. Zugunruhe characteristically commences sometime after twilight, continues through the night, and ends prior to sunrise. Therefore, it is unlikely that a bird would exhibit migratory restlessness earlier than this despite being placed in an orientation cage during the sunset period (SS/ST and SS/NO ST tests), though extraneous activity toward the setting sun might occur (see Bingman & Able in press). It could be argued that at least some of the activity recorded during a SS/ST test occurred before the stars were visible during the first 0.5 to 1 h of cage time. My observations indicate that other than 'noise' level activity when the bird enters the cage, savannah sparrows are generally 'inactive' and initiate Zugunruhe in the cage at the appropriate time.

I conducted a series of orientation tests in which I recorded only activity after the sunset period had ended and the first stars were out. Pieces of construction board were placed over the ink pad of the cage and removed from the bottom of the cage without disturbing the subject after the sun had set. The orientation behaviour of eight sparrows under the SS/ST situation with ink pad covers was compared with the activity records derived from 'normal' (without covers) tests (Fig. 6). Inspection of the distributions suggests that activity recorded during a typical SS/ST test parallels activity known to have been recorded after the sunset period. Only two birds (S04 and S23) concentrated their activity in significantly ($P < 0.05$) different directions according to the Watson–Williams test, and even then the headings are in seasonally appropriate directions.

Sunset: Is It Sufficient?

Compass information derived from the sun at sunset may be necessary but not sufficient in itself to allow migrant savannah sparrows to orient. A plot of the mean nightly headings of individuals tested in spring and fall under the SS/NO ST situation, however, reveals a seasonally well-oriented sample (Fig. 7). Although the spring distribution of means is not as concentrated ($r = 0.595$) as when the SS/ST sample is plotted (1976: $r = 0.682$ and 1977: $r = 0.778$), fall directionality is equally pronounced under either situation (compare fall diagrams, Fig. 2 & Fig. 7).

During the spring migration period (1977), natural overcast (no stars visible) occurred after a sunset (SS/NO ST) enough times that the question of sufficiency could be addressed. Thirteen birds were tested at least once each under this experimental situation on moonless nights (Fig. 8), and in four cases more than once, resulting in 17 tests. More than half (10) of these SS/NO ST tests resulted in statistically significant orientation in a meaningful northerly to northwesterly direction. In addition, the activity of S26 is clearly northward, while most of S22's activity is concentrated in a N–W arc.

The migratory orientation of an additional 11 savannah sparrows was recorded under artificially created night overcast (SS/NO ST) in the fall of 1977 (Fig. 9). One bird failed to show sufficient activity (F13), and two others were disoriented (F33 & F35), but the remaining eight sparrows tested on moonless nights yielded well-oriented activity records.

Comparison of the two test situations (SS/ST & SS/NO ST) indicates that orientation behaviour tends to be directionally more concentrated (higher *r* values) and more often in the appropriate direction when stars are coupled with sunset cues. This is true for spring results (compare SS/ST Figs. 3 and 4 with SS/NO ST Fig. 8) and those for the fall (compare SS/ST Fig. 5 with SS/NO ST Fig. 9). I also noted a decline in the quantity of activity when stars were not coupled with sunset for both spring (1977) and fall (immature birds) tests. Compare the *N*'s for SS/ST tests (Tables I & II) and SS/NO ST tests (Table

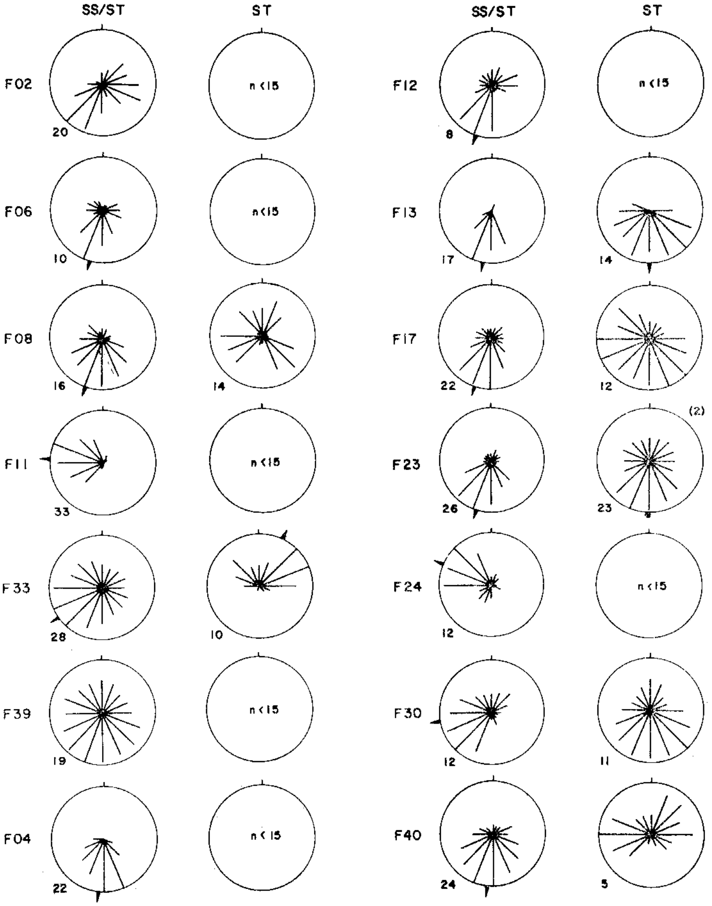

Fig. 5. Orientation behaviour of 14 savannah sparrows tested in the fall of 1977 (Clemson, South Carolina) and allowed to view the sunset plus stars (SS/ST column) and stars only (ST column). All tests were conducted on moonless nights. See Fig. 3 for figure details, and Table III for statistics.

IV). Note that adult birds were tested under the SS/NO ST situation only on moonlit nights. I attribute the difference that does exist to the absence of any visual referent such as stars for maintenance of a pre-selected migratory direction.

Table III. Statistical Results of Fall 1977 Experiments Comparing the Orientation Behaviour of 14 Savannah Sparrows Allowed a View of Sunset and Stars (SS/ST) and Stars Only (ST) on Moonless Nights. Figure 5 Presents Circular Diagrams

Bird	Test	*N*	$\bar{a}$	*r*
F02	SS/ST	53	157°	0.327*
	ST	< 15		
F04	SS/ST	37	186	0.781*
	ST	< 15		
F06	SS/ST	20	193	0.379*
	ST	< 15		
F08	SS/ST	42	198	0.433*
	ST	46	279	0.157
F11	SS/ST	52(2)	277	0.664*
	ST	< 15		
F12	SS/ST	20	198	0.225
	ST	< 15		
F13	SS/ST	22	189	0.739*
	ST	40	180	0.523*
F17	SS/ST	56	199	0.378*
	ST	49	208	0.220
F23	SS/ST	59	197	0.466*
	ST	84(2)	185	0.189
F24	SS/ST	25	293	0.568*
	ST	< 15		
F30	SS/ST	33	261	0.315*
	ST	42	171	0.217
F33	SS/ST	104	237	0.213*
	ST	22	26	0.520*
F39	SS/ST	82	199	0.145
	ST	< 15		
F40	SS/ST	68	186	0.445*
	ST	16	341	0.234

See Table I for symbol explanation.
*Indicates statistical significance at the 0.05 level.

Sunset: How Much Is Necessary?

I would now like to analyse in finer detail the savannah sparrow's use of solar information. Is a view of the actual sun disc required or is the migrant able to gain reliable information from the sun once it has declined below the horizon? Although the sun disc provides a more precisely defined and locatable cue, I imagine that a migrant could determine its direction from the usually distinct character of the sunset horizon glow (see Emlen & Demong 1978). Such is certainly an adequate approximation of the sun's position. The possibility also exists that migrants are determining the sun's position on partly cloudy evenings or when the disc is below the horizon through reception of polarized light.

A first step is taken toward analysing these capabilities by comparing orientation behaviour when the sun disc is visible (SS) and when it is below the horizon (Ss). I compared the migratory orientation of spring (1977) and fall (1977) sparrows under the two sunset conditions (Fig. 10). The sample sizes are not large because I excluded birds tested under either starry or moonlit nights. The two distributions of headings are nearly identical in both spring and fall. Examination of the results at the individual level (Table V) does not indicate any obvious differences in behaviour as a function of sunset conditions, though a suggestion does appear. For example, while no differences exist in the mean $\bar{r}$ values for spring (SS $\bar{r} = 0.423$ and Ss $\bar{r} = 0.443$), the 'sun disc visible' $\bar{r}$ value is higher than the Ss $\bar{r}$ for fall (0.512 versus 0.332), suggesting improved orientation when the migrant can see the sun disc. In addition, a few birds were tested under both conditions, allowing further comparison (S03, S06, S13, and S14 in spring and F08 and F23 in fall). Taking *r* values as a measure of being well oriented, four of six of these birds were better oriented under the SS condition. Note also that, though S06 has a higher *r* value under the Ss condition, its activity is hardly appropriate for spring migration ($\bar{a} = 159°$).

I also compared orientation behaviour when the sun disc was visible (SS), and when it was not (Ss), but this time sunset was followed by clear night sky (stars visible). I was able to test 12 birds in the spring of 1977 at least once under both sunset conditions (Fig. 11). These sparrows manifested no apparent difference in behaviour related to the quality of sunset input. I discovered no consistent trend for higher *r* values to be associated with the SS condition.

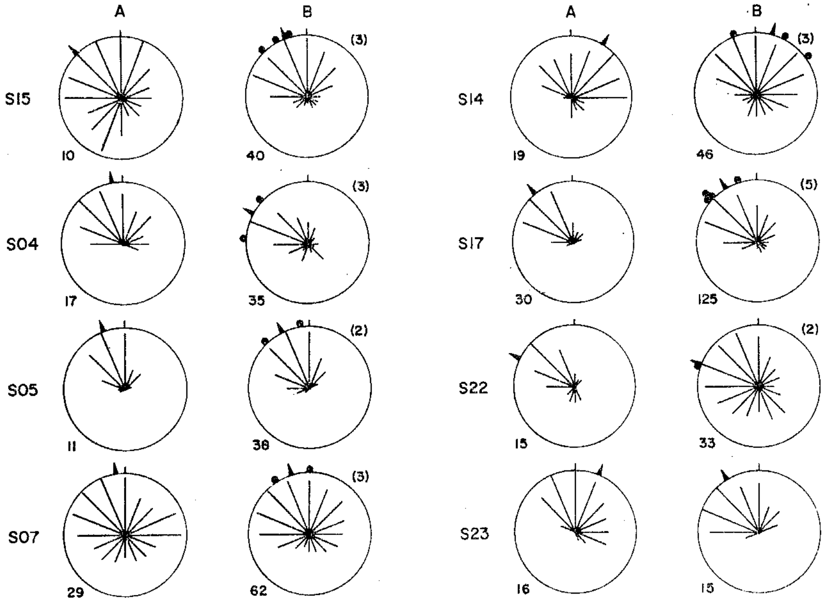

Fig. 6. Orientation behaviour of eight spring (1977) savannah sparrows tested under the SS/ST situation on moonless nights with (A) and without (B) covers over the ink pad during the sunset period. Clearly, no material difference exists between the two conditions. See Fig. 3 for figure details.

Response to Sunset: Menotaxis?

Most nocturnal migrants are otherwise day-animals, and verification of a sun-compass mechanism among these species should not be an especially surprising discovery. A migrant is likely to respond to a directional cue such as the sun in two ways: (i) constant angle orientation (menotaxis), or (ii) constant azimuth orientation involving compensation for the apparent motion of the sun through the course of a day.

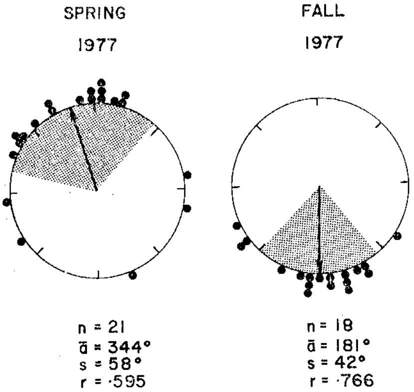

Fig. 7. Directional preferences of individual savannah sparrows tested during the spring and fall of 1977 and allowed only a view of sunset (SS/NO ST situation). Only headings of immature birds tested in Clemson, South Carolina, are plotted for the fall. See Fig. 2 for details.

If savannah sparrows are responding in a fixed-angle manner to the setting sun, no directional change would be expected under a clock-shift regime. I conducted experiments in spring 1977 to determine the effects of a clock-shift on the migratory orientation of this species. I selected six birds (one of which died during the resetting period) whose activity under the SS/ST situation had been well oriented (see control column Fig. 12). The sparrows were moved into an environmental chamber for eight days and phase-shifted 6 h slow. If a knowledge of the time of day is required, a bird whose biological clock has been phase-shifted 6 h slow should exhibit a clockwise deviation in its directional preference of approximately 90°.

The first test night after the phase shift, the savannah sparrows were tested with a clear view of the sun disc prior to sunset. No stars were visible after sunset as a result of natural overcast, but the moon was faintly visible to the SSE. The overcast precluded any stellar bias on this first night. Unfortunately, the moon was present,

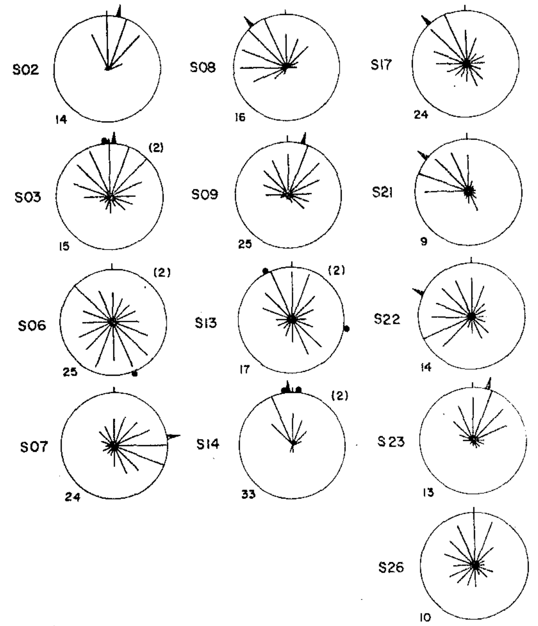

Fig. 8. Spring (1977) orientation behaviour of 13 savannah sparrows tested under natural overcast (no stars visible), but allowed a view of sunset (SS/NO ST situation). Tests were conducted on moonless nights. See Fig. 3 for figure details, and Table IV for statistics.

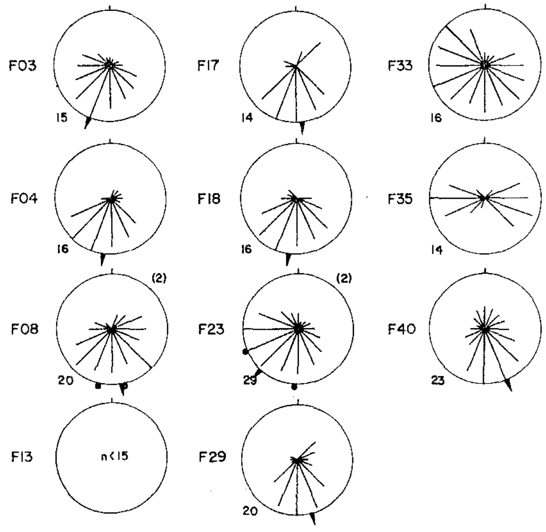

Fig. 9. Fall (1977) orientation behaviour of 11 savannah sparrows tested on moonless nights under artificial night overcast (no stars visible), but allowed a view of sunset (SS/NO ST situation). See Fig. 3 for figure details, and Table IV for statistics.

though it is unlikely that this migrant possesses any form of lunar compass (Moore 1978b, unpublished data). The predicted clockwise shift in orientation failed to materialize (Fig. 12). S16 and S17 were apparently influenced by the moon and displayed bimodal patterns of activity. Note that the direction associated with the dominant mode coincides nicely with the bird's activity prior to the clock-shift. Likewise, the orientation behaviour of the other birds, with the exception of S05, revealed no suggestion of a directional shift in orientation. The birds were returned to the 6 h slow regime and retested the following night. Again the moon was present, but so also were the stars (Fig. 12). Once again, orientation was only marginally different from the pre-phase-shift behaviour, discounting apparent lunar influence (S05 and S17). The 24° clockwise directional shift noted for S23 results in a statistically significant difference between the means ($0.025 < P < 0.05$) according to a Watson–Williams two-sample F test, but falls far short of the 90° deviation predicted (Table VI).

Role of the Stars

I analysed the orientation data in more detail, searching for subtle indications that savannah

Table IV. Statistical Results of Spring (S) and Fall (F) Experiments Conducted under the SS/NO ST Situation on Moonless Nights. See also Figs. 8 and 9

Bird	N	$\bar{a}$	s	r
S02	21	13°	33°	0.846*
S03	51(2)	6	81	0.371*
S06	102(2)	205	121	0.109
S07	70	83	82	0.356*
S08	43	319	64	0.541*
S09	68	17	75	0.421*
S13	58(2)	bimodal		
S14	45(2)	356	53	0.649*
S17	69	319	94	0.259*
S21	20	309	73	0.440*
S22	46	296	94	0.260*
S23	29	16	61	0.564*
S26	32	306	70	0.473*
F03	42	203	75	0.426*
F04	39	189	64	0.541*
F08	63(2)	170	82	0.363*
F13	$N < 15$			
F17	32	174	66	0.514*
F18	39	189	56	0.618*
F23	98(2)	222	81	0.368*
F29	44	165	62	0.555*
F33	68	220	103	0.196
F35	36	177	113	0.141
F40	70	154	90	0.293*

See Table I for symbol explanation.
*Indicates statistical significance at the 0.05 level.

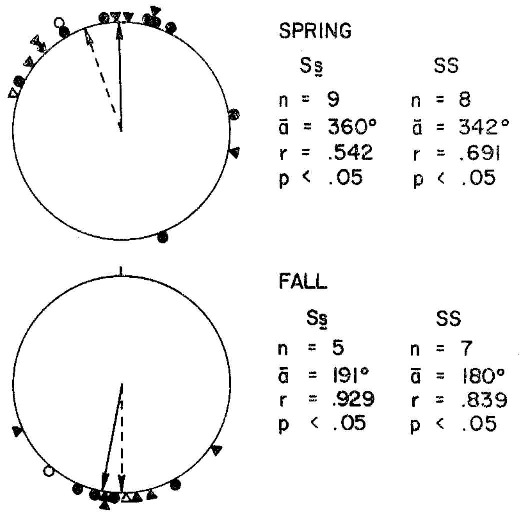

Fig. 10. Directional preferences of savannah sparrows tested under either the Ss/NO ST (triangles: dashed vector) or SS/NO ST (circles: solid vector) situation where Ss symbolizes 'only sunset horizon glow visible' and SS 'sun disc visible to bird above horizon'. Open circles and triangles mean non-significant ($P > 0.05$) individual mean headings. All tests were conducted on moonless nights.

sparrows are capable of using stars without first seeing sunset. First, I looked at pooled stars-only data, both mean of means and summed activity (Fig. 13). I performed Rayleigh tests on the pooled means for the three seasons regardless of whether or not the mean directions were individually significant (black dots $P < 0.05$; white dots $P > 0.05$). ST situations in which the moon was a factor were kept separate from moonless nights. Only in the spring 1977 data set did the mean of means procedure yield a statistically significant heading ($\bar{a} = 54°$). Note that not one of the seven individual means itself was significant for that season. Turn now to the summed activity treatment, where activity was summed for each compass sector across all bird-nights (Fig. 13). Statistically uniform distributions characterize the ST situation for all three seasons.

I next reasoned that if a view of the sunset is critical, the more often a bird is exposed to the stars coupled with sunset during an experimental test, might not the bird gain some proficiency at using stars alone as orientation cues (see Wiltschko & Wiltschko 1975a, 1975b, 1976). Many savannah sparrows, especially from the

Table V. Comparative Statistics Are Shown for Two Sunset Conditions: Ss (Sunset Horizon Glow Visible) and SS (Sun Disc Visible). Neither the Stars nor the Moon were Visible during These Tests

		Ss			SS	
Bird	*N*	*ā*	*r*	*N*	*ā*	*r*
Spring						
S02	21	13°	0.846*			
S03	21	26	0.285	30	358	0.446*
S06	45	159	0.331	57	291	0.188
S07	70	83	0.356*			
S08	< 15			43	319	0.541*
S09				68	17	0.421*
S13	42	333	0.322*	16	101	0.571*
S14	30	353	0.758*	15	5	0.518*
S17				69	319	0.259*
S21				20	309	0.440*
S22	46	296	0.260*			
S23	29	16	0.564*			
S26	30	332	0.263*			
Fall						
F03	42	203	0.426*			
F04	< 15			39	189	0.541*
F08	42	193	0.419	21	123	0.460*
F17				32	174	0.514*
F18				39	189	0.618*
F23	66	184	0.325*	29	247	0.753*
F29				44	165	0.555*
F33	68	220	0.196			
F35				36	177	0.141
F40	70	154	0.293*			

See Table I for symbol explanation.
Bird F13 was 'inactive' when tested under SS/NO ST (not shown here).

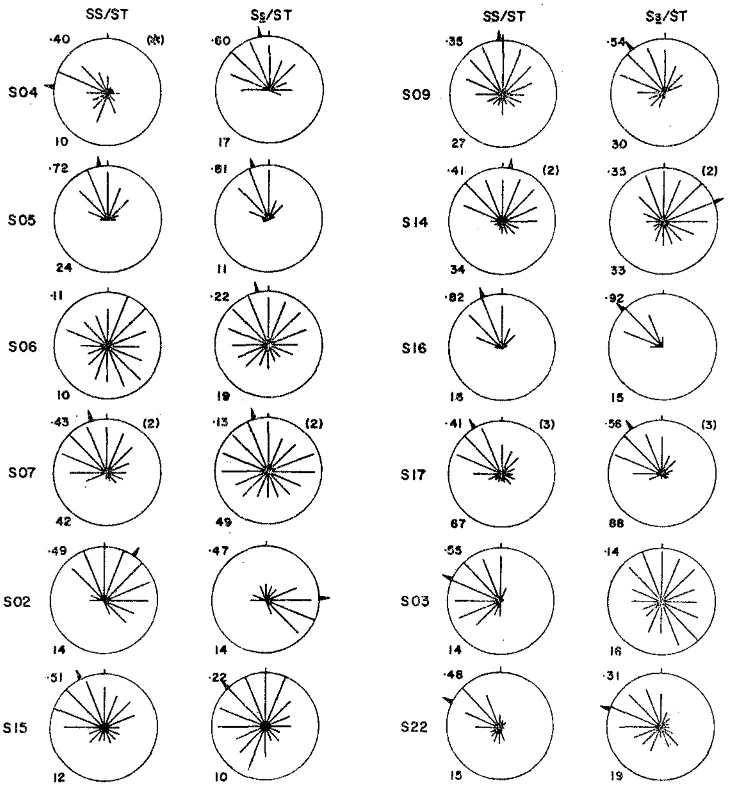

Fig. 11. Spring (1977) orientation behaviour of 12 savannah sparrows tested at least once under conditions varying the nature of sunset exposure: Ss/ST versus SS/ST. The *r* values are presented in the upper left of each circle. See Fig. 3 for figure details.

spring and fall 1977 experiments, met the criterion of a ST situation test preceded by at least two SS/ST situation tests. I found no evidence that orientation behaviour was improved as a result of repeated test exposure to sunset, though both instances of seasonally well-oriented behaviour in the fall (1977) were recorded following at least two test exposures to sunset.

Finally, I decided to analyse the 'orientation' records of birds displaying low ($N < 15$) levels of activity under the ST situation. I remain sceptical, however, that such behaviour is in any way related to migration. The 27 cases are grouped by season in Fig. 14. Only one individual mean heading was statistically significant (black dot, spring 1976), and summing the activity for each season failed to yield meaningful results.

When results from the SS/NO ST and SS/ST situations are compared, directional and quantitative differences in orientation behaviour are revealed. More spring birds were seasonally well oriented on at least one occasion for individuals tested more than once under a situation, when stars were available (SS/ST): 15 of 17 (88%) versus 15 of 21 (71%). I included birds tested on moonlit nights among the SS/NO ST birds because three well-oriented birds (S16, S17, and S37) actually displayed bimodal patterns, but with the dominant mode in a seasonally appropriate direction. A look at the fall 1977 data discloses a similar discrepancy when stars are absent: 15 of 18 birds (83%) were well oriented on at least one SS/ST occasion, while only 11 (55%) were so oriented under the SS/NO ST situation (including birds tested on moonlit nights).

I also noticed that the strength of the directional preference (*r*) typically declined under the SS/NO ST situation. The highest *r* value was

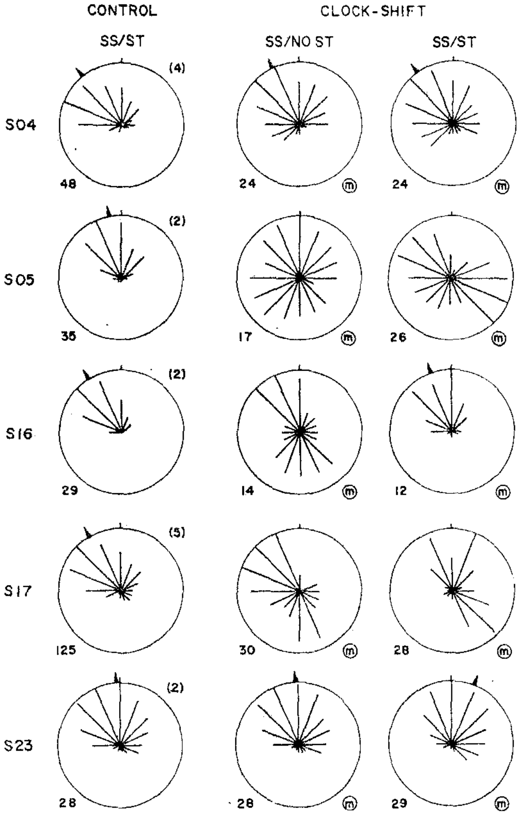

Fig. 12. Orientation behaviour of five savannah sparrows tested in spring (1977) prior to clock-shift (control column) and following an eight-day period during which the birds were clock-shifted 6 h slow (clock-shift column). The first post-shift test was conducted under SS/NO ST conditions and the second test on the next night under SS/ST conditions. See Fig. 3 for figure details, and Table VI for statistics.

associated with the SS/ST situation for the majority (59%) of the 22 spring (1977) birds tested under both situations (where a bird was tested more than once, the highest *r* value was used). In all 13 birds where the SS/ST *r* was highest, the activity was sufficiently concentrated to be deemed statistically significant ($P < 0.05$). Moreover, the heading was northward or northwestward in keeping with spring migration. Appropriate directionality was not always the case for the nine birds characterized by higher *r* values under the SS/NO ST situation. The directional preferences of S06 and S18 were not statistically significant under the SS/NO ST situation despite higher *r* values, while S18's activity was well oriented and in an appropriate direction under the SS/ST situation. The behaviour of S19 was directionally appropriate when stars followed sunset, and inappropriate in the SS/NO ST situation, despite a higher *r* associated with the latter. The 18 fall sparrows for which *r* values could be compared between the two test situations displayed a similar trend. More concentrated orientation was noted for 61% (11) of the birds when stars were available after sunset.

Table VI. Statistical Results of Spring Clock-Shift Experiments Comparing Behaviour of Savannah Sparrows Tested under SS/ST Situation prior to a 6-h Slow Shift (Control) and following the Clock-Shift (exp 1 and exp 2). See Fig. 12

Bird	Test	*N*	*ā*	*r*
S04	Control	110(4)	323°	0.430*
	Exp 1	67	334	0.456*
	Exp 2	73	325	0.456*
S05	Control	94(3)	337	0.703*
	Exp 1	72	313	0.129
	Exp 2	102	bimodal	
S16	Control	41(2)	328	0.838*
	Exp 1	47	268	0.102
	Exp 2	22	342	0.687*
S17	Control	353(5)	328	0.483*
	Exp 1	95	bimodal	
	Exp 2	72	bimodal	
S23	Control	75(2)	356	0.529*
	Exp 1	79	359	0.466*
	Exp 2	79	21	0.493*

See Table I for symbol explanation.
*Indicates statistical significance at the 0.05 level.

Discussion

This study provides information about the orientation behaviour of a nocturnal migrant, the savannah sparrow, and more significantly how such a migrant makes use of the setting sun as an orientation cue. The setting sun is apparently necessary as a source of directional information for migratory orientation in this species. Savannah sparrows allowed a view of both sunset and stars displayed well-oriented behaviour in biologically meaningful directions in both spring and fall. When the same individuals were denied a view of sunset, and tested under the stars alone, disoriented behaviour was the rule. I was understandably surprised that a view of the setting sun was apparently required for seasonally appropriate orientation, but further analysis of the results derived from experiments conducted under the stars only situation failed to uncover even subtle indications of an independent star compass. Additional experiments are planned to clarify the role of stars in the migratory orientation of this species.

I also discovered that sunset is a sufficient source of directional information. Birds allowed a view of sunset, but tested under 'overcast' night skies (no stars visible), displayed well-oriented behaviour in both spring and fall. Orientation behaviour under this SS/NO ST situation corresponds for the most part with that found when both cues were available. At this point, let us assume that savannah sparrows take a compass reading at the time of sunset and subsequently experience a visually cueless (overcast) environment. The longer the bird is without a referent, the more likely the animals will experience deterioration of orientation. Results comparing SS/ST and SS/NO ST tests revealed directional and quantitative differences in orientation behaviour supporting the above view. I suspect the differences are attributable to the absence of stars in the SS/NO ST situation. Evaluating the sufficiency of sunset is beset with a methodological problem. The birds were tested over a 2- to 3-h period; their orientation behaviour was examined by the experimenter after the test period and not sequentially over the course of a test. If the migrant experiences difficulty maintaining a compass direction, well-oriented activity recorded early in the test period shortly after the onset of the overcast may be masked to a greater or lesser degree by later disoriented behaviour. A solution to this problem and one that would yield information on possible deterioration of orientation is to record systematically activity during a progressively longer portion of a test period since seeing the compass reference (sunset). A removable cover (such as that used in the ink pad cover tests) could be placed over the ink pad at the beginning of a SS/NO ST test and removed at prescribed times, perhaps after 0.5 h the first night, 1 h the second night, 1.5 h the third night, and so on. A comparison of the activity records should disclose whether or not orientation behaviour is affected. These experiments are underway.

Furthermore, a view of the actual disc of the sun is not required for appropriate orientation. Birds expressed little more than a subtle difference in orientation behaviour as a function of sunset quality. Results suggest that the horizon glow from the setting sun may be used as a directional cue, though my experiments could not reject the possibility that migrants fix the sun's position by means of the pattern of polarized light. When the actual sun disc is out of view, whether behind a cloud bank or below the horizon at sunset, a migrant capable of perceiv-

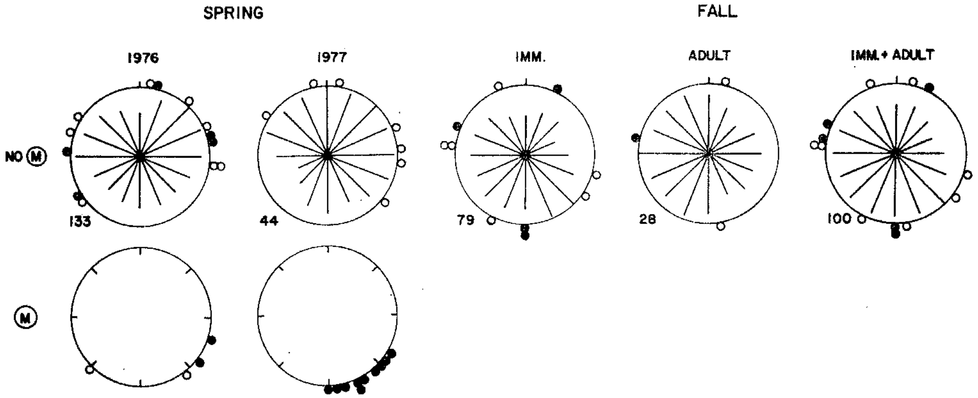

Fig. 13. Spring and fall orientation behaviour of savannah sparrows allowed to view only the stars (ST situation). Vector diagrams represent the summed activity on moonless nights for a season (or age), and are drawn such that the radius equals the greatest number of activity units in any one 22.5° sector (lower left of each circle). The dots on the circumference represent the mean headings of the individual bird-nights where a black dot indicates a statistically significant ($P < 0.05$) heading and a white dot non-significance ($P > 0.05$). Arrows indicating the mean direction of summed activity are not shown on the circumference because none of the distributions are statistically significant ($P < 0.05$). Individual mean headings for moonlit nights are plotted for the two springs.

ing polarized light could discern the sun's position by responding to predictable patterns of polarized light (see von Frisch 1967; Kreithen & Keeton 1974; Kreithen 1978), as long as a requisite patch of blue sky is visible. It should be noted that the polarization pattern is most difficult to interpret at sunset with respect to discerning the sun's position (see von Frisch 1967), and consequently the 'polarized light' hypothesis loses some of its attractiveness. One other means of determining the sun's position once it has set (and in turn derive directional information at that time) is theoretically available to the migrant: ultraviolet radiation. Von Frisch (1967) demonstrated that bees are able to perceive the sun through complete overcast long after the sun has ceased to be visible to the experimenter, and Kreithen (1978) reported pigeons sensitive to UV light. If the capabilities I have mentioned are realized, the sunset becomes a ubiquitous cue for the nocturnal migrant.

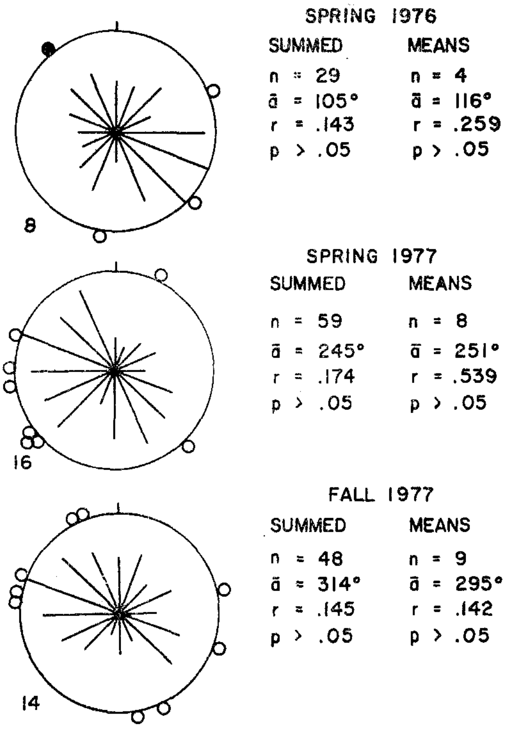

Fig. 14. Spring (1976 and 1977) and fall 'orientation' behaviour of savannah sparrows allowed to see only the stars (ST situation) and failed to display activity levels greater than or equal to criterion ($N < 15$ tests). See Fig. 13 for figure details. Statistics are presented for both summed and mean of means procedures: a = mean direction of activity or headings (given even when distribution statistically uniform) and r = length of mean vector.

The compass of this sparrow appears to be based on a constant-angle (menotactic) response to the setting sun. The orientation behaviour of several clock-shifted birds did not show predicted directional changes typical of such experimental manipulations, tending to rule out a time-compensating compass mechanism. I am not particularly surprised by this result given the directional constancy of the setting sun. The fact that the migrants were tested during the early afternoon of their biological day complicates interpretation of the behaviour of the clock-shifted birds assuming Zugunruhe is endogenously controlled (see Berthold 1975). Nonetheless, activity typical of the control tests was recorded. Possibly, the appearance of natural sunset induced migratory activity. In any case, a menotactic response to the sunset is a viable hypothesis worthy of continued attention.

Constant-angle orientation is not uncommon among animals (Fraenkel & Gunn 1961) and, if sunset-dependent, represents an alternative mechanism for selecting a migratory direction among nocturnal migrants. In the northern hemisphere, the sun sets due west at the vernal (20–21 March) and autumnal (22–23 September) equinoxes. Thus the position of the setting sun varies from due west early in the spring migration season to WNW later that season. During the fall migratory period, the sunset position 'moves' from north of west, through due west at the equinox, to just south of west late in the season. The sunset could readily serve as a predictable referent for calculating a migratory compass direction without the need for integration with an internal chronometer. A nocturnal migrant taking a compass reading at sunset need not be concerned with the apparent motion of the sun prior to its setting. This feature takes on added significance in light of the fact that certain nocturnal migrants apparently do not employ time compensation as part of their stellar orientation systems (see Matthews 1968; Emlen 1975). Savannah sparrows may be deriving compass information from the setting sun in a fashion analogous to indigo buntings (*Passerina cyanea*), who depend on the configuration of the stars in the night sky (Emlen 1967b, 1975). If savannah sparrows are dependent on the setting sun for selection of a preferred migratory heading, changing the apparent position of the sun by using mirrors should result in a predictable shift in orientation activity. Such experiments are underway.

The field of avian migratory orientation has now come full circle with respect to the issue of magnetism, and mounting evidence strongly suggests that some migrant birds are utilizing the directional information available from the earth's magnetic field (see Southern 1971; Emlen 1975; Moore 1977). A handful of workers (e.g. Wiltschko & Wiltschko 1975a, 1975b, 1976) now feel that the primary orientation system is a magnetic compass, the parameters of which are inferred from controlled experiments. Some of my results bear on the role of magnetism in the orientation of savannah sparrows and warrant mentioning.

Results show that this species may not be able to gain compass information from the stars alone (see Moore 1978a and this study). I reason that if savannah sparrows possess a magnetic compass operationally independent of sunset, such as the system advanced by the Wiltschkos, seasonally appropriate orientation should characterize the ST situation results. My stars-only experiments, over the course of two springs and a fall, failed to reveal well-oriented behaviour. I found, further, that neither summing the ST activity across individuals tested over one season nor pooling mean headings (even non-significant ones) uncovered statistically meaningful results.

A more ideal experimental approach is to test migrants under overcast conditions when visual cues such as sunset, stars, and the moon are obscured (see Emlen 1967a; Petersen & Rabøl 1972) If savannah sparrows are able to gain directional information from the geomagnetic field independent of other cue systems, I would expect nocturnal restlessness to be oriented in a seasonally appropriate direction on overcast nights. Results reported elsewhere (Moore 1978b) do not support the existence of an independent magnetic compass in this species.

Consider for a moment the cue attributes of the setting sun. (i) Sunset is highly reliable. Seldom is the sun's position totally obscured from view, and even when it is, the ability to perceive UV light might enable the migrant to locate a 'hidden' sun. Unless an unusually prolonged overcast prevails, the migrant could also determine a direction earlier in the day and employ local landmarks to retain that information should the sunset position become obscured (see Emlen in press). (ii) Compass information is easily extracted from the setting sun. A simple, constant-angle response is sufficient given the predictable westerly direction of the cue. The migrant is not burdened with compensating for the sun's apparent motion (though it is unlikely the bird could not do so). (iii) The temporal relationship between sunset and when a migrant normally initiates a night's flight is an important attribute. The sun is setting at the very time the bird must select its migratory direction as well as decide whether or not even to migrate that night (see Emlen in press). While on the ground, prior to take-off, the migrant could take advantage of various sources of directional information (sunset, wind direction, nearby topographical features, early evening star pattern, geomagnetic cues).

Since the early 1950s when the sun was nominated as one of the primary orientation cues, much has transpired; and workers no longer seriously entertain hypotheses based solely on a single orientation cue. The consensus in the field of avian migratory orientation suggests the existence of multi-cue systems of orientation (see Keeton 1974; Emlen 1975). Now migrating birds are thought to depend on directional information derived from an array of environmental sources. Multi-cue systems could assume at least two forms: (i) a redundant or cue equivalent system wherein orientational information is dependent on the availability of cues and, when conditions permit, pooling of information from a variety of cue sources, or (ii) a hierarchical or weighted system wherein the migrant relies on a primary orientation cue from which other systems are dependent or calibrated. For example, the Wiltschkos (1975a, 1975b, 1976) have investigated the functional relationship between magnetic and stellar cues in certain European warblers (especially *Sylvia borin*) and the European robin (*Erithacus rubecula*), and have found a hierarchical arrangement.

If solar and stellar cues are equivalent sources of compass information for the savannah sparrow, migratory activity should have been well oriented under either system. Such was not the case. Savannah sparrows orient very poorly in the absence of solar information at sunset. I hypothesize that this species, in fact, may not possess an independent star compass. Possibly a hierarchical relationship exists between the primary cue, setting sun, and a secondary cue (stars). Orientational information derived from the former is transferred to the latter in a fashion analogous to taking a reading on a magnetic compass and sighting on some distant landmark, such as a tree, and monitoring a course with respect to the secondary or calibrated cue.

A similar system involving solar cues and wind was proposed some time ago by Vleugel (1954). The migrant supposedly selected its departure direction from compass information available at sunset, and once aloft maintained this course by flying at a constant angle to the wind. The orientation value of the wind was derived initially from the primary reference, the setting sun. More recently, Able (1978) reported evidence based on radar tracks of migrants aloft that lends some credence to Vleugel's model. He found that birds with access to sunset flew in seasonally appropriate directions on overcast nights, despite opposing winds. Possibly the migrants were flying at some angle to the wind so as to maintain a direction determined earlier at sunset. When overcast conditions preceded sunset and continued into the night, effectively precluding access to sunset input, migrants oriented downwind.

Able (1978) refers to the relationship between celestial and wind cues in his study as hierarchical, but the cues actually represent equivalent sources of information weighted by relative availabilities. A hierarchy should be thought of as a set of elements defined by the relation 'is boss of' (see Dawkins 1976). A hierarchy is a set of elements that satisfies two necessary and sufficient conditions: (i) there is no element in the set that is superior to itself (no circular relationships), and (ii) there is one element in the set that is superior to all other elements in the set. In orientation systems (sets), 'is boss of' could mean 'calibrates' or, conversely, 'is bossed by' means 'dependent upon' (see Koestler 1967 for an entertaining yet informative discussion of hierarchical organization).

The relationship betwen solar and stellar cues is probably hierarchical in the savannah sparrow. Information necessary to *select* the appropriate migratory direction is gained from a primary ('is boss of') cue, the setting sun, while *maintenance* of that heading is dependent on a secondary cue, probably the stars (for a discussion of selection versus maintenance see Emlen 1975, in press). By definition, then, the secondary or dependent cue may function only in the maintenance process, while the primary cue may carry out either function. The setting sun can not be a cue used in the maintenance of a pre-selected direction among nocturnal migrants for obvious reasons, but the stars and geomagnetic stimuli are both theoretically capable of performing both processes. White-throated sparrows (*Zonotrichia albicollis*), however, seem capable of making equivalent use of both astronomical cues (see Emlen & Demong 1978), and possibly stars are functioning both in the selection and in the maintenance of migratory direction. This 'white-throat' picture is clouded somewhat by recent cage orientation work with this species (Bingman & Able in press) suggesting the primacy of solar information. Now I must wonder how savannah sparrows would orient if experimentally released and tracked with radar under various cue conditions as Emlen & Demong did with the white-throated sparrow. Recently, the Wiltschkos (1978) suggested that the selection and maintenance of a direction are functionally separate processes in the European robin (*Erithacus rubecula*): the determination of the migratory direction depends mainly on the magnetic compass, whereas the maintenance of a direction strongly depends on the presence of stars.

If a separate cue system is responsible for the maintenance of a direction whose selection was dependent on a different cue, orientational information must be transferred from the primary (selector) cue to the dependent (maintainer) cue (see Wiltschko & Wiltschko 1976; Moore 1978a; Emlen in press). How often the dependent cue must be calibrated (information transferred) for appropriate nightly orientation apparently varies from species to species. Savannah sparrows and garden warblers (*Sylvia borin*) must frequently calibrate their star compasses, while European robins do so less regularly (Moore 1978a, Emlen in press).

Finally, I emphasize that because information is available does not mean all migrants make use of it, if they use it at all. I see the setting sun functioning on the one hand as a primary orientation cue against which other cues are calibrated and on the other as an alternative (equivalent) source of compass information important in the determination of a migratory direction.

Acknowledgments

I am particularly grateful to S. A. Gauthreaux, Jr., for his sound advice and unbounded enthusiasm throughout this study. My work also profited from discussions with K. Able, P. Hamel, B. Beason, S. Emlen, and C. Helms. L. Oring and P. Kannowski, in association with the Institute of Ecology, University of North Dakota, kindly provided logistical support for my fall work in North Dakota. C. Moore, B. Alexander, A. Ross, and H. LeGrand helped in netting birds and maintaining them throughout the study. C. Moore also assisted during orientation experiments and helped analyse data. J. Evans of the Department of Farms, Clemson University, arranged access to an ideal site for my orientation experiments. I received financial support for portions of my work from the American Museum of Natural History (Frank M. Chapman Memorial Fund), the USAF Office of Scientific Research (grant to S. A. Gauthreaux, Jr.), and the Department of Zoology, Clemson University. This study was part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Clemson University.

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(*Received* 19 *April* 1979; *revised* 31 *July* 1979; *MS. number:* A 2305)