

ORIENTATION OF MIGRATORY RESTLESSNESS IN ZONOTRICHIA

By L. RICHARD MEWALDT, MARTIN L. MORTON, and IRENE L. BROWN

The night migratory restlessness (*Zugunruhe*) of White-crowned Sparrows (*Zonotrichia leucophrys*) caged at San Jose, California, is oriented generally to the north in spring and to the south in fall (Mewaldt and Rose, 1960). We have now obtained results from several taxa of *Zonotrichia* and report here upon those migratory members of the genus which winter in the vicinity of San Jose in central coastal California. These include two races of the White-crowned Sparrow (*Z. l. gambelii* and *Z. l. pugetensis*) and the Golden-crowned Sparrow (*Z. atricapilla*); there are a few data on the White-throated Sparrow (*Z. albicollis*).

By using automatic sensing and recording devices we have been able to make continuous records (day and night) for months at a time of the orientation of the motor activities of these migratory sparrows. They respond to their environment, with little apparent frustration due to confinement, in a manner which reveals much concerning the psycho-physiological mechanism which must account for properly oriented migration.

Systematic and quantitative assessments of migratory restlessness, including its experimental manipulation with altered diets, artificial photoperiods, and the injection of hormones have been reviewed by Farner (1955, 1960). Kramer (1949, 1951 and 1961) was the first to make effective use of essentially circular cages constructed to determine directional characteristics of day and night migratory restlessness. During daylight hours, Starlings (*Sturnus vulgaris*) oriented northeasterly at the same time that free-flying Starlings were migrating in a northeasterly direction. In autumn, they showed a southwesterly orientation when free-flying birds were moving toward the southwest. Starlings were demonstrated to have the ability to select a direction under a clear sky with the sun visible and also with only small portions of the sky visible through windows. Mirrors used to shift the view of the sky 90° caused a compensatory shift of 90° in the orientation of the activity of the Starlings. Kramer showed that some Starlings were able to use the sun as a compass and to compensate for its changing position during the day.

Kramer (1949, 1950) studied the autumnal responses of nocturnal migrants (Red-backed Shrike, *Lanius collurio*; Whitethroat, *Sylvia communis*; and Blackcap, *Sylvia articapilla*) in circular cages under an open sky. The reflection of city lights in the night sky apparently influenced the birds to orient their movements toward the light. When, however, a Blackcap was moved to an area free of city lights, its movements in fall were oriented toward the south. These experiments suggested that an observed directional tendency by a caged nocturnal migratory bird might be an immediate expression of migratory orientation.

Hoffmann (1960) and Schmidt-Koenig (1960) review their own and related investigations on the experimental manipulation of the orientational clock in birds. The work, primarily with Starlings and pigeons (*Columba livia*), confirms the presence of an internal clock (physiological chronometer) which operates in harmony with the sun to enable the birds to use the sun to make directional "choices." This clock may be reset by altering daily photoperiods. It will drift in its setting when the birds are placed on constant light and other *Zeitgebers* or time-setters are excluded. Resettings of the internal clock have resulted in predicted shifts of 90° and even 180° (Schmidt-Koenig, 1960) in orientation of activity in the test cage or in free flight. Work with an artificial sun has provided results largely consistent with observations using the natural sun, but some deviations in behavior remain unexplained. They concluded that findings to date

indicate that birds can determine compass directions by using some form of celestial clues.

Fromme (1961), on the other hand, reports that European Robins (*Erithacus rubecula*) are able to select the proper migratory direction without celestial clues, so long as they are not completely surrounded by sheet steel. His results thus far have defied satisfactory explanation.

The Sauers (Sauer and Sauer, 1955, and Sauer, 1957, 1961) observed the actions of Palearctic warblers (Sylviidae) in a circular experimental cage under an open sky and in a planetarium. A bird on the perching ring near the floor of the cage could see a circular section of sky of approximately 68° through the plexiglass roof of the cage. The observer lay in darkness beneath the plexiglass floor of the cage. Birds were judged to be "migrating" *in situ* when they fluttered their wings and oriented their bodies in a given direction. Time spent in such an oriented nervous attitude was recorded to provide the quantitative data. Under a natural night sky in August, September, and October, Garden Warblers (*Sylvia borin*) and Blackcaps oriented their actions toward the south-southwest and southwest, their natural autumnal migration direction. Rather limited data taken in April showed Blackcaps orienting toward the north-northeast and northeast. Under a cover of clouds the birds failed to correct for rotation of the cage and their actions became nearly random. Of even greater significance are planetarium experiments which demonstrated that these birds could orient their migratory restlessness in accordance with an artificial night sky. The full impact of these planetarium investigations has not yet been felt and their interpretation is most challenging.

It seems certain that many migratory birds possess at least two different mechanisms to accomplish orientation of long distance movements (Rüppell, 1944; Griffin, 1952; Matthews, 1955; Perdeck, 1958; and Hoffmann, 1960). (1) Young birds displaced a hundred or more miles laterally prior to or during their first migration to wintering quarters fly on in the original ancestral direction and winter in a new area. These birds must inherit a kind of compass mechanism and directional sense. This has been called one-directional orientation (Lack and Williamson, 1959) or Type II navigation by Griffin (1952). (2) Adult birds, so displaced, home to the breeding and/or wintering quarters over areas unknown to them. The incidence of return and the speed of return in many cases suggest that they perform a kind of bi-coordinate navigation or goal orientation (Type III navigation of Griffin, 1952). It is probable that most of the experimental birds, reported in this paper, combine these two types of mechanisms in their orientation because (a) the azimuth of the summer home and (b) the compass bearing along the migratory route at the test latitude are approximately the same.

Zonotrichia return to the same clump of bushes, weed patch, or banding station on the wintering grounds with great consistency after a season of residence. The rate of return reaches 50 per cent in some populations, probably representing nearly all birds that survive from one year to the next (Mewaldt, 1962). However, return to banding stations along the migratory route is at a rate of less than 0.01 per cent or less than 1 in 10,000 bandings (Fisher and Gill, 1946; Stevens, 1956; Cortopassi and Mewaldt, 1965). It is therefore likely that *Zonotrichia* migrate in a broad front over the great distances between the general localities of breeding and wintering.

Of some interest are returns of *Zonotrichia* to their established winter homes from displacements of great and small distances. Returns of from 700 miles (Mewaldt and Farner, 1957) to more than 2400 miles (Mewaldt, 1963, 1964) of substantial numbers of *Zonotrichia* have been demonstrated. Returns from shorter distances are also substantial in numbers (Sumner, 1938; Roadcap, 1962) but reliability of return in relation to distance displaced has not yet been established for *Zonotrichia*.

We gratefully acknowledge the technical advice of Lester Brubaker and Alfred Einarsson in the development of equipment and data processing techniques. Technical and/or clerical assistance in the field and the laboratory were provided by William Bjorge, Girard Charbonneau, Russel Cropley, Elizabeth Dewey, Evelyn English, John Freitas, Mildred Fujimoto, Robert Hamby, Edward Keller, Dennis King, Ray Marsh, John MacDonald, James McCammon, Frances Mewaldt, William Mewaldt, Herbert Royse, Robert Smith, Doris Tengan, George Tengan and Daryle M. Webb. Stimulating and fruitful discussions resulted when each of the following scientists visited our project: Richard Banks, Mary Erickson, Donald S. Farner, William J. Hamilton III, James R. King, Brian Lofts, G. V. T. Matthews, Friedrich W. Merkel, Alden H. Miller, Franz Sauer, Klaus Schmidt-Koenig, Charles G. Sibley, and Albert Wolfson. This project has been supported in part by National Science Foundation grants 7137 and 20745.

MATERIALS AND METHODS

Our plan has been to develop techniques which gather data in quantity on the orientation of day and night activities of small passerines and which make possible the experimental manipulation of *Zugunruhe* and its orientation. To record the orientation of activity, including migratory restlessness or *Zugunruhe*, we have used a circular cage with activity-sensitive perches around the periphery. These activity-orientation cages and the recording system incorporate certain features of systems used by Kramer (1950 and 1952), Farner and Mewaldt (1953) and Rawson (1954). We have five of these cages and one or more has been in nearly continuous operation since August of 1958. In the next four years, we tested more than 100 birds and accumulated more than 140,000 bird hours of data.

Cage design.—Our activity-orientation cage (henceforth referred to as an A-O cage) is designed for continuous automatic recording of activity and has been described briefly (Mewaldt and Rose,

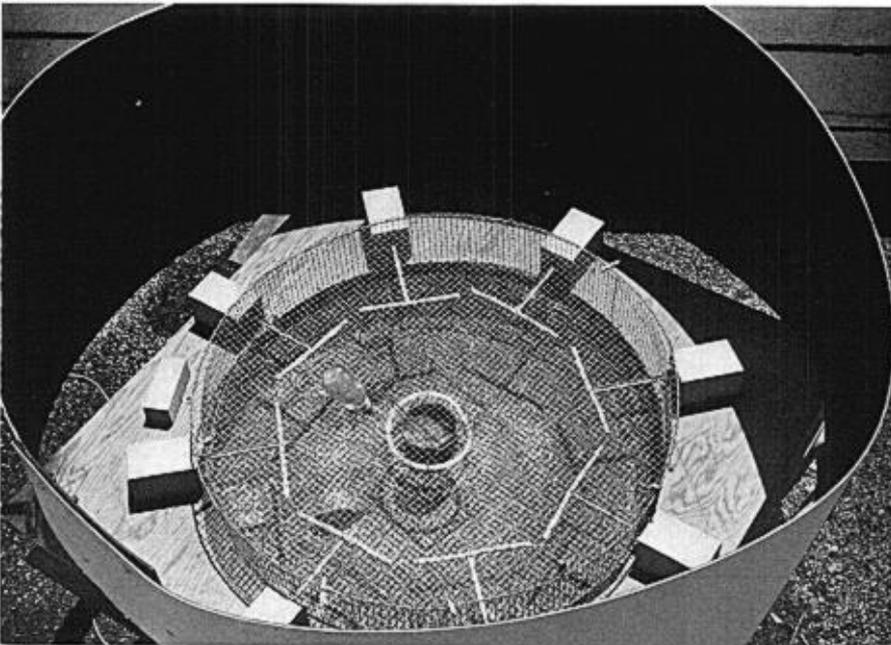


Fig. 1. Activity-orientation cage.

1960). The A-O cage (fig. 1) is made of half-inch mesh steel hardware cloth. It is 91 cm. in diameter and was 27 cm. high until December of 1960 when the height was lowered to 14 cm. This was done to reduce the tendency of some birds to jump over the perch to the side of the cage. Lowering the top of the cage has effectively eliminated this tendency. The cage attaches at the bottom edge to a piece of half-inch plywood 112 cm. square with a circular hole the size of the cage. The circular hole is covered with half-inch mesh hardware cloth to form the floor of the cage. Sixteen centimeters below the cage is a solid piece of plywood that acts as a catch-board for droppings. Four wooden legs, 56 cm. long, are attached to the bottom of the catch-board. The open construction permits free circulation of air. In warm weather a 15 cm. disc of plywood over the center of the cage provides shade. A 25 cm. square of plate glass replaces the disc in wet weather to provide shelter for the bird and to protect the food.

A masonite screen 58 cm. high and 152 cm. in diameter surrounds each cage. This serves to obstruct the horizon and associated landmarks. With the screen in place the bird can see an arc of sky, depending on its position in the cage, of 105° to 117° .

A proportionally smaller cage, 60 cm. in diameter and 14 cm. high, has yielded results which appear comparable to those obtained with the larger units. In addition, three dummy A-O cages were constructed to the same dimensions as those of the activated A-O cages. Routinely a bird was held in a dummy A-O cage for at least a week before it was installed in an activated A-O cage. This procedure served to familiarize the bird with the cage type.

Water is provided by hanging drop from a tube extending from an inverted bottle on the top of the cage. Crumbled dry dog food (Walter Kendall Burger Bits made by Standard Brands Inc., New York) is continuously available. Weekly supplements of chick scratch, red millet, grit, and chopped lettuce are provided and readily taken by most birds. The birds live continuously in the A-O cage except when removed for weekly weighing and plumage inspection. Conditions in the aviary permitted the birds to maintain reasonably normal weight, molt and gonadal cycles.

Eight separate perches 23 cm. long, 8 cm. above the cage floor, and 15 cm. from the circular vertical wall are peripherally arranged so that each occupies just under 45° of the circle. Normally four of the perches are centered on cardinal directions and four mid-way between the cardinal directions. Thus the perch centering on east records activity of the bird between about 68° and 112° . Except as noted, the cages remain stationary and are not rotated. The perches are made from the stem of a local weed, poison hemlock (*Conium maculatum*), which is both lightweight and relatively strong. Each is attached to one end of an aluminum arm extended 15 cm. into the cage. The other end of the arm pivots over a single-pole double-throw contact micro-switch housed under a sheet metal box $8 \times 9 \times 13$ cm. A bird landing on the perch depresses the arm over the micro-switch. This closes the circuit and an impulse is monitored by a remotely located Esterline-Angus 20-pen recorder. When the bird leaves the perch the circuit is opened and one unit of activity has been recorded on the continuously moving recorder tape. Each Esterline-Angus recorder monitors the activity from two A-O cages by accepting signals from eight perches of one cage on lines 1 to 8 and from the other on lines 11 to 18. Tapes were usually run at three inches per hour. At this speed there is overlapping of pen marks when a bird is extremely active. When solidly inked, the record was interpreted as 15 perch registrations every two minutes. Since January, 1961, some records have been accumulated with Elmeg automatic print-out counters, some wired in parallel with the Esterline-Angus recorders. The Elmeg recorders with their ten five-digit channels have the advantage of providing the full count of registrations for each perch each hour. Comparison of simultaneous records makes it apparent that the assignment of a maximum of 15 perch registrations per two minutes (to a maximum of 450 perch registrations per hour) for each perch is very conservative. The directional tendencies exhibited by birds monitored on the Esterline-Angus recorders were actually stronger than we can represent them, especially in cases where the birds exhibited heavy activity. Most of the data used in this report were obtained by use of these reliable Esterline-Angus recorders.

Birds in A-O cages were normally serviced once each day. The automatically accumulated data for hours when disturbance was present were discarded and interpolations were made when the disturbance and its apparent effect (or other interruption of the recording procedure) did not exceed three consecutive hours. When record interruptions of more than three hours occurred, the entire day's or night's data were discarded.

All experimental work reported herein was done on the roof (fourth level) of the Natural Sciences Building on the campus of San Jose State College in mid-town San Jose, California. All records were made with a single bird in each cage. The night sky visible to the birds is apparently quite natural and free of reflected light when there are no clouds. Effects of city light reflections from low scattered clouds are apparently unimportant in the orientation of night activity. Under conditions of more or less solid cloud cover it is possible that some birds exhibit a photo-taxis toward the area of greatest light reflection to the west-northwest of the aviary.

The tops of two or three American elms (*Ulmus americana*) were at times visible to the birds over the tops of the masonite screens. When bare of leaves (December to March) these trees seemed to have no effect on orientation. When the trees were leafed out, A-O cages were moved to that portion of the roof which left the trees to be seen almost completely below the masonite horizon. The tips of these trees could be seen only from the extreme west parts of the A-O cages. No other landmarks interrupted the horizon.

Data on local weather conditions were obtained from the Monthly Meteorological Summaries of the San Jose weather station located one and one-half miles northwest of the college. Gross observations on weather conditions and cloud cover were also noted daily in our aviary journal.

Birds left in an A-O cage for weeks or months could orient their night activity by using environmental clues other than those present in the night sky. When the A-O cages of experienced birds were rotated 90° or 180°, but otherwise left in the same location, the responses of individual birds varied. The most common response was to continue orientation of night restlessness in the same direction, therefore to a new sector of the cage, when the night sky was clear or partly clear. Responses under a cloudy sky varied from individuals that oriented to the same part of the cage, regardless of direction, suggesting reference to a part of the cage, to individuals that corrected for the rotation apparently using reference clues in the vicinity of the cage. Such clues probably included sounds from mechanical devices, for example, hood fans, street noises and perhaps calls of birds in nearby orientation cages (Hamilton, 1962).

To further assess the importance of an unobstructed view of the night sky we placed a pale yellow translucent vinyl sheet (shower curtain) with an embossed pattern over the top of the A-O cage assembly of a White-crowned Sparrow of the race *oriantha*. This bird (adult female 26-199274) had demonstrated a particularly strong tendency to orient its night activity in the direction of its breeding ground toward east-northeast in spite of cage rotations in clear or cloudy weather. (Birds of the race *oriantha* transported from their breeding grounds some hundreds of miles east of San Jose apparently mix a species tendency for spring-northerly and fall-southerly orientation with an easterly orientation toward their breeding ground. Detailed consideration of our considerable data on this taxon must appear subsequently.) To our eyes, this vinyl sheet prevented resolution of any celestial bodies except the general positions of the sun and the moon. It also reduced the amount of light reaching the bird.

Covering the A-O cage assembly with the vinyl reduced the quantity of night activity to less than half. A reduction in activity related to a reduction in illumination below usual night level has been demonstrated for the European Robin by Wagner (1937) and similarly confirmed for *Zonotrichia* in our laboratories. While the cage was left in the same location relative to the parapet wall, other A-O cages, and roof hood-fan assemblies, which could provide auditory locator clues, the bird maintained the same orientation upon rotation of the cage. However, when the cage was moved to a new location activity first ceased entirely for two nights and then was resumed at a reduced

level. After a period of time the bird regained its northeast orientation in this new location with the vinyl cover in place continuously except for a few minutes each day during the servicing. This suggests that the bird might have been using clues other than the night sky in this homing type of orientation. Perhaps memory of the position of the sun during daylight hours was retained into the night hours. When the vinyl cover was removed the bird oriented northwest for a few nights, the same response it showed to the shift in location of the cage and to its rotation while the cover was in place. This initial northwest orientation was probably a phototaxic response to city lights.

These observations on the *oriantha* suggest to us that our method of continuously testing birds in their living cages is adaptable to a wide range of experimental modifications which potentially can reveal much about directional mechanisms. Detailed accounts of such experiments will appear subsequently. In this paper we have described responses of birds in living cages subjected only to occasional cage rotations, in the way of experimental modifications.

One A-O cage was equipped with a plate glass catch tray and canvas drapes reaching from the floor level to the ground. This permitted us, during hours of darkness, to lie quietly below and observe the bird. The birds were disturbed by our entrance to this sub-cage blind, but apparently they "forgot" it in 5 to 15 minutes. Birds exhibiting oriented activity were alert and animated. They seemed to "study" the sky by cocking their heads from side to side. These birds expressed their restlessness by moving about in the selected sector of the cage rather than by sitting on the perch and fluttering their wings as reported by Sauer (1957) for European sylviaids.

Movements in the cage followed a number of patterns. Most birds moved from the center ring to the floor to the perch and back again to the floor. Some birds moved back and forth in an arc involving three or even four perches. These individuals appeared to direct their attention near the center of this arc. Some birds moved more widely in the cage but tended to keep coming back to certain perches more frequently. One thing seemed nearly universal—the birds exhibiting directional preference for a particular sector of the cage were directing attention to "something" overhead in the direction of this greater activity. We did not observe birds facing the center of the cage and thus activating the perch opposite the direction actually chosen.

The quantity of activity recorded provides an index to total activity and to the relative amounts in each of the eight directions. Quantitative comparisons utilizing various periods for an individual bird appear justified. Comparisons between individ-

TABLE 1
SUMMARY OF ALL ACTIVITY-ORIENTATION CAGE RECORDS FROM MIGRATORY *Zonotrichia* WHICH WINTER IN THE SAN JOSE AREA AND WHICH WERE NOT SUBJECTED TO PHOTOPERIOD MANIPULATION

Bird	Date of capture	Age Sex	Period in A-O cage	Bird-nights recorded	Quantity and characteristics of night activity
<i>Z. l. gambelii</i>					
25-199313	Dec. 26, '57	A —	Aug. '58	1	Light—S
385	Jan. 1, '58	I ♀	Aug.-Sept. '58	10	Heavy—equivocal—lunar influence
601 ¹	Dec. 26, '57	A ♂	Aug.-Oct. '58	33	Light to medium—NW then S and SE
602	Dec. 26, '57	A ♂	Aug.-Sept. '58	8	None to medium—NW
26-123496 ¹	Feb. 5, '59	A ♂	Mar.-Nov. '59	258	None to heavy—N in spring to mostly S in fall
806	Jan. 18, '59	A —	June-July '59	15	None
834	Feb. 1, '59	A —	June-Aug. '59	68	Light—NW to W
26-199252	Mar. 21, '59	I ♀	July-Aug. '59	38	None to heavy—equivocal
27-189145	Nov. 18, '60	I ♂	Nov. '60	13	None to light—random

Bird	Date of capture	Age Sex	Period in A-O cage	Bird-nights recorded	Quantity and characteristics of night activity
146	Nov. 18, '60	I ♂	Nov. '60	13	Light—N
150	Nov. 18, '60	I ♂	Nov. '60	13	Light—SW
29-154347	Mar. 5, '61	I ♂	Mar.-June '61	81	None to medium—mostly equivocal—lunar
349	Mar. 5, '61	A ♂	Mar.-June '61	97	None to heavy—mostly N and NE
29-154351 ¹	Mar. 5, '61	A ♂	July '61-Feb. '62	223	None to medium—NW to SE (Sept.) to NE
31-138833 ²	Oct. 19, '62	A ♂	Oct.-Dec. '62	73	Heavy—NW to N
<i>Z. l. pugetensis</i>					
25-199501	Sept. 14, '58	A ♂	Sept. '58	4	None
26-199099	Feb. 22, '59	A ♀	May '59	14	Medium to light—W to NE
103	Feb. 22, '59	A ♂	Apr.-Aug. '59	102	Medium to light—N to NW to SW
131 ¹	Feb. 22, '59	A ♂	Mar.-Apr. '59	29	None to heavy—N
147 ¹	Feb. 22, '59	A ♂	Mar.-Apr. '59	29	Light to medium—NE
27-104227 ³	June 22, '60	A ♂	July-Nov. '60	105	Light—N to SW (Sept.) to SE (Oct.)
231 ³	June 22, '60	A ♂	Oct.-Nov. '60	21	Light—SW
233 ⁴	June 24, '60	A ♂	July-Aug. '60	35	Medium to none—SW
27-188981 ⁵	Aug. 3, '60	A ♂	Aug.-Nov. '60	70	Medium to heavy—N and NW to SW
988 ⁵	Aug. 3, '60	A ♂	Oct.-Nov. '60	28	None
<i>Z. atricapilla</i>					
55-192216	Feb. 26, '60	A ♀	Feb.-Mar. '60	14	Light to medium—equivocal—lunar
251	Mar. 13, '59	I ♂	May '59	7	Medium—N to random
255	Mar. 13, '59	I ♀	May-June '59	33	Medium—equivocal—lunar
363	Mar. 4, '60	A **	Mar. '60	7	Medium—random
380	Mar. 4, '60	A **	Mar. '60	7	Medium—NW
56-164234	Mar. 11, '60	A **	May '60	16	Medium to light—random
241	Mar. 11, '60	I ♂	Mar.-May '60	39	None to heavy—NW to NE
601	Dec. 26, '57	A ♂	Sept. '58	4	Light—random to N
603	Dec. 26, '57	A —	Aug. '58	3	None
655	Dec. 24, '60	I *	June '61	9	Light to medium—N
662	Jan. 12, '61	I *	June '61	9	Medium—NE
672	Feb. 1, '61	A ♂	June '61	9	Light—NE
679 ¹	Feb. 1, '61	A ♂	Mar.-May '61	72	Medium to heavy—N to NE
683	Feb. 1, '61	A **	May '61	3	Light—N
687 ¹	Feb. 1, '61	A ♂	Mar.-June '61	87	Medium to heavy—S to NE
691	Feb. 1, '61	A **	June '61	12	Light to heavy—random to NE
693	Feb. 1, '61	I *	June '61	12	Light—N
<i>Z. albicollis</i>					
26-123664 ¹	Nov. 11, '58	— ♀	Mar.-June '61	83	None to heavy—N—details in text
31-138201 ¹	Dec. 21, '61	— ♀	Feb.-Oct. '62	247	None to heavy—details in text

* Partial male castrate.

** Male castrate.

¹ Individual results analyzed in detail in this report. The 2054 bird-nights from the 44 birds were converted to 276 bird-quarter-months and represented as bird-weeks in figure 3.

² Had recently returned from displacement to Baton Rouge, Louisiana, in April of 1962 (Mewaldt and Newman, MS).

³ Captured on Vancouver Island, British Columbia.

⁴ Captured in Grays Harbor County, Washington.

⁵ Captured in Mendocino County, California.

uals are very hazardous because of individual variation in cage movements (see also King and Farner, 1963:201). Because the activity-sensitive perches are nearly always included in movements in the cage, there seems to be ample justification to compare patterns of activity of several birds under similar conditions in cages of the same design. The hazards involved should not prohibit making certain cautious quantitative comparisons in the activity data of different birds.

The remote monitoring of activity has the obvious advantage of excluding possible interference from an observer. The use of electrical monitoring devices permits continuous, essentially uninterrupted, accumulation of data. The fact that the bird lives in the cage at all times prevents it from being disturbed by handling just before a test session. It also, however, allows the bird to learn to use cues in his cage and immediate locale.

Except in the case of *Zonotrichia albicollis* where the only two birds captured locally were tested, those placed in the A-O cages were not randomly selected (table 1). Of several birds available when a change was contemplated, the bird chosen was usually one judged by weight and plumage condition to be in good health and well adapted to captivity. Also in the six cases out of 44 when birds were introduced directly to the A-O cage from the wild, these birds were judged to be in good health.

In some instances birds were replaced when they exhibited no or very little night restlessness. A few were removed when it became evident from the monitored record that the orientation of their night activity was influenced by the progression of the moon across the night sky. It also follows that a few birds providing quantities of apparently interpretable data were retained in the A-O cages longer than less responsive birds.

Except as noted in the footnotes to table 1, all birds tested were captured in the south San Francisco Bay area. Most were captured with Japanese mist nets from populations of wintering *Zonotrichia*. The results of banding studies (Cortopassi and Me-waldt, 1965) suggest that those *Z. l. pugetensis* captured on the breeding grounds in Washington and British Columbia probably wintered in central California, possibly within 150 miles of San Jose.

INTERPRETATION OF DATA

We have employed a form of vector analysis to interpret the directional choices taken by each bird in its activity orientation cage. This permits us to use choices in all eight directions in the determination of the mean azimuth. Our vector value is a measure of the concentration of choices in the direction of the mean azimuth. Letting choices equal distance (one choice equals one unit of distance), then the vector value is the resultant of the vectors expressed as per cent of total distance traveled. A vector value of 100 would result if all activity were concentrated on but one perch. If activity were such that all eight perches were chosen the same number of times, the vector value would be 0. A very low vector value is also the result when the bird uses as few as two perches, but ones which are on opposite sides of the cage.

Letting m equal number (or per cent) of choices in a given direction we calculate the resultant vectors in the X and Y axes (x and y) as follows:

$$\Sigma m = m_E + m_{SE} + m_S + m_{SW} + m_W + m_{NW} + m_N + m_{NE}$$

$$m_1 = m_E - m_W$$

$$m_2 = m_{SE} - m_{NW}$$

$$m_3 = m_S - m_N$$

$$m_4 = m_{SW} - m_{NE}$$

} Calculation of resultants of opposing vectors

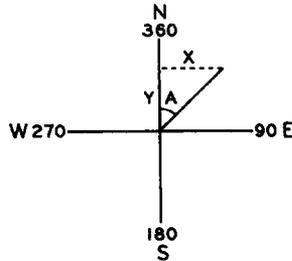
$$x = \frac{m_1 + 0.7m_2 - 0.7m_4}{\Sigma m}$$

$$y = \frac{-0.7m_2 - m_3 - 0.7m_4}{\Sigma m}$$

Then, the tangent of the mean azimuth ($\tan A$) is calculated from:

$$\tan A = \frac{x}{y}$$

Using the coordinate system:



the angle corresponding to $\tan A$ (the mean azimuth) may be selected from a table of natural trigonometric functions (0° to 360°). In this coordinate system it is apparent that the angle falls between 0° and 90° (NE sector) when both x and y are positive (example above); between 90° and 180° (SE sector) when x is positive and y is negative; between 180° and 270° (SW sector) when both are negative; and between 270° and 360° (NW sector) when x is negative and y is positive. It is usually apparent from inspection of the data in which sector the mean azimuth will fall. The vector value is calculated from:

$$\text{vec} = 100\sqrt{x^2 + y^2}$$

VECTOR VALUES

The frequency distributions (fig. 2) of selected groups of vector values provide useful information on the relative concentration of activity in the cage. Although it appears that these vector values have a Poisson distribution, it is far more practical to treat the distributions as normal. We eliminated from analysis those data from nights in March when patterns were atypical, probably because the activity occurred prior to the normal season of migration, and data from days and nights when (1) experimental cage rotations affected the mean azimuths and reduced vector values or (2) the bird showed evidence of a phototaxis in response to the progression of the moon across the night sky. Data from 12 different birds of four races of *Zonotrichia leucophrys*, including the nonmigratory *nutalli* (fig. 2B), and data from *Zonotrichia atricapilla* are included. Many data for vector values by days or nights taken singly come from the same pool of perch registrations used for the weekly vector values. The same individual birds provided data for day and night vector values.

To study the possible vector values for randomness a table of random numbers (Hodgman, 1959) was used. Each of the eight compass directions was given a number E, 1; SE, 2; . . . NE, 8) and a tally was made for each direction tallying one for E whenever "one" appeared in the random number table and so forth. We omitted all zeros and nines. A nearly normal distribution (fig. 2A) around a mean vector value of 10 was obtained. This is the theoretical result, in each case, of 100 non-biased independent choices of perches from the center of the cage. A value of 10 would also result from the calculation of a Random Walk where the number of random turns is 100 and the mean projection in the X and Y axes is one. Such a situation does not in fact exist; in fact, regular patterns of behavior are observed; for example, once the bird has reached a perch it is more likely to again depress that same perch, or an adjacent perch, in its

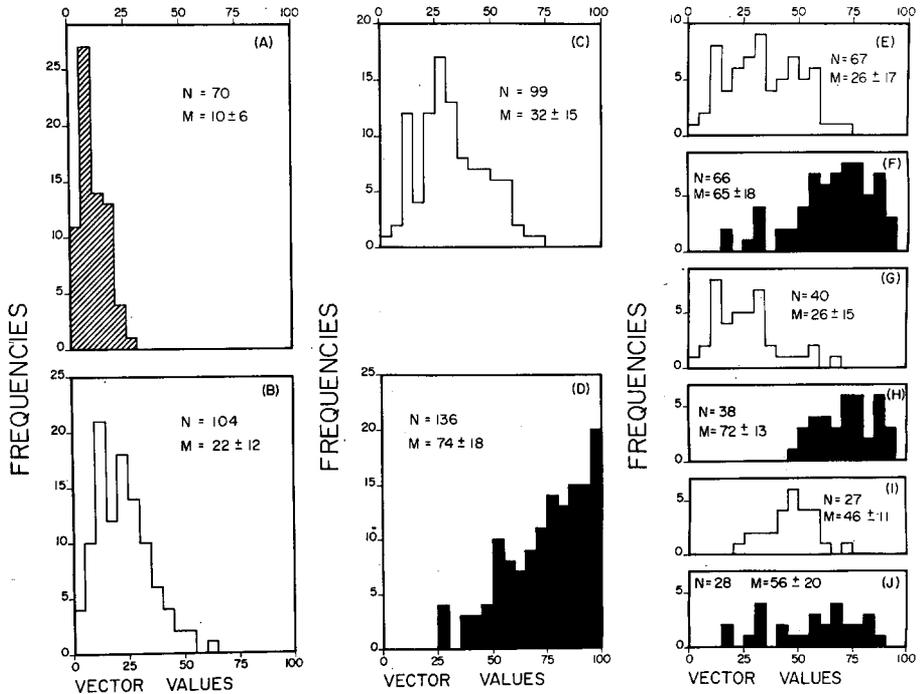


Fig. 2. Frequency distributions of vector values of hypothetical random activity and of day and of night activity of *Zonotrichia*. (A) Random, see text; (B) days for two *Z. l. nuttalli* by days in all months—not included in C to J; (C) days by days, March to November; (D) nights singly, April to November; (E) days by weeks, March to November; (F) nights by weeks, April to November; (G) days by weeks, March to July; (H) nights by weeks, April to July; (I) days by weeks, August to November; (J) nights by weeks, August to November. N = number of days or nights by days or by weeks. M = arithmetic mean \pm one standard deviation.

next movement, than to depress a perch in another sector of the cage. This bias in favor of the perch already depressed is confirmed by our observation of the bird's behavior and must operate to increase vector values above 10. A further analysis to assess this effect is complex and will be treated elsewhere. It is perhaps significant that B, C, and G of figure 2 each show a secondary peak in the frequency interval 10 to 14. The mean vector value of each of these groups (fig. 2B, C, G) is, however, significantly larger (greater than 3 standard errors of the difference between means) than the mean vector value of the random sample A.

The interaction of a number of factors which operate in the daylight hours further bias the vector values but tend to keep them well below 50 (fig. 2B, C, G). Some of the likely factors are: (1) the progressive distribution of sun and shade in the cage through the day; (2) wind directions; and (3) individual preferences for certain sectors of the cage for preening and for periods of exercise which often alternate with periods of feeding. The exception is the sample of days by weeks from August through November (fig. 2I). In this period there was frequently a carryover of oriented activity through the dawn until one or two hours after sunrise. This dawn carryover of migratory restlessness was seldom evident in the spring months.

Night vector values are characteristically higher than day values and are usually well above 50. Standard errors of the difference between means of paired day and night vector values as represented in figure 2 are: C and D, 19.5; E and F, 10.2; G and H, 14.6; I and J, 2.5. Three standard errors of the difference indicate significance at the 99.7 per cent level. These higher nighttime vector values are the product of behavioral patterns which our observations through the glass bottomed cage suggest are directed toward a specific sector of the sky. Our *Zonotrichia* repeatedly move from the floor of the cage to the perch in that sector of the cage toward the portion of the sky which they appear to inspect by looking upward. Some variations in behavioral pattern, noted in our direct observations and combined with careful studies of the Esterline-Angus tapes, include: (1) floor—perch—side of cage—same perch—floor—same perch, and so forth; (2) floor—perch—lean backward and return to floor—same perch—lean backward, and so forth; (3) floor—perch—side of cage—adjacent perch—floor—perch—side of cage, and so on; (4) floor—adjacent perch (usually)—perch—other adjacent perch (usually)—floor—adjacent perch—perch—other adjacent perch, and so on; and (5) food ring—floor—perch—side of cage—perch—floor—food ring—floor on opposite side of cage—opposite perch—opposite floor—food ring—floor—perch. Careful observation and study of the records make it evident that variations of these patterns are common. A single bird may in fact use two or three of these patterns in succession, or less frequently it may engage in activity which does not seem to have a pattern.

The very high vector values in figure 2D are the consequence of such patterns as (1) and (2) just mentioned. More than 95 per cent of several thousand perch depressions may be on one perch resulting in vector values well over 50. Some birds habitually have much higher nighttime vector values than others. In figure 2D, the 16 of 20 vector values in the frequency interval 95 to 100 came from the data from a single bird (*Z. l. orientalis*, 26-199274). We include some data in this figure from taxa other than those detailed in table 1. Because such concentration on the same perch is seldom sustained every night for as much as a week, the highest vector values of nights by weeks (fig. 2F, H, J) are somewhat lower than for nights singly (fig. 2D). This is especially true in fall (fig. 2J) when the mean azimuth often changes substantially in a period of seven days (see later sections in this paper). Vector values of night activity tend also to be well above 50 because the birds usually concentrate their attention and activity on the northerly perches in spring and somewhat less consistently the southerly perches in fall.

In summary, the two quantities, mean azimuth and vector value, provide a quantitative expression of an important characteristic, the directional tendency or orientation, of the migratory restlessness. For purposes of interpretation, we shall consider that azimuths with vector values of greater than 50 should warrant considerable confidence. These values apparently result from oriented behavior patterns most common at night and significantly different from behavior patterns exhibited during the day. These daytime vector values are, in turn, significantly different from the vector values for the hypothetical model of randomness which we have calculated. The daytime patterns will not, however, be subject to detailed analyses in this paper because *Zonotrichia* are nocturnal migrants.

MEAN AZIMUTH

Our calculation of a mean azimuth for any particular period does not necessarily mean that we judged the bird to be orienting his movement in response to a migratory urge during that period. The mean azimuth may simply indicate a preference for that sector of the cage. This was especially true during daylight hours when either shade or

sunshine was obviously sought. Our observations of night activity through the glass-floored cage confirm that most night activity being recorded is oriented migratory restlessness or *Zugunruhe* as described by Kramer (1950) and Sauer (1957). During the night the birds usually roosted on the center perching ring where there was some protection. *Zugunruhe* tended to radiate from this central perch area. When activity was light, the bird spent much of its time sitting quietly on the perch, apparently awake, and occasionally cocked its head as though to look at the sky. Heavier activity was expressed as motor activity from the central perching ring and/or from the floor to a directional perch and perhaps from the directional perch to the adjacent side of the cage and back to the perch. The fluttering in place, so important in the observations of Sauer (1957) with members of the Sylviidae and of Hamilton (1962) with the Bobolink (*Dolichonyx oryzivorus*), is apparently of minor importance in the *Zonotrichia* investigated. Although the wings were occasionally held in a partly open position, the birds expressed the greatest portion of their restlessness as motor activity detected by the directional perches. We are confident the data obtained provide a useful index of the quantity of restlessness and that the orientation of the activity provides additional useful information.

Daytime activity data include all perch registrations from about the beginning of civil twilight in the morning to the end of civil twilight in the evening. Because of its more nearly random nature it could be sharply differentiated on the monitoring tapes from night activity in both twilight periods.

RESULTS

Between August, 1958, and December, 1962, a total of 841 bird-weeks (141,000 bird-hours or 1,128,000 perch-hours) were recorded in our activity orientation cages. This report covers the 293 bird-weeks, including 2054 bird-nights summarized in table 1 obtained for the migratory *Zonotrichia* (44 individuals) of taxa which winter in the San Francisco Bay area and which were not subjected to photoperiod manipulation. The 293 bird-weeks of data considered represent more than 49,000 bird-hours, including both active and inactive hours, recorded from eight perches (more than 392,000 perch-hours). It has not been possible or practical to make detailed analyses of all these data. Several thousand man-hours were required to extract the data from the tapes and apply the accompanying analyses to only nine of these birds. Because analyses were in progress already in 1959, it was not possible to take an overview of all data collected through 1962 to select the most appropriate subjects for analysis. Bias resulting from such adventitious selection is minimal in our opinion. The relatively detailed analysis which follows on one *Z. l. gambelii* (26-123496), although expensive because of the 258 days it tied up an A-O cage and monitoring equipment, has been especially rewarding because it shows long term trends in the orientation of migratory restlessness. Naturally the most extensive analyses were made on birds with temporally longer records in the A-O cages and also on those whose responses were quantitatively large enough and sufficiently orientated to be interpretable.

It should also be noted that under our experimental set-up it is possible, but rare according to our observations, for a bird to exhibit strongly oriented behavior and for its tape to show a quantitatively low and weakly oriented record simply because of its avoidance of the recording perches except for an occasional inadvertent hop. Such behavior was detected in the case of a *Z. l. oriantha* (not considered in this report) which regularly ducked under the perch in its pattern of motor activity. Individual variability in behavior is certainly present in birds although perhaps it is not as well

developed as in mammals. Recent evidence (unpublished data) suggests that there may be a very real difference between individual birds in their abilities to "navigate." It would be most surprising if under the limitations and distractions of captivity each and every individual showed strongly oriented behavior at all appropriate times. The spread seen in figure 3, which includes all data from the 44 birds, thus seems partly explainable by these considerations. The birds which we have analyzed in detail show trends similar to those illustrated in figure 3 and represent, we believe, a fair sampling of that body of data.

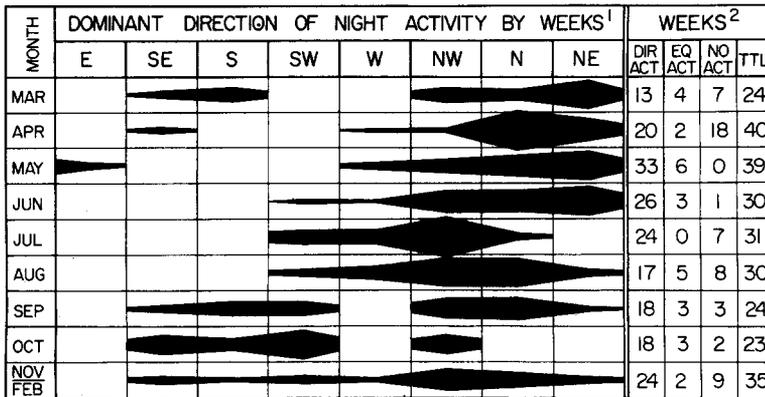


Fig. 3. Summary (by per cent of total active non-equivocal weeks) of dominant direction of night activity of *Zonotrichia* by weeks for 276 bird-weeks (actually bird-quarter-months) between August, 1958, and December, 1962. Vertical interval between horizontal lines represents 50 per cent. ¹Percentage of total weeks in which night activity was present and directional; ²includes weeks when activity was directional, equivocal (see text), or when there was no activity.

To prepare figure 3, tapes for each of the 2054 bird-nights from the 44 individuals were examined, and a statement of quantity of activity and its orientation was prepared for each night. These are summarized by weeks (actually quarter months). Most birds exhibited no significant night activity or at least exhibited greatly reduced night activity when they were in molt, for example, in April, July and August. When activity was present but when no dominant direction could be definitely determined, it was classed as equivocal. The presence of the moon in the night sky was responsible for some of this equivocal activity. Data for the months of November to February were combined because of their small numbers and similar nature.

The dominant directional tendency was northerly from March through August. From September through February there was a tendency for many birds to orient activity in the southerly portion of the cage even though most of these same birds oriented their activity toward the northwest and north in other weeks of the fall season. This southerly orientation perhaps lacks strength because the birds tested were already on their wintering ground and the drive to proceed farther south may have been weak.

Results in figure 3 suggest possibility of phototaxis toward the west-northwest where city lights were reflected from low lying clouds. Any such influence was certainly minimal in April and May when the migratory urge presumably has its greatest development. This is consistent with the experience of Fromme (1961) who reports that the

direction of "migration" of caged *Erithacus rubecula* and *Sylvia communis* in Europe is apparently held more precisely in spring than in fall. A greater incidence of activity in the northwest sector in July and August may have been influenced by such city lights reflected from the frequent low overcast in the hours between midnight and dawn. Comparison of cloud cover data from Moffett Field (Naval Air Station) and our crude empirical nighttime observations at San Jose only serve to emphasize the great variation in local sky conditions in the San Francisco Bay area.

Because of individual variation in this rather complex behavioral response (orientation of night activity) to the environment, we have found it advisable to do detailed analyses of all birds individually. Temporal and directional behavioral responses even to the same environment in the same year make combinations unprofitable while consideration of the same records individually may be very rewarding. For example, some birds seem to ignore the moon in the night sky while the orientation of the activity of other birds is obviously influenced. The role of the moon should not be overlooked in our interpretation of the results from either group. We have not allowed indiscriminate combinations of data from several different birds to screen experimentally predictable or explicable results from individuals.

ZONOTRICHIA LEUCOPHRYS GAMBELII

Birds of this race breed from extreme north-central Washington to northern Alaska and from extreme western mainland Alaska to Hudson Bay in Canada. They winter from as far north as southeastern Washington to Texas and northern México. We consider *gambelii* the most strongly migratory of the races of *Zonotrichia leucophrys*. Our *gambelii* were captured on their winter range in the vicinity of San Jose, where they remain from late September to early April. Although the evidence is thus far largely subjective, our *gambelii* from the San Francisco Bay area are probably wintering about 2000 miles south of their breeding grounds.

What is known of the responses of free-flying *gambelii* may be summarized as follows: We have regularly observed vernal weight increase and prenuptial molt in free-flying birds captured in this area shortly before migration begins, from April 10 to May 13 (see also Blanchard and Erickson, 1949). As a result of handling some thousands of wild birds for banding, it is our distinct impression that molt and migration in *Zonotrichia* are virtually mutually exclusive. In spring some birds seem to leave the San Jose area with their feathers still in sheaths, but not apparently until the feathers have their full growth. Birds captured en route to the breeding grounds are fat (Blanchard and Erickson, 1949; King and Farner, 1959). Upon arrival on the breeding grounds in Alaska in mid-May, the birds have lost their migratory fat (Oakeson, 1954). On the other hand, most *Zonotrichia* held captive in our aviaries during the summer months lose the "migratory" fat only gradually (see also King, 1961; King and Farner, 1963). Apparently *gambelii* complete the postnuptial molt before leaving the breeding grounds in mid-August (Oakeson, 1954). We have found the birds arrive lean at San Jose between September 10 and about October 1 (Blanchard and Erickson, 1949).

Adult male (26-123496) weighed 28 gm. upon capture on February 5, 1959, near Gilroy, about 30 miles southeast of San Jose. This bird was part of a mixed wintering flock of about two hundred *gambelii* and *pugetensis*. He was kept continuously in an A-O cage from March 8 to November 21, 1959, except for a few minutes weekly when removed for weighing and inspection for molt. These 37 weeks included a period of 6 weeks prior to and during the prenuptial molt, the spring migration and breeding season which extended 11 weeks, the postnuptial molt with a duration of 7 weeks, about

12 weeks of fall migratory activity and finally one partial week of the winter activity. His prenuptial and postnuptial molts, and his weight cycle (fig. 4) followed generally the typical pattern for the species in captivity (Farner, 1960). The increase in weight to 34.5 gm. in August and September was less than the 38.5 gm. reached in the spring.

His responses to the experimental conditions also appear to parallel, with certain limitations, the responses of free-flying wild birds even though he was kept at 37° north latitude instead of somewhere north of 50° north latitude where the species breeds during the summer months. The absence of a breeding and nesting experience and other restrictions of cage life at 37° latitude appear not to have interfered with these responses (see Wagner and Thomas, 1957) except for the weight cycle.

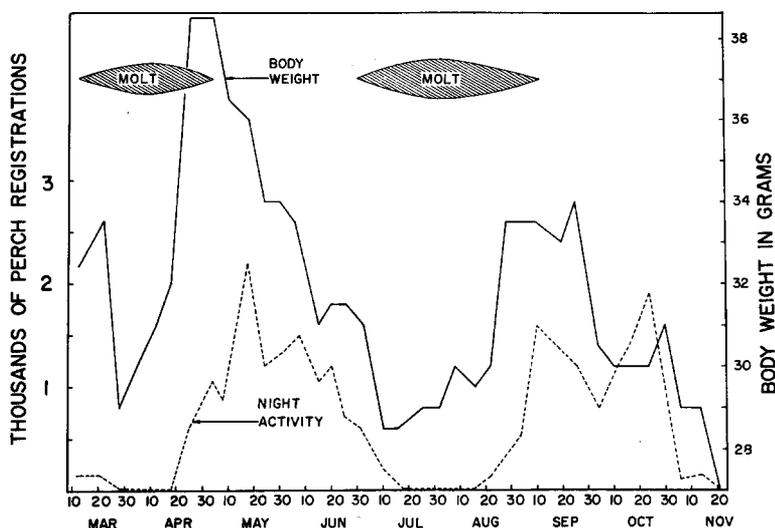


Fig. 4. Body weight, molt, and migratory restlessness in an adult male Gambel White-crowned Sparrow (*Z. l. gambelii*, 26-123496).

BODY WEIGHT AND NIGHT ACTIVITY

In spring night activity and body weight both increased to peaks and then gradually declined to late summer minima. The curves which describe these changes (fig. 4) are similar in shape but are temporally displaced. The curve describing intensity of night activity best correlates with the curve of the body weight that occurs three weeks earlier (table 2). Because of the displacement of these curves, it is unlikely that night activity is directly dependent on body weight. This strongly supports the findings of King and Farner (1963) and Lofts, Marshall, and Wolfson (1963) who suggest that neither fat deposition nor *Zugunruhe* is a direct functional consequence of the other but that they may have parallel relationships as photoperiodically controlled mechanisms. It is very unlikely that weight increases are dependent on night activity as suggested by Kendeigh, West, and Cox (1960). It is perhaps noteworthy that two resurgences in night activity (June 4 to 10 and 18 to 24) are each associated (three weeks later) with an arrest in the otherwise regular decrease in weight toward the postnuptial minimum.

The last significant night activity (259 moves between 1:00 a.m. and 5:00 a.m.)

TABLE 2
CORRELATION COEFFICIENTS BETWEEN CURVES OF BODY WEIGHT AND
NIGHT ACTIVITY FOR *Z. l. gambelii* 26-123496

	Correlation coefficient
Actual timing of events	0.70
Activity displaced one week after weight	0.72
two weeks	0.83
three weeks	0.89
four weeks	0.61
five weeks	0.39

was recorded on the night of July 11-12, about one week after the start of the postnuptial molt. Primaries one (3 cm.) to three ($\frac{1}{2}$ cm.) were in growth on July 10. Two days before this last night's activity the bird's weight reached its summer low of 28.5 gm. The persistence of night activity through the breeding season has been noted by others including Merkel (1958). He suggests the summer night restlessness seen in caged sylviiids in Europe probably does not exist in free-flying birds because their experiences after reaching the breeding grounds tend to end migratory restlessness.

From July 12 to August 22, night activity was absent (0-5 perch registrations) on 25 nights and present (7-54 perch registrations with mean of 22) on 16 nights. Some 460 moves were recorded (3:00 to 6:00 a.m.) on the night of August 22-23, but activity was insignificant the next three nights. Strong, persistent night activity commenced on the night of August 26-27. Some body contour feathers remained in sheaths on August 28, but all feathers were hardened by September 4. Weight increased from 30.0 gm. on August 21 to 33.5 gm. on August 28.

It appears that the demands of the prenuptial and postnuptial molts were sufficient to block *Zugunruhe*. During both molts, however, some night activity occurred when only a few flight feathers were growing, or when body molt was found to be "light." This is consistent with the findings of Weise (1956) and Millar (thesis, Univ. Wisconsin) in caged *albicollis*.

The onset of night activity in the autumn again closely parallels the gain in body weight, but it is displaced about two weeks. Feathers over extensive portions of the body were still in sheaths during the periods of greatest weight increase in spring and autumn. However, significant night activity did not occur until after body molt was nearly complete. At maximum molt there was a complete absence of night activity. Maximum in body weight was reached before molt was complete in both seasons, and peak in night activity was not reached until after the completion of the molt.

CIRCADIAN ACTIVITY PATTERNS

The term "circadian activity pattern" [(L) *circa* = about and (L) *dies* = day] is used to describe the 24-hour pattern of activity exhibited by these birds. The patterns display certain temporal and quantitative (relative) aspects of the 24-hour activity cycle. This usage appears in harmony with "circadian rhythms" and "circadian behavior" as discussed by Halberg (1960). In birds, several of the components of the circadian pattern exhibit a circadian rhythm or period (whether endogenous or exogenous cannot be discussed at this time) when photoperiod is eliminated as a *Zeitgeber* (for example, Aschoff and Wever, 1963).

The median circadian activity patterns for *gambelii* 26-123496 were determined for nine selected periods from March to November (fig. 5). They were selected to exhibit the contrasting patterns which develop in and out of the periods of migration. During

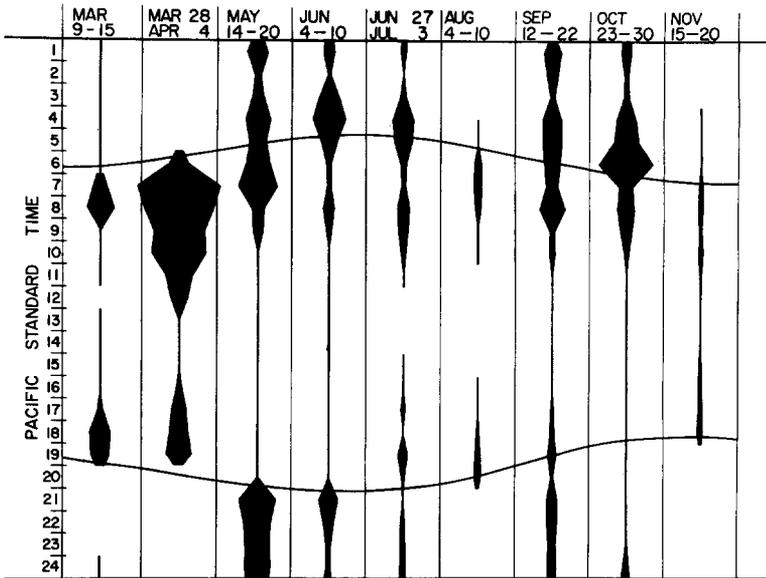


Fig. 5. Circadian activity patterns of an adult male Gambel White-crowned Sparrow (*Z. l. gambelii*, 26-123496) for selected weeks. Dawn and dusk (civil twilight) are represented by the curved lines. The width of the solid black areas represents perch registration per hour; distance between vertical lines represents approximately 1000 perch registrations.

the week of March 28 to April 4, while the prenuptial molt was still in progress, the morning and evening peaks are typical of the patterns seen outside the season of migration in *Zonotrichia* and in many other species tested (see, for example, Eyster, 1954; Farner, Mewaldt, and King, 1954; Weise, 1956; and Merkel, 1958). In mid-May, during the height of migration, the evening peak is absent, the period of greatest sustained activity is at night prior to 1:00 a.m., and the total number of perch registrations is greater during the nine night hours (2180) than during the fifteen daylight hours (1681). In late June and early July when the night activity persisted, as is typical in many species (Weise, 1956), there was in this bird a restoration of the evening peak in activity, and the relative amount of activity prior to 1:00 a.m. was greatly diminished. During the period of postnuptial molt, total activity was greatly reduced. The bird spent several hours in mid-day perched on or near the central circular perch. Patterns in September and October are very similar to those in May and June except for some persistence of the evening peak in activity in September. In September this particular bird exhibited more activity at sunset than do most of our birds. By mid-November, activity had fallen off and the circadian pattern had assumed the morning and evening peaks characteristic of a nonmigratory season.

ORIENTATION OF ACTIVITY—SPRING AND SUMMER

The details of the onset of night activity in late April (fig. 6) are especially significant. There was no important night activity until April 26 and 27 when 284 perch registrations were scattered over all eight perches. Randomness prior to midnight gave way to N and NE activity between 2 and 6 a.m. The vector value of 27 is relatively low. Both the quantity of the night activity and its concentration in the north sector of the cage increased the next two nights. The record for the night of April 27-28 showed 1240 perch registrations with activity in every hour except 5 and 6 a.m. A

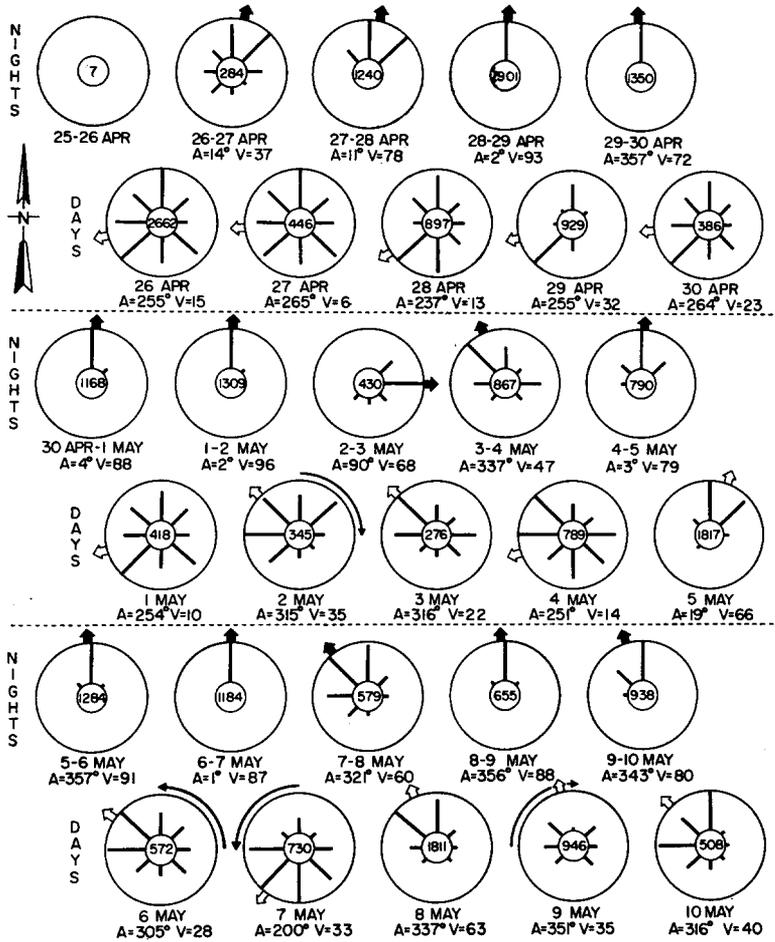


Fig. 6. Onset of Spring Migratory Restlessness of an adult male *gambelii* (26-123496). The number of perch registrations during an entire night or day appears in the inner circle. A = mean azimuth; V = vector value (see text). One-quarter circles with arrows on May 2, 6, 7 and 9 represent 90° cage rotations in the directions indicated.

tendency to orient toward the NW and N around midnight shifted to the N and NE by 2 a.m. More than 1000 of the registrations the second night were between 1 and 5 a.m. On the third night of significant restlessness, nearly all the activity was confined to the north perch. The occasional activity in other parts of the cage was registered at widely scattered time intervals. This apparent progression or improvement in the mechanism of orientation suggests that restlessness may develop before a sense of orientation has materialized or may be necessary to permit the development of the mechanism of orientation (Mewaldt and Rose, 1960). During this period, daytime activity fell off sharply and remained essentially random in nature.

The orientation of the total recorded activity for nights and for days is presented by weeks for the period from March 12 to November 21 (figs. 7 and 8 and table 3). Numbers of recorded perch depressions are nightly or daily arithmetic means. Progressive changes in the orientation of night activity and its degree of fidelity in the

TABLE 3

SUMMARY OF ACTIVITY OF *Z. l. gambelii* 26-123496 FROM MARCH TO NOVEMBER, 1959

Week	Activity index*	Nights		Days		
		Mean azimuth	Vector value	Activity index*	Mean azimuth	Vector value
Mar. 12-18	109	126°	5	991	280°	31
19-25	114	38°	16	885	272°	32
26-Apr. 1	19	6892	29°	33
Apr. 2-8	3	2776	299°	19
9-15	2	4628	53°	46
16-22	6	1176	228°	17
23-29	598	4°	77	1164	245°	12
30-May 6	1043	2°	78	646	356°	30
May 7-13	852	333°	85	1179	310°	33
14-20	2180	315°	90	1681	289°	58
21-27	1195	302°	82	810	252°	22
28-June 3	1283	300°	79	600	245°	29
June 4-10	1369	312°	91	926	11°	13
11-17	1009	304°	73	633	311°	14
18-24	1230	312°	91	755	10°	24
25-July 1	668	333°	61	1474	273°	17
July 2-8	542	332°	60	1241	305°	22
9-15	264	302°	87	1561	295°	18
16-22	0	2800	234°	23
23-29	12	2125	260°	33
30-Aug. 5	10	812	268°	43
Aug. 6-12	7	842	293°	17
13-19	14	1035	231°	20
20-26	126	284°	58	4309	216°	52
27-Sept. 2	345	318°	58	1560	202°	42
Sept. 3-9	584	343°	31	2541	225°	45
10-16	1614	227°	51	2535	231°	36
17-23	1395	222°	55	1553	255°	54
24-30	1170	197°	79	2572	268°	51
Oct. 1-7	778	202°	82	3422	232°	57
8-14	1150	234°	66	3731	238°	47
15-21	1416	239°	67	1542	233°	29
22-28	1905	243°	70	1570	237°	42
29-Nov. 4	1210	250°	83	698	242°	30
Nov. 5-11	121	299°	72	426	292°	41
12-18	184	318°	47	577	217°	29
19-21	9	725	201°	33

* Arithmetic means of perch registrations per night.

direction of "choice" inspire confidence and invite interpretation. This is evident even when data are considered by weeks. We shall later consider the patterns for a series of individual nights to observe hour-to-hour changes.

Night activity from March 12 to 25, although not great in quantity, was regular and significant in quantity and was occurring in the early stages of the prenuptial molt. This activity was almost perfectly random, especially during the first of the two weeks. The energy demands of feather growth evidently prevented significant night activity for the next four weeks.

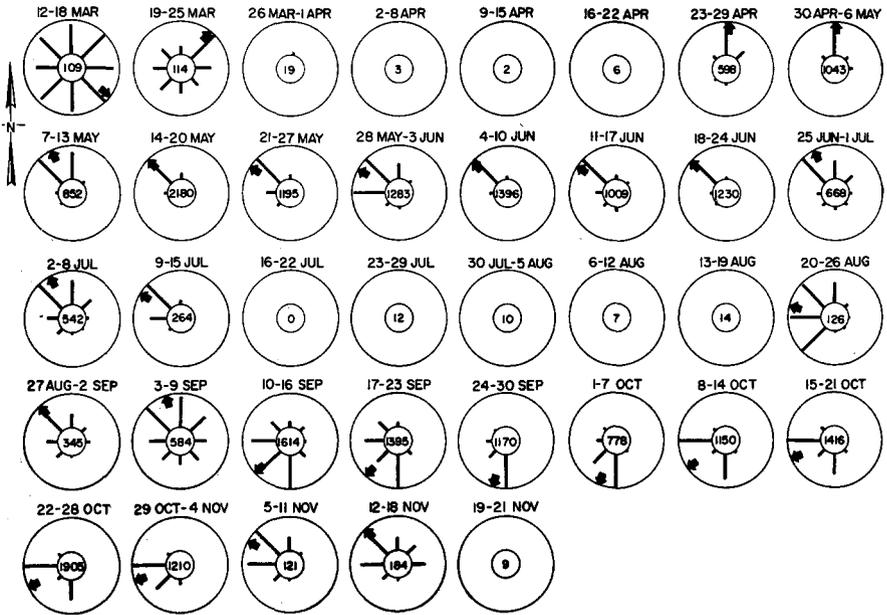


Fig. 7. Night orientation of activity of an adult male *gambelii* (26-123496).

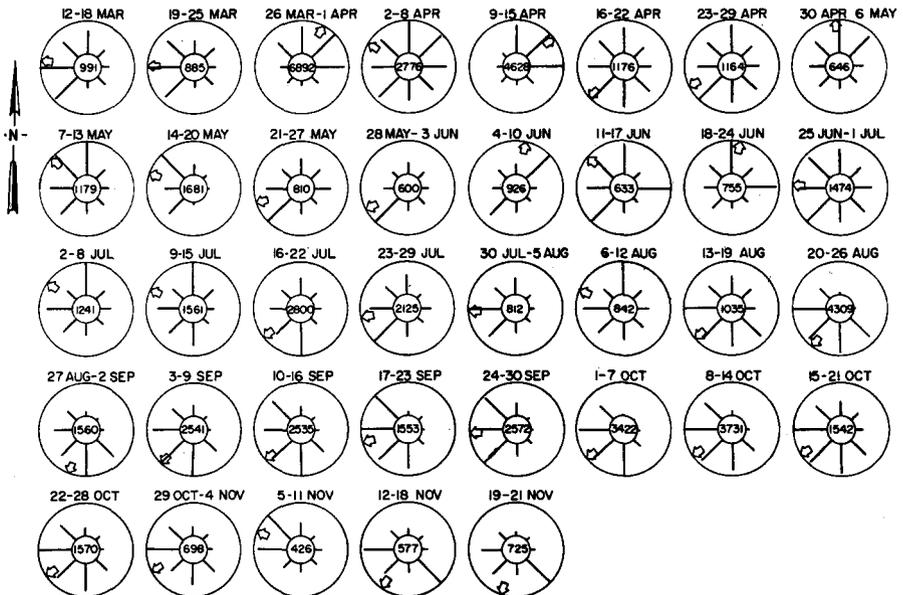


Fig. 8. Day orientation of activity of an adult male *gambelii* (26-123496).

Persistent night activity began on the night of April 26–27 and continued nightly until July 12. Initially the activity was almost true north. At the end of the first week of May a shift toward the northwest began. This shift was progressive until into the first week of June. A northwesterly tendency persisted until night activity ceased simultaneously with the start of the postnuptial molt. No significant night activity occurred during the five weeks from July 12 to August 21 when the bird was in heaviest molt.

ORIENTATION OF ACTIVITY—AUTUMN

Following the postnuptial molt, night activity began gradually. It is of considerable interest that it was northwesterly at first and then shifted northerly by the week of September 3 to 9. Quite suddenly, however, there was a shift to the southwest on the night of September 10–11. The direction of choice was more and more southerly until October 9–10. This southerly (SSW) orientation was strongest between September 19–20 and October 9–10, the period when the race normally completes its southward migration at this latitude. After October 9–10 the trend was reversed and the direction of choice became more nearly westerly until November 5–6 when a northwesterly orientation appeared and persisted until significant night activity ceased on November 18–19. Of some interest is the bimodal curve representing the intensity of fall *Zugunruhe* (fig. 4). Activity making up the first peak (early September) was predominantly southerly. Activity producing the second peak (late October) was predominantly westerly. This suggests a rather sharp change in directional response to the environment when the bird's weight dropped from a plateau of about 33.5 gm. to a lower plateau of about 30.0 gm. in late September.

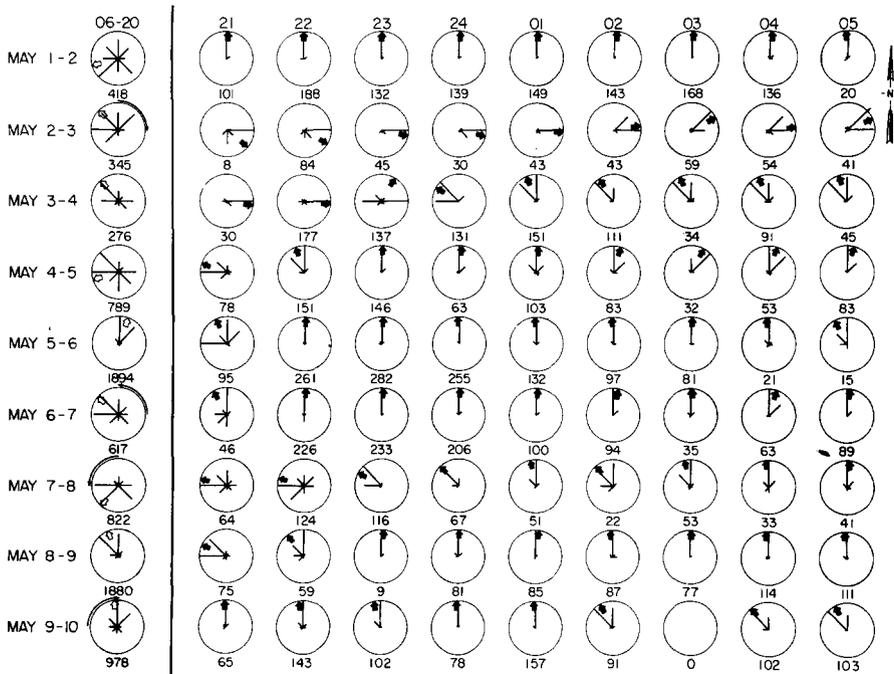


Fig. 9. Night orientation of activity of an adult male *Z. l. gambelii* (26–123496) by hours. The mean azimuth is indicated by the arrow. The number of perch registrations appears below each circle.

These patterns of shift in the orientation of night activity suggest that some regular cyclic changes in the environment may be serving as orientation guide posts. Those associated with the annual cycle of celestial bodies would be expected to exhibit about seven degrees of change each week. Although mean azimuths of some shifts approximate seven degrees, these birds exhibited rather sudden and persistent reversals which tend to disallow a purely celestial explanation. It seems to us more likely that the bird itself shows a varying response to its changing external environment in accordance with an integrated set of psycho-physiological factors. When these are in proper balance the bird responds by moving in the direction of its ancestral breeding area in spring and its ancestral wintering area in fall.

Daytime vector values were substantially below 50 except for a short period in spring and again for a more extended period in the fall (table 3). During the week of May 14 to 20, pre-dawn activity in quantity persisted uninterrupted into the early post-dawn hours. The directional choice in these few early morning hours was the same as on the previous night and thus would seem to be migratory restlessness. On the other hand, vector values slightly above 50 in September and early October seem to reflect preference for a particular sector of the cage during the period of active morning feeding and are probably not to be equated with migratory restlessness.

CAGE ROTATION

Four times in early May, the orientation cage was rotated 90° during daylight hours. In each instance, the entire cage assembly, including the platform and circular screen, were rotated 90°. When rotated 90° clockwise at 11:30 a.m. on May 2 (figs. 6, 9) the sky was overcast (fog) and continued mostly overcast the following night. The bird made a gradual correction for this rotation by exhibiting an hour-to-hour shift toward the northeast. Most activity on that night was on the perch which had been to the north from the center of the cage on previous nights and which was

TABLE 4

NIGHT RESTLESSNESS OF AN ADULT MALE WHITE-CROWNED SPARROW,
Zonotrichia leucophrys gambelii 26-123496, IN OCTOBER, 1959

Night	Perch registrations	Mean azimuth	Vector value	Night sky
Oct. 11-12	791	247°	73	Clear
12-13	913	254°	76	Clear
13-14	1025	261°	85	Clear
14-15	1085	263°	84	Clear
Cage rotated 90° clockwise at noon on October 15				
15-16	1026	244°	77	Clear
Cage rotated 180° at 10:00 a.m. on October 16				
16-17	1180	262°	79	Clear
17-18	3433	230°	58	Clear to partly cloudy
18-19	909	230°	74	Partly cloudy
19-20	841	239°	72	Clear
20-21	488	265°	87	Clear to partly cloudy
Cage rotated 90° clockwise at 3:00 p.m. on October 21—return to original position				
21-22	745	253°	75	Partly cloudy
22-23	1365	252°	77	Clear
23-24	1071	259°	85	Clear
24-25	1387	260°	84	Clear

now east. Correction for this rotation was accomplished by midnight on the second night (which was mostly clear) following the rotation. Counter clockwise cage rotations of 90° were made at 11:00 a.m. on May 6 and at 8:30 a.m. on May 7; both days were clear. Full compensation was accomplished on the clear night of May 6-7, but there was considerable scatter in the activity (vector value of 60) on the night of May 7-8, when there was some haze in the night sky. Full correction was accomplished, however, by 4:00 a.m. on that night and by 11:00 p.m. on the night of May 8-9. A 90° clockwise rotation at 1:15 p.m. on May 9, which returned the cage to its normal position, was corrected for with only a slight drop in the vector value (from 88 to 80) on the clear night of May 9-10. The quantity of activity dropped significantly (1309 to 430 perch registrations and 1184 to 579 perch registrations) on nights following a rotation for which the bird did not completely correct.

In October another series of cage rotations was made. The results are shown in table 4. In this period the bird was orienting west-southwest, part of his gradual change from southerly orientation to northwest orientation which was previously discussed. The sky was at least partly clear the night following each of the three rotations (90° clockwise, 180° and 90° clockwise). It is apparent from table 4 that neither perch registrations, mean azimuth or vector value, was significantly affected by rotation of the cage in this period. This result indicates that in this case the bird was apparently not using cues in the cage itself in choosing direction.

These findings suggest the bird was using visual cues in the night sky to orient his night activity. These cues were apparently not available when the sky was overcast and on such occasions the bird used mostly the perch which had been to the north on the previous night. Points of reference in the rotated cage were probably used when the night sky was overcast. It is likewise possible that such points of reference are used to reinforce direction finding on clear nights and probably account for the display of good orientation on cloudy nights when the position of the cage is not changed.

The impact of cage rotation on daytime activity could not be well assessed because rotation of the cage disturbed the bird and because most of each day's activity was recorded in the hours prior to rotation.

OTHER Z. L. GAMBELII

Gambel Sparrow 25-199601, an adult male, was captured in March, 1958, at Sonora, California, about 90 miles east-northeast of San Jose. It was placed in an A-O cage for limited periods in the fall of 1958 (fig. 10). In each of the five periods represented, there was a distinct choice for the southeast sector. The circadian pattern of activity resembles that of bird 26-123496 in September and October (fig. 5). Our observations suggest that in autumn most of the night activity occurs in the hours after midnight rather than in the hours prior to midnight, as is more characteristic of the pattern in late April and May.

Adult bird 29-154351, also a Gambel Sparrow, was captured on March 5, 1961, near Moss Landing, Monterey County, about 40 miles south of San Jose. During April, May, and June it passed through the prenuptial molt and maintained a weight of more than 35 gm. (usual weight about 27 gm.) from April 29 to June 10. It was kept in a dummy (training) A-O cage from April 29 until June 26 when it was placed in a recording A-O cage.

Night activity in late June (fig. 11), and what light night activity persisted during the postnuptial molt (July 15 to August 26), was strongly oriented toward the north and northwest. There had been a gradual shift toward the west which reached 285° during the week of July 15 to 22, followed by a gradual shift back toward the north

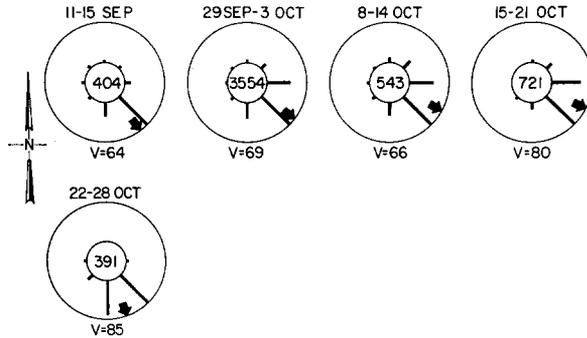


Fig. 10. Night orientation of activity of an adult male *gambelii* (25-199601).

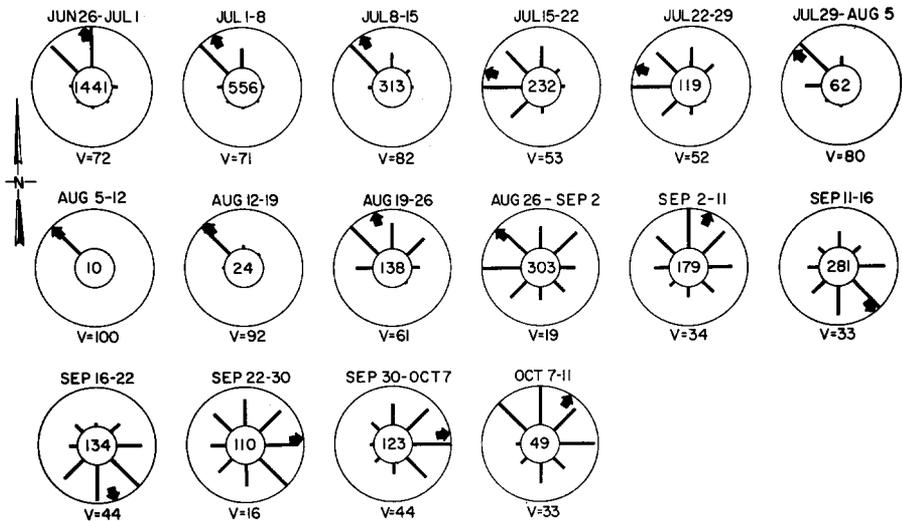


Fig. 11. Night orientation of activity of an adult male *gambelii* (29-154351).

until completion of the molt in the last week of August. At this time a clockwise shift in the choices of direction began which culminated in a mean azimuth of 162° (SSE) during the week of September 16 to 22. A 90° clockwise rotation of the cage on September 16 and a 90° counterclockwise rotation on September 22 were both followed by a night or two of disoriented behavior contributing somewhat to the low vector values observed during this part of the southward orientation. This southerly tendency faded rather quickly and there was a shift back toward the east and north reaching 32° (NNE) during the nights of October 7 to 11, just prior to temporary replacement by another bird. That this tendency to choose a southerly direction was not fully developed is suggested by the relatively low vector values (fig. 11) starting in late August.

It is of some interest to note that whereas bird 26-123496 showed a counterclockwise shift to a south-southwest bearing (fig. 7), bird 29-154351 showed a clockwise shift to its south-southeast bearing (fig. 11). The significance of these opposing shifts remains obscure.

The failure of bird 29-154351 to increase its body weight as did birds 26-123496 and 25-199601 (fig. 12) suggests a correlation between body weight and the strength

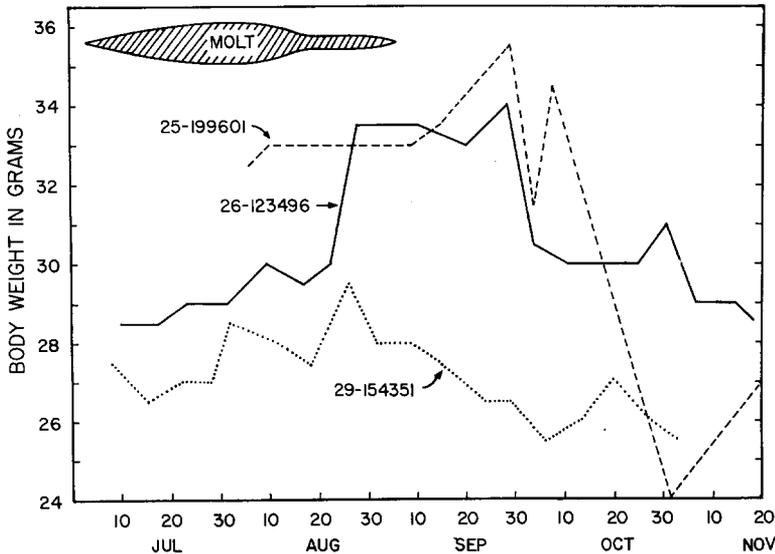


Fig. 12. Body weights of three adult *gambelii* during the fall migratory period.

of the migratory behavior pattern. This is similar to the situation described by Wolfson (1942) in which only fat juncos (*Junco oreganus*) migrated when released after photostimulation in winter. Both birds which showed an increase in weight also exhibited southerly oriented night restlessness for seven or eight weeks whereas bird 29-154351 showed a southerly orientation only for a period of less than two weeks. Vector values also are interesting; the two birds which increased their weights have vector values of from 51 to 67 and from 64 to 85, respectively, during the period of southerly orientation. Bird 29-154351 on the other hand had vector values of from 16 to 44 during its period of southerly orientation. Our data suggest that completion of the post-nuptial molt, accumulation of metabolic reserve in the form of fat, the incidence of night activity and the tendency to orientation of activity toward the south are some of the elements of a neurophysiological apparatus which normally result in southward migration.

ZONOTRICHIA LEUCOPHRYS PUGETENSIS

Birds of this race breed in northern coastal California, western Oregon and Washington and southwestern British Columbia; they winter in the southwestern United States and northwestern México. Bird banding recovery records from our San Jose station suggest that a substantial portion of the *pugetensis* which winter in the San Jose area breed in the rather limited area from Seattle, Washington, to Vancouver, British Columbia. In our aviaries these birds do not generally show as substantial a vernal weight gain as do birds of the race *gambelii* which fly substantially farther to their breeding grounds. This is in agreement with Odum, Connell, and Stoddard (1961) who found that long distance migrants tend to acquire greater fat reserves prior to migration. In this characteristic, *pugetensis* resemble the nonmigratory race *nutalli* which they adjoin on their breeding ground in northern coastal California. Neither caged (Smith, thesis, San Jose State College) nor free-living *nutalli* show a significant vernal gain in weight. Most, but apparently not all, *pugetensis*, however, show a weight gain prior to leaving the bay area in spring migration (unpublished data in our laboratory).

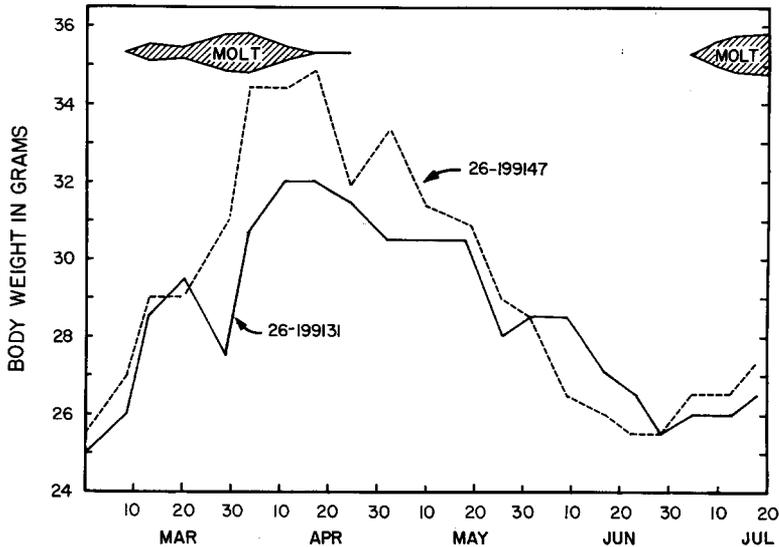


Fig. 13. Body weights of two adult male *Z. l. pugetensis* during the spring migratory period.

They tend here to resemble *albicollis* which may begin migration without a substantial gain in weight (Weise, 1956; Millar, MS). In this respect both *pugetensis* and *albicollis* differ from *gambelii* in which substantial fat is invariably deposited before migration (King and Farner, 1956, 1959).

Activity orientation data were analyzed for two *pugetensis* (26-199131 and 26-199147; see table 1). Both were adult males captured on February 22, 1959, at San Juan Bautista, 40 miles south-southeast of San Jose. They were placed in A-O cages on March 27, and continuous recordings were made until they were removed on April 25. Both of these birds showed a substantial gain in weight (fig. 13). In both birds a light body molt, which may have been in part adventitious, persisted into late April.

The circadian activity patterns (fig. 14) resemble those of *gambelii* 26-123496 (fig. 5). Certain features are worthy of note: (1) Whereas during the week of March 28 to April 3, *pugetensis* 147 had begun to show night restlessness and showed no evening peak in activity, bird 131 exhibited no night restlessness and a pronounced evening peak in activity. The lag of about one week in bird 131's gain in weight (fig. 13) suggests that bird 131 was about one week behind bird 147 in physiological readiness to exhibit migratory restlessness. (2) The evening peak was absent from the patterns of both birds during the week of April 4 to 11, but it reappeared in both birds in the third and fourth weeks of April. (3) The greater quantity of night restlessness takes place prior to midnight. (4) A pre-dawn break in activity is evident in some cases. The accumulation of data by hours usually obscures this break of from 30 to 90 minutes.

The orientation of the night restlessness (fig. 15) of these two birds is certainly northerly, but they exhibit important differences in detail. The birds were in essentially identical cages and were within a few feet of each other. Careful inspection of the Esterline-Angus tape, which recorded the activity of the two birds simultaneously, suggests they responded independently to the environment. Bursts of activity were usually not synchronous. Our direct observations at night of several *Zonotrichia* indicate that they do produce call notes from time to time and seem actually to call in response to another bird in a nearby cage at times. That they may have responded to

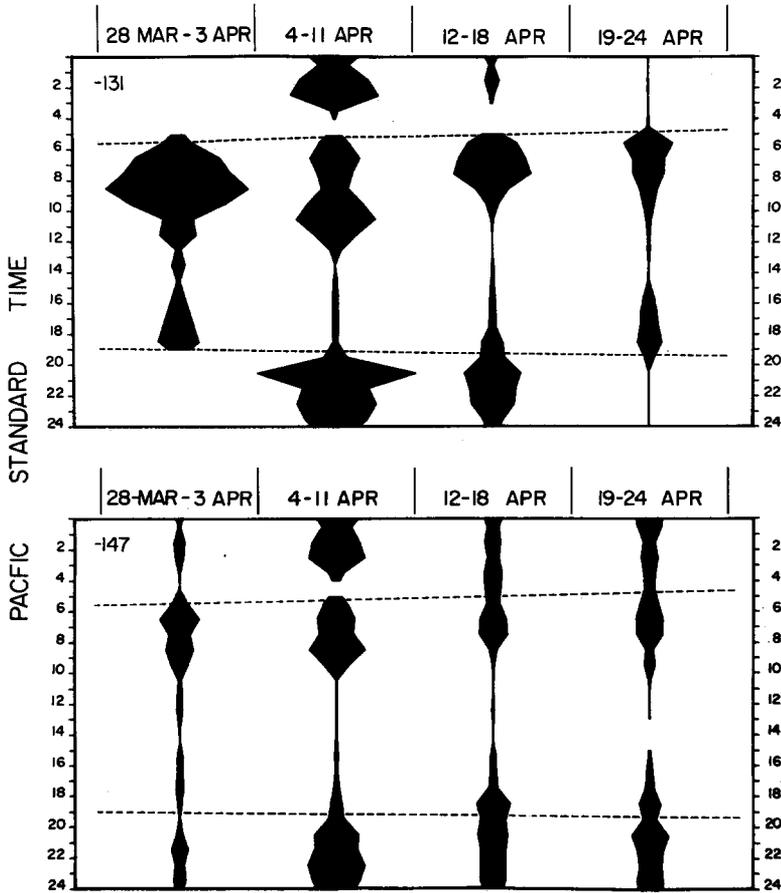


Fig. 14. Circadian activity patterns of two adult *pugetensis* (26-199131, upper; 26-199147, lower). Dawn and dusk (civil twilight) are represented by the dotted lines. A pattern width of $\frac{3}{8}$ inch represents 300 perch registrations per hour.

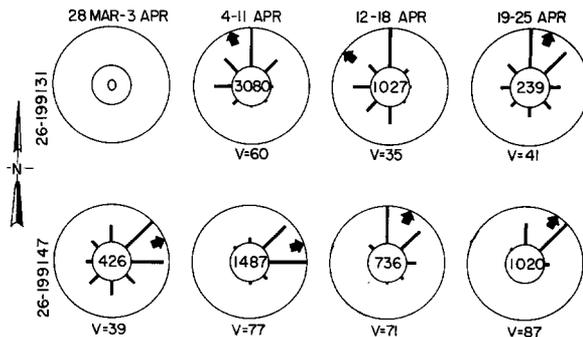


Fig. 15. Night orientation of activity of two adult *pugetensis* in spring.

each other's call is possible as suggested by Hamilton (1962). Such mutual stimulation, if it does actually occur, seems to be effective only when both birds are in fully developed migratory restlessness. We have found no tendency for activity to be directed in a portion of the cage close to other birds which might be calling. It is significant to note that the mean azimuth of the activity of bird 147 was to the east side of north. This was away from the northwest sector of the sky which reflects the most light when there is overcast or fog. Bird 131 did direct activity slightly west of north but then switched to east of north about April 19. There was no unusual tendency to direct activity toward the northwest on those nights when there was a cloud cover during part or all of the hours of darkness.

ZONOTRICHIA ATRICAPILLA

Two males of this species, which breeds mainly in western Canada and Alaska and winters mainly in California, were kept in A-O cages in the spring of 1961 starting on March 18. They were taken in mist nets at San Juan Bautista, 40 miles south-southeast of San Jose, on February 1 and were determined to be males by laparotomy on February 8 and 9. Body weights increased steadily from about 35 gm. in February to 45 to 50 gm. in early May. These birds became exceptionally fat.

The prenuptial molt extended from about March 11 through April 15. This molt was of medium intensity and had little apparent effect on the night restlessness of bird 56-164679 (fig. 16) except that there was a substantial increase in the quantity of activity as feather replacement was completed. The mean azimuths of activity by weeks were within 10° of north from March 29 to May 2. A shift to the northeast and east occurred in early May during and after a series of cage rotations (90° and 180°) from May 6 to 12. The response of this bird to cage rotations was similar to that of some

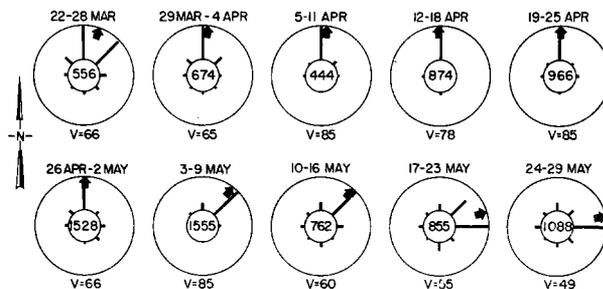


Fig. 16. Night orientation of activity of an adult male Golden-crowned Sparrow (*Z. atricapilla*; 56-164679).

others discussed elsewhere in this paper (birds 26-123496 and 26-123664) in that a 90° clockwise rotation was followed by a shift of the mean azimuth of the bird in that direction. Later as evidenced by vector value, a 90° rotation was followed by essentially random behavior. Therefore vector values and mean azimuths for the two weekly periods affected by these rotations (May 3 to 9 and May 10 to 16) are resultants of combining nights of greatly varying behavioral responses. On May 13 the bird was placed in another cage which further reduced the cumulative vector value for the week of May 10 to 16.

Our records show that bird 56-164687 experienced a prenuptial molt during the same period but of greater intensity, being classified as "heavy" on the body on April 1. The cessation of night activity (fig. 17) in the week of March 28 to April 4 may well

be a consequence of the heavy metabolic drain incident to a heavy body molt. It is perhaps significant that a southerly oriented night restlessness in this bird gave way to a northeasterly orientation just as feather replacement was completed between April 15 and 22. This bird responded to the same set of cage rotations (May 6 to 12) of 90° and 180° by exhibiting nearly random activity. In spite of this apparent randomness as defined by the low vector values ($V = 10$ for the week of May 3 to 9), the mean

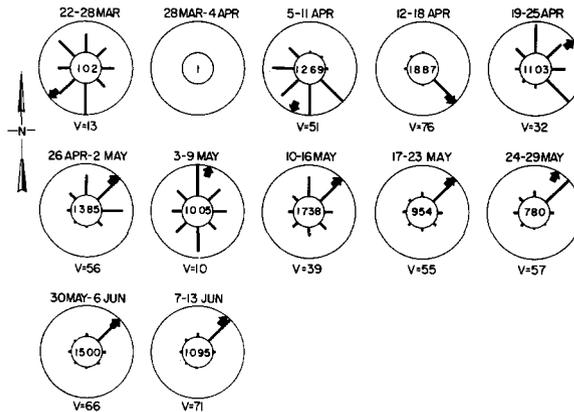


Fig. 17. Night orientation of activity of an adult male Golden-crowned Sparrow (*Z. atricapilla*; 56-164687).

azimuths by weeks remained northeasterly. The circadian activity patterns of these *atricapilla*, which resemble very closely the patterns of *gambelii*, have been described in detail by two of us (Morton and Mewaldt, 1962).

ZONOTRICHIA ALBICOLLIS

White-throated Sparrows winter regularly, but in very small numbers in California. Returns of White-throats banded in California confirm that individuals return to the same specific area each winter. Although we have activity orientation data on only two birds, the nature of these data suggest they may be typical of this species so commonly used in migration studies in middle and eastern North America.

On November 11, 1958, a female White-throated Sparrow (26-123664) was captured at San Juan Bautista about 40 miles south-southeast of San Jose. Kept continuously in an outdoor aviary under natural photoperiods, she underwent three prenuptial and two postnuptial molts at the expected times. Immediately following the prenuptial molt vernal weight increases of 6 to 10 gm. were recorded in April of each of the three springs. There was no weight increase the first autumn (1959). The second autumn (1960) weight increased only to 27.5 gm. The orientation of this female's activity was monitored continuously from March 21, 1961, until June 14, 1961, when she was killed by an unusually high aviary temperature.

The sequence of pertinent events (fig. 18) in the spring of 1961 was typical of the genus except that the onset of *Zugunruhe* and the increase in total activity did not occur until 16 days after body weight had increased to 32 grams and 9 days after the seasonal maximum of 36 grams had been registered. It is clear that vernal fattening in this female was not a consequence of increased activity in daylight or darkness. The prenuptial molt was complete by April 8 and the first significant night activity appeared on the night of April 24-25. This activity was generally random for a period of 7 days

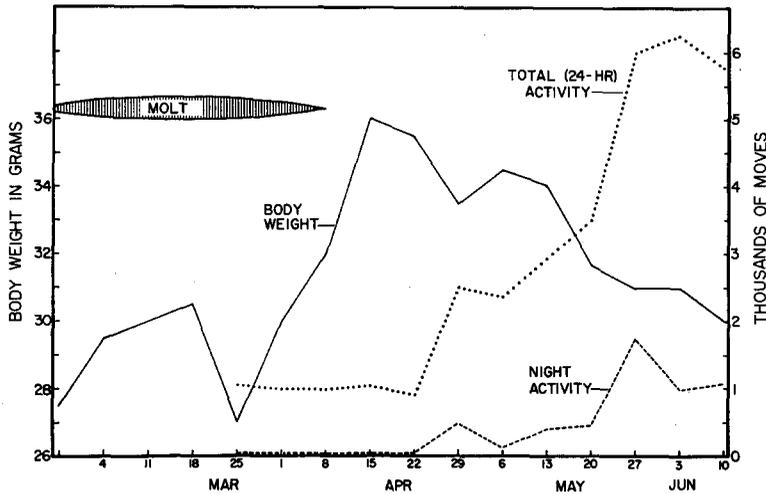


Fig. 18. Body weight, molt, and day and night activity in an adult female White-throated Sparrow (*Z. albicollis*; 26-123664).

(vector values = 10 to 38; table 5). However, by the night of May 1-2 the bird was orienting northwest (342°) with a vector value for the night of 58. This orientation continued ($\pm 1^\circ$) for three nights with a break on the night of May 4-5 when there was no significant activity. The low vector value (39) on the night of May 5-6 is probably due to rain on that night. At 9:00 a.m. on May 6 the cage was rotated 90° clockwise. The result, and results of other rotations, are summarized in table 5.

On the two nights following this first rotation the mean azimuths were 46° and 48° and vector values were low. The night of May 6-7 was cloudy and the night of May 7-8 was foggy. The night of May 8-9, however, was clear and the bird's azimuth that night was 332° , apparently a return to the previously preferred direction. The day of May 6 was cloudy, however, the day of May 7 was clear. Apparently the daytime sun position was not utilized as a cue by the bird in choosing night azimuth. The night of May 9-10 was cloudy again and the azimuth was 312° . These data suggest that following a cage rotation this bird oriented to the favored (previously NW) perch when the clear

TABLE 5

NIGHT RESTLESSNESS OF AN ADULT FEMALE WHITE-THROATED SPARROW, *Zonotrichia albicollis* 26-123664, IN 1961

Night	Perch registrations	Mean azimuth	Vector value	Night sky
Apr. 19-20	2	Partly cloudy
20-21	1	Partly cloudy
21-22	12	Overcast—showers
22-23	16	Partly cloudy—showers
23-24	5	Partly cloudy
24-25	204	250°	15	Clear
25-26	349	2°	23	Clear
26-27	259	326°	34	Clear
27-28	400	270°	19	Clear
28-29	804	11°	24	Clear
29-30	570	26°	10	Clear

Night	Perch registrations	Mean azimuth	Vector value	Night sky
Apr. 30-May 1	386	320°	38	Clear
May 1-2	245	342°	58	Partly cloudy to clear
2-3	122	342°	60	Partly cloudy
3-4	55	343°	53	Clear
4-5	4	Clear to partly cloudy
5-6	52	341°	39	Overcast—showers
Cage rotated 90° clockwise at 9:00 a.m. on May 6				
6-7	101	46°	30	Partly cloudy
7-8	297	48°	35	Clear
8-9	148	332°	35	Clear
9-10	116	312°	60	Cloudy
Cage rotated 180° at 11:00 a.m. on May 10				
10-11	272	257°	45	Partly cloudy to showers
11-12	227	227°	57	Partly cloudy to clear
Cage rotated 90° clockwise at 4:40 p.m. on May 12—return to original position				
12-13	526	234°	68	Clear
13-14	455	282°	41	Clear
14-15	508	299°	39	Partly cloudy
15-16	377	312°	37	Partly cloudy
16-17	224	290°	5	Overcast
17-18	302	22°	36	Overcast
18-19	460	338°	34	Overcast—showers
19-20	318	352°	44	Overcast
20-21	496	348°	55	Overcast
21-22	466	25°	32	Partly cloudy
22-23	1061	357°	53	Partly cloudy
23-24	1578	8°	62	Partly cloudy
24-25	1745	3°	53	Clear
25-26	1706	0°	57	Clear
26-27	1181	342°	71	Overcast
27-28	1846	355°	68	Partly cloudy
28-29	1760	355°	54	Clear
Cage rotated 90° clockwise at 2:00 p.m. on May 29				
29-30	1283	2°	53	Clear
30-31	748	48°	45	Partly cloudy
May 31-June 1	260	345°	21	Partly cloudy—rain
Cage rotated 180° at 10:00 a.m. on June 1				
June 1-2	443	35°	43	Overcast
2-3	1315	3°	37	Overcast
3-4	1024	31°	15	Overcast
4-5	1654	25°	16	Overcast
Cage rotated 90° clockwise at 8:30 a.m. on June 5—return to original position				
5-6	1751	352°	53	Clear to overcast
6-7	1278	40°	33	Clear
7-8	499	10°	10	Overcast
8-9	700	62°	28	Clear to overcast
9-10	1322	8°	51	Clear to overcast
10-11	1823	22°	37	Clear to overcast
11-12	798	342°	5	Clear to overcast
12-13	944	67°	28	Partly cloudy
13-14	1724	62°	40	Clear—hot

night sky was obscured by clouds or fog and corrected for this "error" when the clear night sky was again visible.

Following a 180° rotation on May 10 the mean azimuth was southwest during two cloudy to partly cloudy nights—both days were cloudy but the sun was partly visible through the overcast. The original northwest perch was now southwest and these data suggest that the bird was orienting toward the favored perch again. Another 90° clockwise rotation on May 12 returned the cage to its original position. In spite of the fact that the next night was clear, the bird continued to orient southwest. Only gradually during the next six nights did the bird resume a northerly orientation. Four clear days and two clear nights occurred at the start of this six-day period. However, the night preceding the change to northerly orientation was overcast.

During the next 12 nights, May 17–18 to May 28–29, during which the cage was left in position, the bird's mean azimuth varied from 338° to 25° with a mean azimuth of 358°. (Mean vector value = 52.) During this period both total activity and vector values were generally increasing. On the day of May 29 the cage was rotated 90° clockwise. The following night, which was clear, the mean azimuth was 2°—well within the

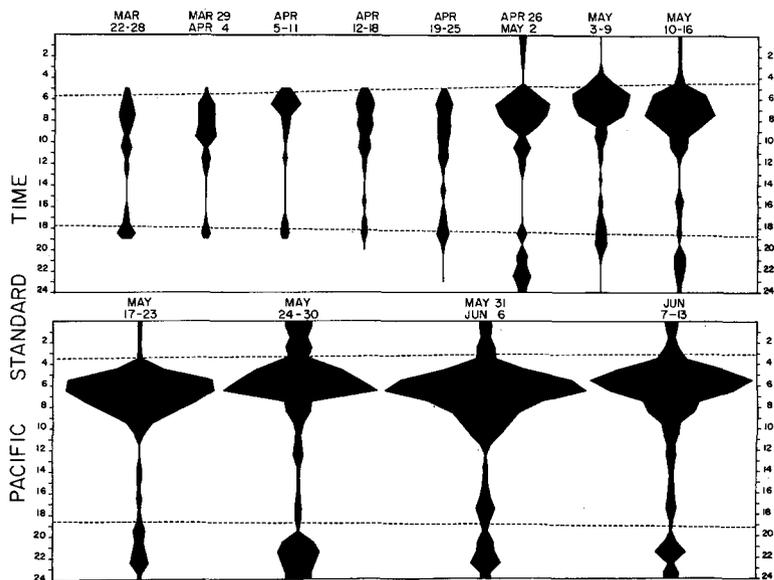


Fig. 19. Circadian activity patterns of an adult female White-throated Sparrow (*Z. albicollis*; 26-123664). Dawn and dusk (civil twilight) are represented by the dotted lines. A pattern width of $\frac{1}{18}$ inch represents 400 perch registrations per hour.

range of variation of the previous 12 nights. Apparently there was some sunshine during both the first and second days. However, the second night after the rotation was overcast and the mean azimuth was 48°, significantly clockwise of the recent azimuths of this bird; and the vector value dropped lower than it had been in eight nights. On the third night, cloudy with rain, the azimuth was northwest but the vector value was so low as to indicate randomness. Total activity also dropped during these three nights.

After a 180° rotation on June 1, vector values continued low with azimuths somewhat clockwise of the range of the 12 nights preceding the earlier 90° clockwise rotation. It was overcast throughout this series of nights and the days were partly cloudy with some sunshine. A 90° clockwise rotation on June 5 returned the cage to its original position. The first night following this last rotation the azimuth was 352°, and the

vector value was 53, an apparent return to behavior which preceded this series of rotations. In subsequent days the vector values were mostly low and the quantity of activity was lower than during the period of strongest orientation, May 22–23 to May 28–29.

In summary, the data in table 5 suggest that the rotation of an orientation cage may temporarily disrupt the behavioral response of an *albicollis* as measured by both azimuth and vector value. There was little or no carryover of direction from daytime sun position to directional choices during the night following. Given a sufficient exposure to one or more nights with clear skies, however, the bird eventually returned to its original behavior pattern.

The circadian activity patterns of bird 26–123664 (fig. 19) are similar to those of our White-crowned Sparrows and closely resemble those obtained for White-throated Sparrows by Weise (1956). Weise summarized activity in units (maximum of 10) per hour. In his units, morning and evening peaks in activity are less conspicuous than in ours which are indices based on total perch depressions per hour. The principal detectable parallel is the higher level of night activity prior to midnight in May and June. This is consistent with the circadian patterns in the other *Zonotrichia* we have tested.

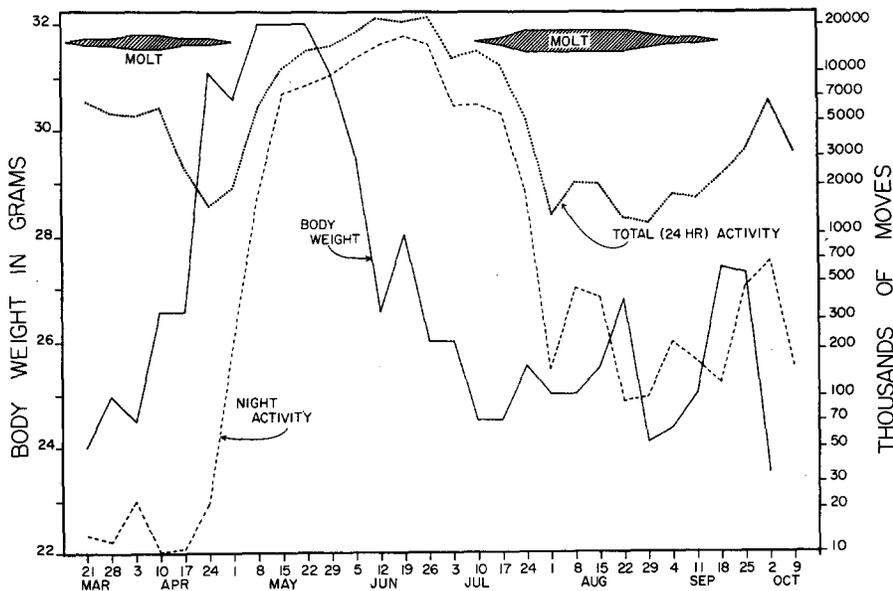


Fig. 20. Body weight, molt, and day and night activity of a female White-throated Sparrow (*Z. albicollis*; 31-138201) in spring.

The second White-throated Sparrow (31-138201) was captured on December 21, 1961, at San Jose. As this female completed the prenuptial molt (March 19 to April 24) she gained weight from a lean 24 to 26 gm. in February and March to 31 to 32 gm. in April and May (fig. 20). The persistence of activity into July is characteristic of *Zonotrichia* tested (Weise, 1956; Millar, MS). During the postnuptial molt night activity continued at a somewhat reduced level. This was also true of some of the birds tested by Millar (MS). This bird did not show a significant aestival weight gain prior to her death in a severe storm on October 13. As in *gambelii* 26-123496, the curves which describe night activity and body weight are similar in shape but temporally displaced. The curve describing night activity best matches the curve of the body weight four weeks earlier (table 6). Again as we did with *gambelii* 496, we may conclude that

it is unlikely that night activity is directly dependent on body weight or that weight increases are dependent on night activity. However, it appears, that some more complex relationship exists between the two.

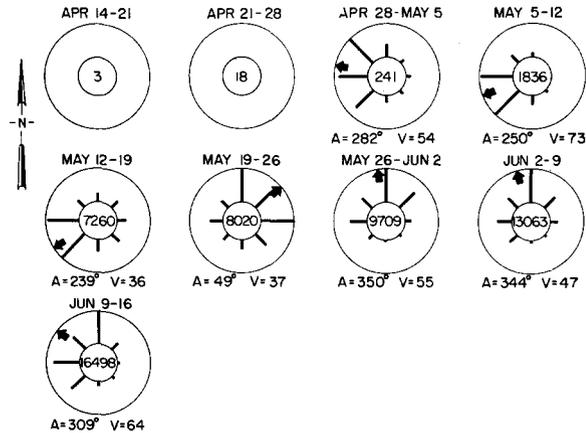


Fig. 21. Night orientation of activity of an adult female White-throated Sparrow (*Z. albicollis*; 31-138201).

The night activity of bird 31-138201 was not significant in quantity until the week of April 28 to May 5 (fig. 21). The azimuth was west (282°) and the vector value was high (54). In the following two weeks, however, during which the moon was visible for some part of the night, the azimuths were west and southwest (250° and 239°). These values are the resultants of hourly data which when analyzed by hour show the bird's azimuth to be different from hour to hour, suggesting that the bird was being influenced by the changing position of the moon during the night. Because of the complex nature of these data further interpretation of the moon influence will be presented in a separate paper. When the moon ceased to be visible to the bird on the night of May 22-23, the orientation changed dramatically as demonstrated during the week of May 19 to 26 when the azimuth was 49° . The week of May 26 to June 2 was completely free of moon influence and the azimuth was now north (350°) with a vector value of 55. For the next two weeks the bird continued to show a reasonably strong northwest tendency. These three weeks of strong north-northwest orientation coincide with a considerable increase in total night activity.

TABLE 6
CORRELATION COEFFICIENTS BETWEEN CURVES OF BODY WEIGHT
AND NIGHT ACTIVITY FOR *Z. albicollis* 31-138201

	Correlation coefficient
Actual timing of events	0.35
Activity displaced one week after weight	0.43
two weeks	0.51
three weeks	0.70
four weeks	0.86
five weeks	0.79
six weeks	0.60

Neither of these female *albicollis* showed (table 5 and fig. 21) as persistent a tendency to orient night activity to the north as have most of our *gambelii* and *atricapilla*. Each bird, however, exhibited reasonably good northerly oriented night activity from mid-May to mid-June.

GENERAL DISCUSSION

It is evident that migratory *Zonotrichia* confined in a suitable cage will exhibit directional behavior at night which may be equated with migratory behavior. It is significant that these birds exhibit oriented *Zugunruhe* for many hours each night, night after night. There is no evidence that the eventual deterioration of this behavior pattern is due to "frustration" because of confinement. On the contrary it is apparently due to the changing environment and the changing psychophysiological state of the bird as it enters another phase of its annual cycle.

Each of the four taxa discussed in detail here show similar responses but individual variation in response is sufficient to make precise combinations of data unprofitable. Our experience suggests, however, that White-crowned Sparrows of the race *gambelii* showed the strongest spring-northerly and fall-southerly migratory restlessness. The strength of response was somewhat diminished, in descending order, in *atricapilla*, *pugetensis*, and *albicollis*. Even less precise are the responses of the nonmigratory *Zonotrichia leucophrys nuttalli* (Smith, MS).

We see then, considerable variation in directional migratory restlessness within the genus *Zonotrichia*. When this variation is considered in combination with variation between individuals of the same taxon and temporal variation in single individuals from one day to the next and one season to the next, it becomes apparent that we are dealing with a complex psychophysiological phenomenon. Our activity records of individual birds in different species (for example, *gambelii* and *atricapilla*) often resemble each other more than they do the records of other individuals in the same species. The overriding similarities in response by birds of the several taxa in the genus suggest a common phyletic origin for most components of the migratory mechanism. Therefore, a common discussion of results from the four taxa seems indicated.

Use of the activity-orientation (A-O) cage provides a device for study of directional components of night restlessness in *Zonotrichia*. We assume that a bird in the A-O cage exhibiting properly oriented night restlessness or *Zugunruhe* is (1) in an appropriate psychophysiological state for migration and (2) in effective sensory contact with its environment. Many of the data presented suggest that as the internal state of the bird changes with time, so does its ability or perhaps its drive to respond to the environment. It is interesting here to consider the relation between body weight and night activity. Our data suggest that the two, while functionally related, are not interdependent. Recent studies (King and Farner, 1963, and Lofts, Marshall, and Wolfson, 1963) show the development of nocturnal unrest in birds (including members of the genus *Zonotrichia*) deprived of enough food to prevent a weight increase. It would be interesting to determine whether these active nonfat individuals exhibited oriented activity. Our findings suggest that strongly oriented behavior may be associated with adequate weight increase at least in autumn.

In the better adapted of the birds reported here, intensity of night restlessness and its concentration (vector value of the mean azimuth) in an appropriate direction (spring-northerly or fall-southerly) increased to a high and then gradually faded in each of the spring and fall migratory periods. In some birds, especially in autumn, the appropriate direction (south) was exhibited for a period of from a few days (*gambelii*, bird 29-154351) to a few weeks (*gambelii*, bird 26-123496).

In spring a northerly or northeasterly direction was exhibited by most birds almost immediately upon commencement of night activity following completion of the pre-nuptial molt. An increasing trend toward a northerly orientation during the first two or three nights in which significant activity occurred suggests that restlessness (1) may develop before a sense of orientation has materialized or (2) may be necessary to per-

mit the development of orientation (Mewaldt and Rose, 1960). After reaching a peak, there was a gradual erosion of the intensity and/or northerly direction through the breeding period in June and July until cessation of night activity at the time the post-nuptial molt commenced.

An abundance of data, reported herein and elsewhere, stress the importance of the internal (physiological) environment to full expression of the migratory habit. It is, however, probably not necessary that all systems (physiological) be in a complete state of readiness for migration to be undertaken. It is well known that all individuals of strongly migratory species migrate except those with incapacitating physical or physiological disabilities. However, at our San Jose banding station there are a few birds each year with disabilities (for example, blind in one eye; poorly healed wing fracture; missing several remiges or several to all rectrices; or foot missing with consequent poor weight and plumage condition). Any of these birds which are surviving at the time of migration disappear and presumably attempt to migrate in spite of handicaps. The observations of Hamilton and Hammond (1960) are noteworthy in this regard. They report that in spring adult pinioned Canada Geese (*Branta canadensis*) which escaped or were released well south of their natural breeding range moved northward on foot.

Although it is perhaps generally understood, we think it pertinent to state that the complexity of the spring-northerly and fall-southerly responses make it apparent that the determination of migratory direction is not an "all or none" phenomenon. A conceptual model which attempts to account for behavior observed following cage rotations is revealing in this context. The hour-to-hour shift in orientation of activity occasionally observed the first night or nights after rotation (for example, fig. 9, May 7 to 9) makes it apparent the bird has not fixed attention on a single environmental object, such as a star. Instead it uses information from more than one object. In practice we have found that reference points within the cage and in the vicinity of the cage are used. It is conceivable that a celestial pattern can provide a number of points of reference and that these in combination with a physiological chronometer cause the bird to assume a directional bearing in flight. Assuming appropriate internal conditions, something in the night sky appears to act as a stimulus in the directional choice of the bird. Since activity in the appropriate direction continued, often increasing in strength for periods of weeks at a time, we may hypothesize a self-reinforcing or positive feedback situation controlling oriented behavior directed by a particular stimulus or cluster of stimuli. At the same time many other stimuli are present which may or may not affect the behavior of the bird at a given moment. The considerable spread we often get about the preferred direction, then, would result from the momentary responses of the bird to other stimuli perhaps functional as directional determinants (for example, the moon) or nonfunctional in themselves as directional determinants such as random motor drives arising from confinement in a cage. The results of our cage rotations show clearly that the bird's behavior is also related to its immediate surroundings.

A simple example accounting for the observed data can be hypothesized from conditioned response theory. Consider a bird in spring orienting in the direction of a particular star in the north sky. After a period of time the unconditioned stimulus, the star, is associated with the conditioned stimulus which we may assume to be a particular perch in the cage which by minor irregularities is recognizably different than the others even to the eyes of the experimenters. The bird then responds to the perch as well as to the star and thus maintains good orientation even on cloudy nights—until the cage is rotated. The bird then continues in most instances, especially on cloudy nights, to orient to this same perch which is now in the "wrong" direction. Lacking the reinforcement of the unconditioned stimulus, the response soon fades, and the other randomizing

stimuli are free to exert a greater influence. Eventually, however, the bird returns to its original directional choice, and the old conditioned response is extinguished permitting formation of a new one. However, the fact that conditioned responses seem never completely lost may account for some of the complex results we have obtained in series of multiple rotations of a bird's cage.

This hypothesis isolates only two of the uncounted number of stimuli available to the bird's sensory input from moment to moment into a highly schematic analysis which tentatively seems to account for some of the observed data. At the same time that the perch is acting as a conditioned releaser, other parts of the cage and other items in the nearby environment, patterns in gravel on the roof surface, the parapet wall, and so on, may also become conditioned stimuli. In rotating the cage we change only some of these. This hypothesis accounts for the more profound disruption of behavior when the entire cage assembly is moved to a new part of the roof (see methods). Without doubt the orientational mechanism includes feedback components which facilitate a weighted response to a complex environment. Indeed the ability to form such conditioned responses to environmental cues might have adaptive value under natural conditions. A particular landmark on the horizon might serve as a conditioned stimulus after an initial association with a celestial pattern and allow enough carryover of response to get the bird through short periods when the celestial pattern was obscured. The observation that the moon has a pronounced phototaxic effect on some of our birds but not on others makes it apparent that interpretation of the environmental cues also varies between individuals.

The celestial pattern in the night sky evolves such that in 6500 years it is materially different, but in 25,800 years it returns again to very nearly the initial pattern. If birds are to respond to this pattern in accordance with an hereditary ability, that ability must evolve in pace with the evolution of the celestial pattern. Agron (1962:527) after considering this problem suggests the "evolutionary change in the bird's behavior occurs at a rate comparable to the speed with which some subspecific anatomical changes are known to occur in higher vertebrates."

It is apparent that the clear or partly clear night sky provides orientational information to our *Zonotrichia* which is not available when the sky is overcast. The responses of our birds to cage rotations under varying meteorological conditions and with a plastic sky screen are consistent with assignment of great importance to the visual contact with the clear night sky. That the celestial pattern provides essential information seems most reasonable, but this is not necessarily proved by our data. Work we have completed, have in progress, and have projected with the manipulation of environment (for example, photoperiod, time shifts, temperature, humidity) of *Zonotrichia* hopefully will further elucidate this problem.

SUMMARY

The responses of individual migratory sparrows in circular activity orientation cages under a natural night sky were recorded. Approximately 49,000 bird-hours of eight-directional-perch activity of 44 birds of four taxa of *Zonotrichia* have been examined in detail. These are part of more than 140,000 bird hours involving more than a million perch hours recorded from August, 1958, to December, 1962. Taxa used were White-crowned Sparrows of two races (*Zonotrichia leucophrys gambelii* and *Z. l. pugetensis*), the Golden-crowned Sparrow (*Z. atricapilla*), and the White-throated Sparrow (*Z. albicollis*). All are night migrants which winter in central California and breed in Washington, the western provinces of Canada and/or in Alaska.

All data were obtained at San Jose, California, and every month of the year is rep-

resented. Major attention was directed to night migratory restlessness (*Zugunruhe*) in the spring and fall migratory periods. Appropriate for migratory birds in the northern hemisphere, spring activity was concentrated in the northerly sectors of the cage. A substantial portion of fall activity was concentrated in the southerly sectors of the cage.

A method of measuring the mean azimuth (mean compass bearing) and vector value (a measure of the concentration of the vectors ranging from 0 to 100) was devised to permit certain quantitative judgments. Both day and night activity appeared to be significantly nonrandom.

Daytime activity vector values were usually low but suggested some preference for various sectors of the cage. These preferences were associated with feeding, simple exercise, sun-seeking, shade-seeking, and wind avoidance and did not include an expression of migratory restlessness except perhaps occasionally in the fall months when pre-dawn migratory restlessness may persist into the post-dawn period. The daytime portion of the circadian activity pattern included mid-morning and evening (sunset) peaks in the quantity of activity. The evening peak disappeared from this pattern when night activity became well developed.

Nighttime activity vector values were usually high. Vector values were highest, and the mean azimuth was most appropriate to the season (spring-northerly and fall-southerly) when free flying birds were in migration. In spring, vector values remained high during the first few weeks after the departure of the local wintering populations. We have no evidence that our caged birds were or were not influenced in any way by free flying migrants. Whereas in spring the greater quantity of night restlessness occurred prior to midnight, in fall the birds were most restless between midnight and dawn.

It is apparent that *Zonotrichia* derive visual information from the clear night sky to orient their *Zugunruhe*. The complex nature of the motor responses makes it likely that the mechanism responsible for orientation includes feedback components. In certain individual birds the orientational mechanism is overwhelmed by a phototactic response to the moon and/or city lights reflected from a low cloud cover. These same birds usually exhibit the appropriate orientational response when the clear night sky is moonless.

Although statistically valid quantitative comparisons are not yet feasible, we found the strongly migratory *gambelii* generally exhibited the strongest spring-northerly and fall-southerly *Zugunruhe*. The strength of response was somewhat diminished in descending order in *atricapilla*, *pugetensis*, and *albicollis*.

A high level of night restlessness is not necessarily associated with a strong directional choice. Indeed some birds showing considerable quantities of night restlessness failed to show a significant directional choice. Our findings suggest that (1) night restlessness *per se* and (2) directional "choice" may be separate components of the behavioral apparatus. It is further possible that (1) night restlessness may develop before a sense of orientation has materialized or (2) that night restlessness may be necessary to permit the development of orientation. Night activity persists beyond the normal spring migratory period into the summer months.

Night restlessness is usually absent or at least greatly reduced during the prenuptial and postnuptial molts. It is most consistent with our results to conclude that the deposition of migratory fat in the vernal period and the onset of night restlessness do not have a cause and effect relationship. They are instead each measurable expressions of the psychophysiological mechanism responsible for migration and as such probably have a functional relationship with each other.

Experimental manipulation of the cage location and appurtenances suggest that

after the original directional "choice" the birds may rely on clues within the cage or closely nearby in maintenance of direction. An unobstructed view of the clear night sky appears to be the most efficacious stimulus enabling the bird to resume normal directional choice after experimental manipulations have confused its response. In experiments of this kind involving caged birds, it is important to be aware of this apparent attachment of the birds to immediate cues in their cage environment. We have discussed an hypothesis in terms of conditioned responses which attempts to account for our observations in this regard.

In the four taxa of *Zonotrichia* tested, the direction of home (northerly) and the appropriate migratory direction in spring (northerly) are the same and may well reinforce each other. The birds used were all already on their wintering ground. This may account for the generally weaker orientational responses we obtained in the fall. The winter-homing component could hardly operate if the bird was already on or very near its specific wintering ground.

LITERATURE CITED

- Agron, S. L.
1962. Evolution of bird navigation and the earth's axial precession. *Evolution*, 16:524-527.
- Aschoff, J., and Wever, R.
1963. Resynchronisation der Tagesperiodik von Vögeln nach Phasensprung des Zeitgebers. *Zeits. f. vergl. Physiol.*, 46:321-335.
- Blanchard, B. D., and Erickson, M. M.
1949. The cycle in the Gambel sparrow. *Univ. Calif. Publ. Zool.*, 47:255-318.
- Cortopassi, A., and Mewaldt, L. R.
1965. Circumannual distribution of white-crowned sparrows. *Bird-Banding*, 36: in press.
- Eyster, M. B.
1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. *Ecol. Monog.*, 24:1-28.
- Farner, D. S.
1955. The annual stimulus for migration: experimental and physiologic aspects. *In Recent Studies in Avian Biol.*, edited by A. Wolfson (Univ. Illinois Press, Urbana), pp. 198-237.
1960. Metabolic adaptations in migration. *Proc. XII Internat. Ornith. Congr., Helsinki, 1958*, pp. 197-208.
- Farner, D. S., and Mewaldt, L. R.
1953. The recording of diurnal activity patterns in caged birds. *Bird-Banding*, 24:55-65.
- Farner, D. S., Mewaldt, L. R., and King, J. R.
1954. The diurnal activity patterns of caged migratory white-crowned sparrows in late winter and spring. *Jour. Comp. Physiol. Psych.*, 47:148-153.
- Fischer, R. B., and Gill, G.
1946. A cooperative study of the white-throated sparrow. *Auk*, 63:402-418.
- Fromme, H. G.
1961. Untersuchungen über das Orientierungsvermögen nächtlich ziehender Kleinvögel (*Erithacus rubecula*, *Sylvia communis*). *Zeits. f. Tierpsych.*, 18:205-220.
- Griffin, D. R.
1952. Bird navigation. *Biol. Rev.*, 27:359-393.
- Halberg, F.
1960. Temporal coordination of physiologic function. *Cold Spring Harbor Symp. Quant. Biol.*, 25:289-310.
- Hamilton, W. J., III
1962. Evidence concerning the function of nocturnal call notes of migratory birds. *Condor*, 64:390-401.
- Hamilton, W. J., III, and Hammond, M. C.
1960. Oriented overland spring migration of pinioned canada geese. *Wilson Bull.*, 72:385-391.

- Hodgman, C. D.
1959. C. R. C. standard mathematical tables (Chemical Rubber Publishing Co., Cleveland, Ohio).
- Hoffmann, K.
1960. Experimental manipulation of the orientational clock in birds. *Cold Spring Harbor Symp. Quant. Biol.*, 25:379-387.
- Kendeigh, C., West, G. C., and Cox, G. W.
1960. Annual stimulus for spring migration in birds. *Anim. Behaviour*, 8:180-185.
- King, J. R.
1961. The bioenergetics of vernal premigratory fat deposition in the white-crowned sparrow. *Condor*, 63:128-142.
- King, J. R., and Farner, D. S.
1956. Bioenergetic basis of light-induced fat deposition in the white-crowned sparrow. *Proc. Soc. Exper. Biol. and Med.*, 93:354-359.
1959. Premigratory changes in body weight and fat in wild and captive male white-crowned sparrows. *Condor*, 61:315-324.
1963. The relationship of fat deposition to *Zugunruhe* and migration. *Condor*, 65:200-223.
- Kramer, G.
1949. Über Richtungstendenzen bei der nächtlichen Zugunruhe gekäfigter Vögel. *In Ornithologie als Biologische Wissenschaft*, edited by E. Mayr and E. Schüz (Carl Winter, Universitätsverlag, Heidelberg), 269-283.
1950. Orientierte Zugaktivität gekäfigter Singvögel. *Naturwissenschaften*, 37:188.
1951. Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse. *Proc. X Internat. Ornith. Congr.*, Uppsala, 1950:269-280.
1952. Experiments in bird orientation. *Ibis*, 94:265-285.
1961. Long-distance orientation. *In Biology and Comparative Physiology of Birds*, edited by A. J. Marshall (Academic Press, London). Vol. II, 341-371.
- Lack, D., and Williamson, K.
1959. Bird-migration terms. *Ibis*, 101:255-256.
- Lofts, B., Marshall, A. J., and Wolfson, A.
1963. The experimental demonstration of pre-migration activity in the absence of fat deposition in birds. *Ibis*, 105:99-105.
- Matthews, G. V. T.
1955. *Bird navigation* (University Press, Cambridge, England).
- Merkel, F. W.
1958. Untersuchungen über tages- und jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. *Zeit. f. vergl. Physiol.*, 41:154-178.
- Mewaldt, L. R.
1962. Displacement of white-crowned sparrows. *Western Bird Bander*, 37:4-6.
1963. California "crowned" sparrows return from Louisiana. *Western Bird Bander*, 38:1-4.
1964. California sparrows return from Maryland. *Science*, in press.
- Mewaldt, L. R., and Farner, D. S.
1957. Translocated golden-crowned sparrows return to winter range. *Condor*, 59:268-269.
- Mewaldt, L. R., and Rose, R. G.
1960. Orientation of migratory restlessness in the white-crowned sparrow. *Science*, 131:105-106.
- Morton, M. L., and Mewaldt, L. R.
1962. Some effects of castration on a migratory sparrow (*Zonotrichia atricapilla*). *Physiol. Zool.*, 35:237-247.
- Oakeson, B. B.
1954. The Gambel's sparrow at Mountain Village, Alaska. *Auk*, 71:351-365.
- Odum, E. P., Connell, C. E., and Stoddard, H. L.
1961. Flight energy and estimated flight ranges of some migratory birds. *Auk*, 78:515-527.
- Perdeck, A. C.
1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea*, 46:1-37.

Rawson, K. S.

1954. Sun compass orientation and endogenous activity rhythms of the starling. *Zeits. f. Tierpsych.*, 11:453-475.

Roadcap, R.

1962. Translocations of white-crowned and golden-crowned sparrows. *Western Bird Bander*, 37:55-57.

Rüppell, W.

1944. Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung. *Jour. f. Ornith.*, 92:106-132.

Sauer, F.

1957. Die Sternorientierung nächtlich ziehender Grasmücken (*Sylvia atricapilla*, *borin* und *curruca*). *Zeits. f. Tierpsych.*, 14:29-70.

1961. Further studies on the stellar orientation of nocturnally migrating birds. *Psychologische Forschung*, 26:224-244.

Sauer, F., and Sauer, E.

1955. Zur Frage der nächtlichen Zugorientierung von Grasmücken. *Rev. Suisse Zool.*, 62:250-259.

Schmidt-Koenig, K.

1960. Internal clocks and homing. *Cold Spring Harbor Symp. Quant. Biol.*, 25:389-393.

Stevens, O. A.

1956. Harris' sparrow transient return; other sparrow records. *Bird-Banding*, 27:33.

Sumner, E. L.

1938. "Homing instinct" in the golden-crowned sparrow. *Condor*, 40:127-128.

Wagner, H. O.

1937. Der Einfluss von Auszenfaktoren auf den Tagesrhythmus während der Zugphase. *Vogelzug*, 8:47-54.

Wagner, H. O., and Thomas, I.

1957. Die hormonale Blockierung des Zugimpulses der Vögel während der Fortpflanzungszeit. *Zeits. f. vergl. Physiol.*, 40:73-84.

Weise, C. M.

1956. Nightly unrest in caged migratory sparrows under outdoor conditions. *Ecology*, 37:274-287.

Wolfson, A.

1942. Regulation of spring migration in juncos. *Condor*, 44:237-263.

Department of Biological Sciences, San Jose State College, San Jose, California, September 26, 1963. (Morton's present address: Department of Zoology, Washington State University, Pullman, Washington).