THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 101 JULY 1984 NO. 3

FACULTATIVE EXTENSION OF FALL MIGRATION BY YELLOW-RUMPED WARBLERS (*DENDROICA CORONATA*)

SCOTT B. TERRILL[1,2] AND ROBERT D. OHMART[3]
[1]*Department of Zoology and*
[3]*The Center for Environmental Studies, Arizona State University,*
Tempe, Arizona 85287 USA

Abstract.—Many nocturnally migrating birds show at least some degree of winter site fidelity. Laboratory tests of nocturnal activity, or *Zugunruhe* patterns, and displacement experiments indicate that migratory distances may be under endogenous control. Yellow-rumped Warblers (*Dendroica coronata auduboni*) displayed a southerly nocturnal orientation well into winter months, past the conventional migratory period. Additionally, population shifts between highly isolated, limited, desert riparian habitats reflected a facultative migration from north to south. The magnitude of movement was correlated with food-resource abundance, which was dependent on climatic conditions. This suggests that the birds maintain a physiological state that enables them to winter as far north as possible but allows for a correctly oriented movement if conditions become unfavorable. Our results indicate considerable plasticity in what is generally considered a more rigidly fixed process. *Received 20 May 1983, accepted 6 February 1984.*

MUCH of the recent work on bird migration has revolved around mechanistic questions, especially those involving orientation, navigation, and physiology. Specifically, studies concerning the ethological aspects of bird migration have emphasized the degree to which behavior is rigidly controlled (Berthold 1975, Gauthreaux 1979, Karr 1980). Although these studies are extremely valuable, there remain numerous questions, virtually unexplored, involving the ecological, demographic, and social aspects of bird migration (Gauthreaux 1979). Of primary importance in gaining a more complete understanding of migration systems is the integration of both areas of endeavor.

Classically, true bird migration has been viewed as consisting of deliberate movements between two relatively fixed sites on the breeding and wintering grounds. Those individuals that survive return to these sites year after year (Lack 1968, Moreau 1972, Berthold 1975). Generally, migrants are believed to traverse the distance between the two sites as rapidly as possible, given certain constraints (Matthews 1968).

The concept of a fixed wintering ground is based upon several lines of evidence, including winter site fidelity of marked individuals and winter displacement experiments (Schwartz 1963, Ralph and Mewaldt 1975). Other experiments have involved displacement of migrating birds (Rüppell and Schüz 1948; Schüz 1949; Perdeck 1958, 1967). These experiments have demonstrated that, in some migrants, distance and direction to the wintering grounds involve a relatively inflexible specific vector movement, at least in first-year birds. Further experiments, primarily with Old World warblers (Sylviinae), have demonstrated that noctural restlessness, or *Zugunruhe*, in fall migrants is correlated well with the timing and duration of migration in the field (Helms 1963; Gwinner 1968, 1972, 1977; Berthold 1973, 1975, 1978, 1979, 1980; Gwinner and Czeschlik 1978;

---

[2] Present address: Department of Biological Sciences, State University of New York, Albany, 1400 Washington Avenue, Albany, New York 12222 USA.

Gwinner and Wiltschko 1978; Berthold and Querner 1981). These experiments imply a mechanism whereby the specific vector movement is fixed. In some species, however, fall *Zugunruhe* has been found to exceed what was thought to be the normal migration period in nature. Several hypotheses have been advanced to address this apparent paradox. One such hypothesis is that in some species, especially in some relatively short- or medium-distance migrants, extended *Zugunruhe* may reflect a physiological condition that is relatively more sensitive to variable environmental cues (Gwinner and Czeschlik 1978).

Large numbers of migrant passerine insectivores that occur from mid-November through March in lowland riparian or riverine habitats in the southwestern United States are generally considered to be wintering birds. Field observations and censusing during winter months from 1973 to 1979 indicated a decrease in numbers following the prolonged or relatively severe cold periods that occur during some winters. When severe cold periods occurred earlier than usual, few insectivorous migrants remained during any winter months. When milder winter conditions prevailed, large numbers of birds, primarily Yellow-rumped Warblers (*Dendroica coronata*), Orange-crowned Warblers (*Vermivora celata*), and lesser numbers of other transient insectivorous passerines, remained throughout the winter period. There was no evidence of mortality, and environments surrounding these habitat islands were unfavorable to local dispersal. Our observations suggested that these parulids have a highly facultative migration system in which migratory behavior may occur during the winter. Three predictions were generated to test this hypothesis. (1) There should be changes in population sizes such that northernmost migratory stopping sites should attain maximum densities, followed by a subsequent decrease, before population peaks at more southerly sites. (2) The timing of population declines, if they were to occur, should be weather related, and the magnitude of the decrease should reflect the severity of the effects of climatic conditions upon food abundance. Potentially, absolute population sizes could vary greatly between sites because of habitat differences. Therefore, the relative patterns at the sites are important. Finally, (3) if these warblers were capable of initiating a continued nocturnal migration, they should maintain a preferred orientation through fall and into winter. This would be necessary in order that additional movements, if brought about by unfavorable conditions, be properly directed.

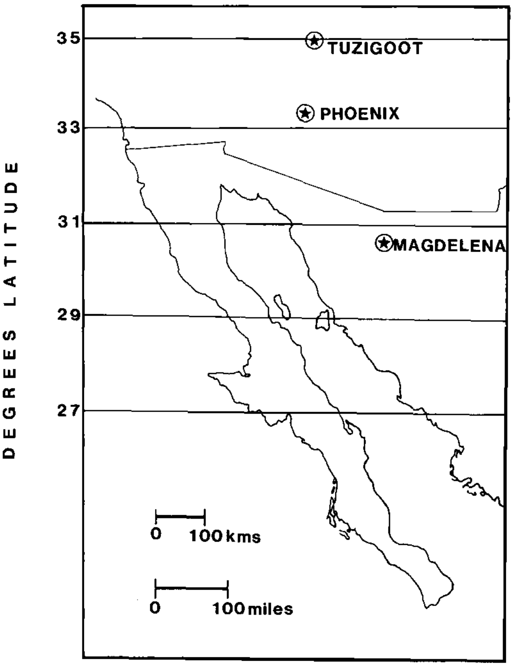


Fig. 1. Map of study-site locations. The Phoenix location included two separate sites: Santa Maria and the Guernsey Ranch. Orientation tests were done primarily at Phoenix. The elevation rises around Phoenix in all directions except to the southwest.

STUDY AREAS AND METHODS

Our selection of study areas (Fig. 1) was based on the following general criteria. (1) All represented highly isolated riparian gallery forests surrounded primarily by arid Sonoran Desert and/or agricultural areas. (2) Each site contained permanent water and clusters of trees. All sites contained cottonwood (*Populus fremontii*), willow (*Salix gooddingii*), and mesquite (*Prosopis glandulosa*) or athel tamarisk (*Tamarix aphylla*) as dominant perennial species. All Arizona study sites contained some salt cedar (*Tamarix chinensis*), whereas the Sonoran site lacked this exotic species. (3) All sites contained clumps or rows of trees small enough and isolated enough to allow direct counts of avian species and calculation of densities.

Field methods.—At each study site, one or two transects of 804.5 × 122 m (0.5 mi × 400 ft) were established. These were censused in early morning. Because riparian strips were so narrow at each site, direct counts of birds were considered to be reliable density estimates. Census numbers were obtained by averaging counts for each census period, usually three consecutive days (Anderson and Ohmart unpubl.).

The only extensive areas in the immediate vicinity of the Phoenix study sites that appeared to be favorable to Yellow-rumped and Orange-crowned warblers were older residential areas. Two transects were established in residential Tempe, near Phoenix, in an area supporting large numbers of introduced shade trees. If birds were dispersing locally rather than continuing south, this would be the most likely area to show an increase in warbler density.

Insect sweep samples were taken along each transect with a canvas net on a hoop 0.3 m in diameter that was mounted on a pole. Each set of sweep samples included 1,000 sweeps per day. Insect samples were taken from the vegetation at heights where warblers were observed feeding. The number of sweeps per unit area was kept constant for each transect during insect sampling. All sampling was undertaken between 1100 and 1300 MST on a given date. Samples were placed in a large plastic bag and were sealed and frozen. In the laboratory, vegetation was separated manually from arthropods, and the latter were identified to the lowest taxon possible.

At the Arizona sites, approximately 100 birds were collected from October to January in 1979–1980 and 1980–1981. These birds were analyzed for stomach contents, lipid content (Wolfson 1945), age, sex, weight, morphological measurements, and other relevant information. Ages were determined by plumage characters and skull ossification.

Bird stomachs, preserved in a 7% ethanol solution, were placed in a graduated cylinder, and the displacement of the full stomach was measured. Next, the contents were extruded, and the volume displacement by the stomach wall was used to measure stomach-content volume. Stomach contents were identified, separated to insect order or family, and then spread over a grid, and the percent volume of the stomach content occupied by each taxon was estimated.

Orientation experiments.—Mist nets were used to capture Yellow-rumped Warblers at each site. Birds were put into solitary, closed, holding cells until 1 h after sunset, when they were quickly measured and weighed, and then placed in a paper orientation funnel for 1 h (Emlen and Emlen 1966). The birds were released the next morning at the site of capture. One night of testing for orientation per individual bird was used. A single night of orientation testing was selected for two reasons. First, it is very difficult to keep small insectivores alive and healthy for several days under field conditions. Second, DeSante tested 23 Blackpoll Warblers (*Dendroica striata*) and compared activity patterns (jumps/night) of the first night after capture with those of consecutive nights. He concluded that no significant difference in activity existed between any of these nights' tests and that nocturnal activity of freshly captured birds is truly representative of *Zugunruhe* (DeSante 1973).

Orientation tests were performed under primarily clear skies. Each test site was chosen to eliminate any horizon glow from adjacent cities. The Tuzigoot site was completely sheltered. The Phoenix birds were transported to an area behind South Mountain (828 m) to eliminate horizon glow.

Ink prints left by the birds in the orientation funnels were analyzed by dividing each funnel into 24 15° wedge-shaped segments. A clear grid divided into 0.5-cm^2 segments was placed over each 15° wedge. For each wedge, the number of squares that were at least half covered by ink were summed. Therefore, each of the 24 segments contained a quantitative value relative to the amount of ink left by the bird in that area of the funnel. These values were analyzed for a mean directional angle, $\bar{a}$, by means of 24 mid-angles derived from each of 24 15° segments. The mean angle was tested with the Rayleigh test (Zar 1974). Although independence of hops cannot be assumed for each bird, significance at $P < 0.05$ by the Rayleigh test was used as an arbitrary method of designating directionality, if present, for each funnel test. Appropriately oriented activity should be indicative of *Zugunruhe* rather than escape activity.

RESULTS

Population changes.—During the 1979–1980 study period, peaks in abundance at more northerly sites were followed by decreases at those sites and increases at more southerly sites (Fig. 2). Yellow-rumped Warbler numbers at the northermost site, Tuzigoot, peaked in October, and then declined to near zero in November, a pattern that might be considered typical of a "normal" fall migration. At the Santa Maria site (33°N), the maximum population occurred in mid-December, when nearly 450 birds/40 ha were detected. This population peak was followed by a decrease in bird numbers from mid-December through early January. The decline continued, from 285 birds/40 ha to 34 birds in 11 days. By early February, only six birds were found at the site.

The Rio Magdelena site was censused only 2 days per visit in 1979–1980. There was an increase from 11 Yellow-rumped Warblers/40 ha on 17 January to 90/40 ha on 27 January. This increase corresponded well with the decline in the north.

A different situation occurred in 1980–1981. Increases similar to those of the previous season at Phoenix (33°N) took place from early

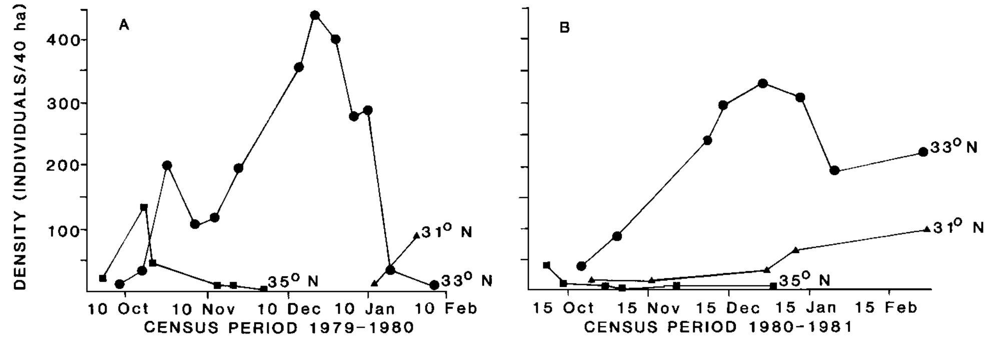


Fig. 2. Yellow-rumped Warbler densities in highly isolated patches of riparian habitat in Arizona (Tuzigoot, 35°N; Phoenix, 33°N) and Mexico (Magdelena, 31°N). Densities were derived from 3-day count periods. Note the dramatic decrease in (A) mid-winter 1979-1980 in the wake of a major cold front versus a much lesser decrease in (B) 1980-1981 (no major front). Increases in the south correspond to decreases in the north, indicating population shifts. These shifts are occurring during a time period (December-January) when these birds were formerly considered to be winter residents at a given site.

November into December. The peak, however, occurred approximately 2 weeks later in 1980 than in 1979 (Fig. 3). This peak was followed by a decrease of approximately 42% (compared to 92% in December to January 1979-1980). Numbers declined until around 20 January and the population then remained at approximately the same level into late February (208 birds in 1981 compared to 6 birds in 1980).

Rio Magdelena was censused throughout the 1980-1981 period, with at least 3 days per census period. The number of Yellow-rumped Warblers remained fairly constant, with a slight increase from October into very late December. From the first of January, however, a steady increase was noted until at least 7 February.

Local dispersal was not detected on the urban transects. Rather, mid-winter decreases were similar to those at the riparian sites (Fig. 3).

Study sites in Arizona lie along major river corridors. The vast majority of the wintering habitats of Yellow-rumped Warblers along the floodplains of these rivers have been eliminated (Ohmart and Anderson 1982). Only remnant, isolated pockets of riparian vegetation have been left. Areas surrounding the Phoenix sites are all higher in elevation, which correlates with a decrease in temperature, and, therefore, these areas are less suitable winter habitat for the warblers. The one exception to

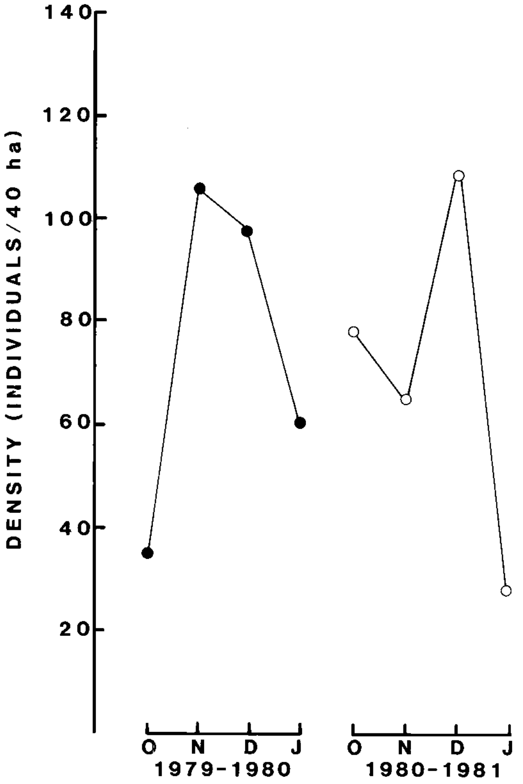


Fig. 3. Fall and winter mean densities of Yellow-rumped Warblers from two residential transects in Tempe, Maricopa County, Arizona. O = October, N = November, D = December, and J = January.

TABLE 1. Total numbers of insects per 1,000 sweep samples taken at Santa Maria, Maricopa County, Arizona (approximately 33°N).

Order	15 Nov 1979[a]	12 Dec 1979	24 Jan 1980	10 Nov 1980	13 Dec 1980	10 Jan 1981	24 Jan 1981	Total
Araneida	223	21	205	54	88	355	43	989
Coleoptera	218	21	97	65	227	116	8	752
Diptera	533	33	122	1,323	750	695	90	3,546
Hemiptera	39	3	11	31	43	50	4	181
Homoptera	7,729	15,181	442	585	13,581	7,045	2,866	47,429
Hymenoptera	159	4	40	70	314	160	20	767
Lepidoptera	10	0	2	5	4	7	2	30
Neuroptera	98	11	17	20	43	67	2	258
Orthoptera	5		6	5	4	9		29
Thysanoptera				2	5		1	8
Trichoptera	1							1
Total	9,015	15,274	942	2,160	15,059	8,504	3,036	53,990

[a] Each date represents 1,000 sweeps.

this general surrounding elevational increase is to be found in the Gila River basin, where the Gila River flows southwest of the Phoenix area and eventually empties into the lower Colorado River. Warblers could, in theory, move from habitat island to habitat island down the Gila River to the lower Colorado River (lower in elevation than Phoenix). With extensive censusing in all habitats along the entire lower Colorado River, however, we did not detect any mid-winter increase in Yellow-rumped Warblers (Anderson et al. MS). In fact, patterns of numerical decreases similar to those described for the Phoenix area occurred, indicating a pattern in other species of migrant insectivores similar to that in Yellow-rumped Warblers (Anderson and Ohmart 1977, Laurenzi et al. 1982). To the south of Phoenix (330 m) is a rise in elevation to Nogales, Arizona (1,178 m). From Nogales, the elevation drops to the south and west. The birds would have to fly south at least into north-central Sonora to search for more favorable environmental conditions. In fact, the first area south of Nogales to support leafed riparian vegetation in 1979-1980 was a small riparian area at Magdelena, Sonora, Mexico. This area was probably kept relatively mild by moist, warm air from the Gulf of California. Therefore, population changes, combined with information about the elevation and temperature gradients, indicate a fairly long-distance movement over relatively unfavorable habitat (e.g. actual migration) versus short flights through favorable habitat (dispersal).

Resource abundance.—Numbers of insects collected at the Phoenix and Tuzigoot sites are summarized in Tables 1-3. Stomach contents of Yellow-rumped Warblers are summarized in Table 4. In general, insect sweep samples reflected the diets of the birds collected. For example, of the 47,429 Homoptera collected at Santa Maria, 43,380 were in the family Aphididae. Therefore, aphids made up the vast majority of insects there. Aphids, when summed up for those months, represented the greatest relative percent volume of the diets. At the Guernsey Ranch in 1980-1981, Chironomidae (Homoptera) represented by far the majority of

TABLE 2. Total numbers of insects per 1,000 sweep samples taken at Guernsey Ranch, Maricopa County, Arizona (approximately 33°N).

Order	22 Oct 1980[a]	12 Nov 1980	15 Dec 1980	22 Jan 1981	Total
Araneida	21	95	270	79	465
Coleoptera	27	135	103	50	315
Diptera	54	495	661	575	1,785
Hemiptera	4	11	3	2	20
Homoptera	17	194	281	275	767
Hymenoptera	7	31	78	13	129
Lepidoptera	3			1	4
Neuroptera		4	1	3	8
Psocoptera				2	2
Trichoptera		1			1
Total	133	966	1,397	1,000	3,496

[a] Each date represents 1,000 sweeps.

TABLE 3. Total numbers of insects per 1,000 sweep samples taken at Tuzigoot National Monument, Yavapai County, Arizona (approximately 35°N).

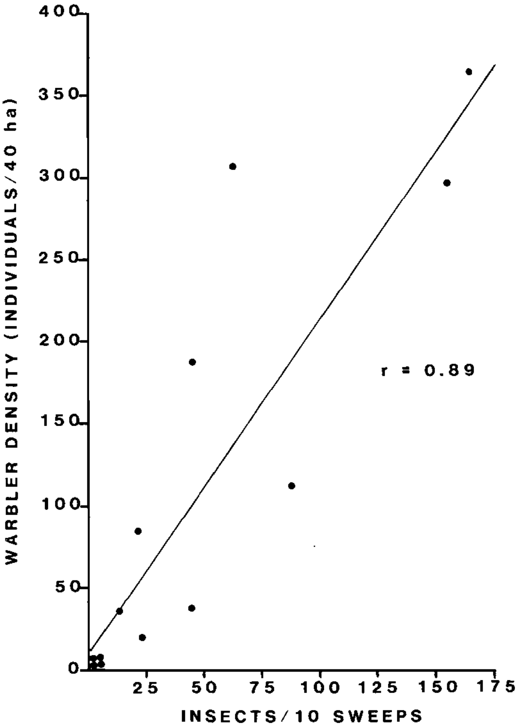
Order	24 Oct 1979[a]	18 Nov 1979	23 Nov 1979	19 Oct 1980	8 Nov 1980	25 Nov 1980	Total
Araneida	497	41	28	42	22	19	649
Coleoptera	289	14	15	54	23	12	407
Diptera	1,332	307	59	121	97	92	2,008
Hemiptera	159	7	0	14	8	12	200
Homoptera	1,498	53	47	1,973	261	85	3,917
Hymenoptera	450	26	3	49	20	5	553
Lepidoptera	35		1	1		2	39
Neuroptera	21	1			2		25
Odonata	8			1			9
Orthoptera	63	1	4	14	5	7	94
Psocoptera	8				1		9
Thysanoptera	17	1		1	1		20
Trichoptera	6			1			1
Total	4,383	451	157	2,271	440	234	7,931

[a] Each date represents 1,000 sweeps.

insects in all sweeps. Chironomidae consistently represented the greatest relative percent volume of stomach contents of birds collected at the Guernsey Ranch. A breakdown of the insect sweep data presented in Tables 1-3 into families is available upon request from the senior author.

Sweep samples were therefore considered reliable estimates of relative resource abundance for warblers. A highly significant correlation ($P < 0.001$) exists between numbers of birds and numbers of insects (Fig. 4) at the sites. None of the Yellow-rumped Warblers captured or collected had any substantial fat accumulation at any time during the study period.

Weather at the sites.—In 1979, a cold front moved through Arizona on 31 October. The temperature at Tuzigoot dropped from an average minimum temperature in October of 27.8°C to an average minimum temperature of 18.5°C in November. During the cold front, the temperature at Santa Maria dropped to approximately 19.5°C. Within a day, the temperatures returned to minimums of 22-32°C until 21-25 November, when freezing temperatures occurred at Santa Maria on 21 and 29 November.



⟶

Fig. 4. Correlation (significant at $P < 0.001$) between numbers of insects and numbers of birds at Arizona riparian sites from October through early February for two years. Each point represents the mean number of warblers from a 3-day census period against a 1,000-insect sweep sample taken during the same period at a given site. Stomach analyses ($n = 100$) indicated that the sweep contents represented warbler diets. Changes in insect populations appeared to be strongly associated with climatic variables (at least in mid-winter). Southerly population shifts (Fig. 2A, B) corresponded to drops in insect abundance, which varied greatly between years.

TABLE 4. Percent volumes occupied by insect groups in the stomachs of Yellow-rumped Warblers from three riparian sites in Arizona. (A) = adult; (L) = larvae.

Tuzigoot (35°N) Sample size = 14		Guernsey Ranch (33°N) Sample size = 22		Santa Maria (33°N) Sample size = 27	
Cicadellidae	34.7	Chironomidae	55.0	Aphididae	46.5
Aphididae	17.8	Cicadellidae	16.4	Hymenoptera	23.0
Hymenoptera	17.4	Reduviidae	91.0	Cicadellidae	5.6
Coleoptera	15.9	Coleoptera	7.0	Curculionidae	5.6
Lepidoptera (A)	5.6	Lepidoptera (A)	5.4	Coleoptera	4.8
Lepidoptera (L)	5.1	Membracidae	2.4	Araneae	3.4
Formicidae	1.4	Curculionidae	1.7	Chironomidae	2.9
Buprestidae	1.2	Syrphidae	1.6	Reduviidae	2.0
Curculionidae	0.5	Formicidae	0.8	Lepidoptera (L)	1.8
Araneae	0.2	Nitidulidae	0.4	Buprestidae	1.5
Hemiptera	0.1	Araneae	0.2	Membracidae	1.1
				Formicidae	0.6
				Nitidulidae	0.6
				Lepidoptera (A)	0.6

No freezing temperatures occurred at the southwest Phoenix site in December 1979.

Several cold fronts moved through the state in January 1980. Freezing temperatures, high winds, and hail occurred at the Santa Maria site from 17 January through 19 January (the most severe conditions during the entire study). The only day that snow was in sight of the transect was 20 January 1980. During this storm, leaves fell from all trees at the Santa Maria site, and insect and bird numbers dropped dramatically. Although the month was otherwise generally mild, leaves did not return until late February.

In November and December 1980 and in January 1981, there were no major cold fronts. For the most part, trees remained in leaf throughout the winter (although cottonwoods lost approximately 50% of their leaves in mid-January). Willows remained in leaf, with buds and new leaves emerging throughout December and January. Both insects and birds decreased during January but to a much lesser degree than in January 1980. The relative role of various weather variables in the system is unclear.

Orientation results.—Yellow-rumped Warblers were tested from October or early November through early January. Throughout both study seasons, they were consistently active in the funnels at night. Of 84 birds tested, a high degree of orientation was shown by 52 birds (Fig. 5). This test population generally showed a significant southerly orientation into early January (1981), with the exception of early to mid-December 1980 (Table 5). There was, however, a decrease in the degree of orientation shown by these birds from October through early January. Unfortunately, no mid-January tests were performed.

DISCUSSION

During the winter of 1979–1980 in central Arizona, a major cold front in January was immediately followed by a substantial decrease in insect abundance and a significant decrease in the number of birds present at the Phoenix site. The next winter (1980–1981) was milder in that no such fronts occurred. Numbers of warblers at Phoenix remained relatively high into March. There was a decrease in January in both insect and bird numbers, but this decrease was much less pronounced than that of the previous winter. January decreases in Arizona were reciprocated by increases in the number of Yellow-rumped Warblers to the south, in northern Sonora, Mexico. A similar pattern was found, earlier in the fall, between northern Arizona (Tuzigoot) and central Arizona (Phoenix). Changes in numbers of birds correlated with changes in numbers of insects. Nocturnal orientation corresponded to the southward shifts in bird populations. These results support the hypothesis that these populations represent insectivores for which wintering sites are relatively plastic within and between winters. Furthermore, these data support an hypothesis of a physiological threshold model. In some migrants, endogenous systems may induce migratory behavior with the aspects of a relatively inflexible pattern, whereas in other birds, such

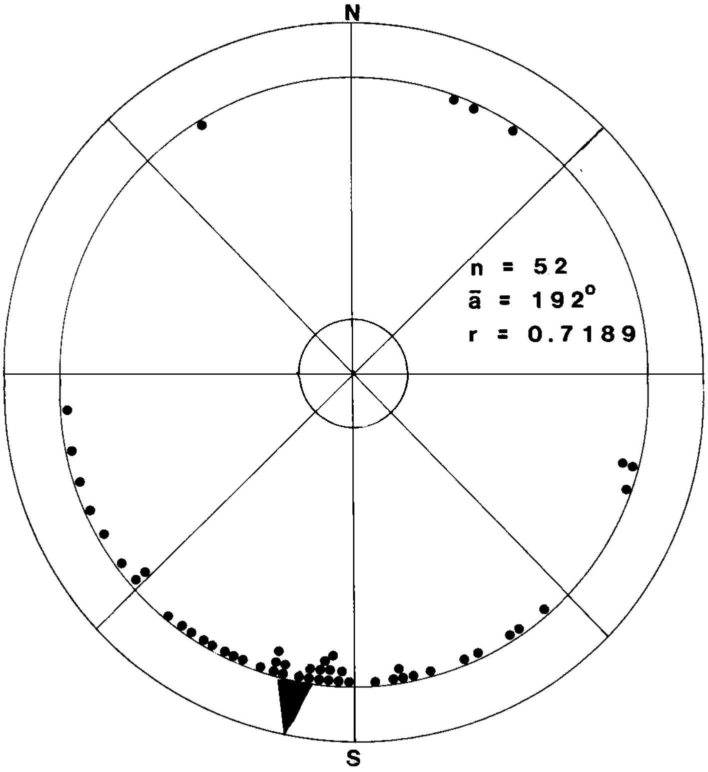


Fig. 5. Orientation of Yellow-rumped Warblers tested outdoors approximately 1 h after sunset. Individual birds were tested for a single night (1 h) from late fall into mid-winter (Table 4). The distribution of pooled mean directions was significantly oriented ($Z = 26.87$, $P < 0.001$) to the south well into the winter period.

as Yellow-rumped Warblers, the migratory state might represent more of a threshold that causes migration if conditions dictate movement. Such thresholds might change with time or distance of migration.

In the Yellow-rumped Warbler, the threshold hypothesis seems appropriate in light of the suddenness with which weather conditions can change. Not all fronts passing through Arizona affect environmental suitability equally. Furthermore, variance in the overall climate over a given winter season may affect the de-

TABLE 5. Mean angles ($\bar{a}$), measures of dispersion (r), scales of Z, and significance level (P) from nocturnal orientation tests on Yellow-rumped Warblers near Phoenix, Arizona. The samples include birds lumped together by temporal periods. NS = nonsignificant.

Date	Number of birds	$\bar{a}$	r	Z	P
November 1979	7	204°	0.74	3.91	$0.01 < P < 0.02$
Early to mid-December 1979	6	190°	0.97	5.72	$P < 0.001$
Late December 1979	4	156°	0.87	3.06	$0.02 < P < 0.05$
October 1980	11	210°	0.86	8.21	$P < 0.001$
November 1980	8	182°	0.88	6.27	$P < 0.001$
Early to mid-December 1980	6	217°	0.66	2.66	NS
Late December 1980 to early January 1981	10	163°	0.54	3.02	$0.02 < P < 0.05$

gree of change created by relatively similar frontal systems between seasons. If the birds had to "gear up" from a nonmigratory state, the time element involved in changing to a migratory state might be too great. Therefore, an extended, low-level maintenance of the migratory state enabling a rapid response would be advantageous.

The span between a highly facultative migration and a highly fixed one may represent differences in the degree of suitability of habitats along the migration route. Many migrants, such as those that cross the Mediterranean and Sahara or the Gulf of Mexico, might be considered as birds that migrate a mandatory distance. One tradeoff might be that these birds consistently wind up in a relatively benign environment at the end of this movement. On the other hand, some species apparently have developed the ability to shift the wintering area along the route, depending upon the current suitability of given areas. Underlying this concept is the assumption that there is an energetic cost associated with migration and that a reduction in migratory distance, where feasible, would be advantageous. In addition, it has been suggested that birds wintering closer to the breeding grounds gain an advantage by earlier arrival when conditions on the breeding grounds permit habitation (Ketterson and Nolan 1976, Gauthreaux 1978, Myers 1980).

Yellow-rumped Warblers are known to be late migrants, especially for parulids (Keast 1980a). In a seasonal comparison among 14 species of northeastern North American breeding wood warblers, the longest fall migration period and shortest wintering period were attributed to Yellow-rumped Warblers. Lack and Lack (1972) noted that Yellow-rumped Warblers may not arrive in Jamaica until January. Numbers of Yellow-rumped Warblers have been found at nocturnal tower kills in December and January (Crawford 1981). This species has arrived at and departed from the Farallon Islands, California, relatively frequently in mid-winter (DeSante and Ainley 1980). These data, although indicating mid-winter movement, are unable to address whether these movements were facultative or "late" typical migration.

Some ducks and shorebirds appear to remain as far north as possible, moving southward in stages as freezes occur (Shuford and DeSante 1979). So-called "weather migrants" are well known. In general, these are not "typical" migrants or insectivores but include birds such as siskins, crossbills, grosbeaks, redpolls, and other "irruptive species." Some species of migrant sparrows appear to show facultative migration, including Field Sparrows (*Spizella pusilla;* Fretwell 1980) and White-crowned Sparrows (*Zonotrichia leucophrys;* Gauthreaux pers. comm.). Chipping Sparrows (*Spizella passerina*) continue to migrate south into the Sierra Madre Occidental of Mexico from potential wintering areas in southeastern Arizona if low summer rainfall has not produced an abundance of winter seeds (Pulliam and Parker 1979). Individual Dark-eyed Juncos (*Junco hyemalis*) have been found after December in vastly different areas between winters, with most of these shifts being to the south (Ketterson and Nolan 1982). European Starlings (*Sturnus vulgaris*) that were displaced to favorable wintering areas ceased their migration, whereas other individuals that were transferred to unfavorable surroundings showed an induced prolongation of migration (Perdeck 1964). Several species of Old World *Turdus* are known to extend or initiate facultative fall (winter) migration (Lack 1944). Some recent observations indicate that other Old World long-distance migrants may be pausing or decelerating in their fall migration and then continuing if conditions dictate further movement. Some species that are destined for South America may linger in Panama before proceeding to their wintering grounds (Morton 1980). In Africa, at least some of these migrants move southward in stages, pausing for weeks or even months before proceeding (Moreau 1972, Morel 1973, Pearson and Blackhurst 1976, Moreau and Dolp 1970). Experimental evidence suggests that the birds in Arizona were actually showing a propensity for nocturnal migration rather than diurnal movements. There is evidence that very late movements by these other species are also of the classical nocturnal type. Included in these are Marsh Warblers (*Acrocephalus palustris*), which were observed repeatedly coming to lighted windows at Amani, Tanganyika in December and January (Moreau 1972). Observations of this species in that area occurred only at night. In Isavo, Kenya, 12 species of nocturnal migrants were found at brightly lighted windows on the north side of a building in December. Four of these species were migrants that have also shown winter site fidelity (Moreau 1972).

Food-resource abundance is probably extremely important in the evolution of migration systems (Dingle 1980, Keast 1980b). Energetically, migration is very costly (Tucker 1971, Blem 1980). Therefore, it appears selectively advantageous for migrant birds to reduce as much as possible the distance between adequate food resources in the breeding and nonbreeding periods. In addition, many factors would enter into the distance variable: winter site predictability, suitability of habitats, renewability or lack of renewability of a food resource, competition, and morphological and physiological limitations. Regardless, it would be selectively advantageous for an individual migrant to be able to leave its present location should unfavorable conditions occur and the probability of mortality become high. Movements of this type may not always be more beneficial than staying (depending upon the probability of finding a better area as opposed to the probability of dying if they remain). Many factors would enter into the movement process, not the least of which would be how many other individuals might be leaving an area, and how this might affect the habitat suitability. Thus, there is the likelihood, or at least the possibility, of mixed populations of site-flexible and site-fixed individuals that may involve different trade-off relationships, depending upon, for example, different breeding populations or age or sex groups, dominance relationships, and other factors (Ketterson and Nolan 1976, 1979, 1982; Gauthreaux 1978). Finally, even the same individuals might vary between years, depending not only upon past experience (or lack thereof) but upon fluctuating conditions as well. Winter site fidelity is a relatively prominent phenomenon in at least some migrant species. This fidelity should occur in areas where past winter survivability was achieved. There are many benefits derived from returning to a familiar area as well. It does seem, however, that few data exist concerning between-year site suitability in areas where individuals recur in winter. The observation that a bird recurs does not address the question of whether or not the bird possesses the capability to move if the habitat changes for the worse.

Just as migrants are known to accelerate their rate of movement as they approach the breeding grounds if conditions are favorable (Lincoln 1952), we are suggesting that some, at least, decelerate their rate of movement in late fall migration if conditions are favorable, stopping to winter if conditions remain favorable. Decelerating the rate of movement, when feasible, may reduce the energetic cost of migration and allow for an overall reduction in the distance between the breeding and wintering area. By maintaining a relatively low-level migratory state, movement can be elicited with a minimum amount of preparatory time, and movements, if necessitated, can be properly oriented.

ACKNOWLEDGMENTS

We thank K. P. Able, J. L. Brown, H. R. Pulliam, and S. Martindale for their valuable comments and S. T. Emlen, S. A. Gauthreaux, Jr., C. J. Ralph, A. T. Smith, and G. E. Walsberg for their input during the course of this study. K. V. and G. Rosenberg, L. Terrill, and J. Wielgus helped extensively in the field and in the laboratory. E. W. Minch identified arthropods from both the stomachs and sweep samples. C. D. Zisner typed the manuscript, J. R. Durham and S. M. Cook helped with the editing, and L. G. Ginn and C. D. Zisner prepared the figures. We also thank P. Berthold and D. DeSante for their helpful criticisms and comments in reviewing the manuscript.

LITERATURE CITED

BERTHOLD, P. 1973. Relationships between migratory restlessness and migration distance in six *Sylvia* species. Ibis 115: 594–599.

———. 1975. Migration: control and metabolic physiology. Pp. 77–128 *in* Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

———. 1978. Concept of endogenous control of migration in warblers. Pp. 275–282 *in* Animal migration, navigation and homing (K. Schmidt-Koenig and W. T. Keeton, Eds.). Berlin, Springer-Verlag.

———. 1979. Beziehungen zwischen Zugunruhe und Zug bei die Sperbergrasmuche *Sylvia nisdria*: eine ökiphysiologische Untersuchung. Vogelwarte 30: 77–84.

———. 1980. Beziehungen zwischen Nachtunruhe und Zugverhalten bei der Brillengrasmüche *Sylvia conspicillata*. Vogelwarte 30: 276–277.

———, & U. QUERNER. 1981. Genetic basis of migratory behavior in European warblers. Science 212: 77–78.

BLEM, C. R. 1980. The energetics of migration. Pp. 175–244 *in* Animal migration, orientation and navigation (S. A. Gauthreaux, Jr., Ed.). New York, Academic Press.

CRAWFORD, R. L. 1981. Bird casualties at a Leon County, Florida TV tower: a 25-year migration study. Bull. Tall Timbers Res. Sta. 22: 1–30.

DESANTE, D. F. 1973. An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California. Unpublished Ph.D. dissertation, Stanford, California, Stanford Univ.

———, & D. G. Ainley. 1980. The avifauna of the South Farallon Islands, California. Studies Avian Biol. No. 4.

DINGLE, H. 1980. Ecology and evolution of migration. Pp. 2–101 *in* Animal migration, orientation and navigation (S. A. Gauthreaux, Jr., Ed.). New York, Academic Press.

EMLEN, S. T., & J. T. EMLEN. 1966. A technique for recording migratory orientation of captive birds. Auk 83: 361–367.

FRETWELL, S. D. 1980. Evolution of migration in relation to factors regulating bird numbers. Pp. 517–528 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.

GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance. Pp. 17–54 *in* Perspectives in ethology (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Publ.

———. 1979. Priorities in bird migration studies. Auk 96: 813–815.

GWINNER, E. 1968. Circannuale Periodik als Grunollage des jahreszeitlichen am Fitis (*Phylloscopus trochilus*) und am Waldlaubsänger (*P. siliatrix*). J. Ornithol. 109: 70–95.

———. 1972. Endogenous timing factors in bird migration. Pp. 321–338 *in* Animal orientation and navigation (S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and P. E. Belleville, Eds.). Washington, D.C., U.S. GPO, NASA Sp-626.

———. 1977. Circannual rhythms in bird navigation. Ann. Rev. Ecol. Syst. 8: 381–405.

———, & D. CZESCHLIK. 1978. On the significance of spring migratory restlessness in caged birds. Oikos 30: 364–372.

———, & W. WILTSCHKO. 1978. Endogenously controlled changes in migratory direction of the Garden Warbler, *Sylvia borin*. J. Comp. Physiol. 125: 267–273.

HELMS, C. W. 1963. The annual cycle and *Zugunruhe* in birds. Proc. 13th Intern. Ornithol. Congr.: 925–939.

KARR, J. R. 1980. Patterns in the migration system between the north temperate zone and the tropics. Pp. 529–543 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. J. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.

KEAST, A. 1980a. Migratory Parulidae: what can species co-occurrence in the north reveal about ecological plasticity and wintering patterns? Pp. 457–476 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. J. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.

———. 1980b. Synthesis: ecological basis and evolution of the nearctic-neotropical bird migration system. Pp. 559–576 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. J. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.

KETTERSON, E. D., & V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis*). Ecology 57: 679–693.

———, & ———. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). Auk 96: 532–536.

———, & ———. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. Auk 99: 243–259.

LACK, D. 1944. The problem of partial migration. Brit. Birds 37: 122–130, 143–150.

———. 1968. Bird migration and natural selection. Oikos 19: 1–9.

———, & P. LACK. 1972. Wintering warblers in Jamaica. Living Bird 11: 129–153.

LAURENZI, A. W., B. W. ANDERSON, & R. D. OHMART. 1982. Wintering biology of Ruby-crowned Kinglets in the lower Colorado River valley. Condor 84: 385–398.

LINCOLN, F. C. 1952. Migration of birds. Washington, D.C., U.S. Dept. Int., Fish Wildl. Serv.

MATTHEWS, G. V. T. 1968. Bird navigation. Cambridge, Massachusetts, Cambridge Univ. Press.

MOREAU, R. E. 1972. The Palearctic-African bird migration system. New York, Academic Press.

———, & R. M. DOLP. 1970. Fat, water, weight, and wing length of autumn migrants in transit on the northwest coast of Egypt. Ibis 112: 209–228.

MOREL, G. 1973. The Sahel Zone as an environment for palearctic migrants. Ibis 115: 413–417.

MORTON, E. S. 1980. Adaptations to seasonal changes by migrant land birds in the Panama Canal Zone. Pp. 437–453 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservations (A. J. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.

MYERS, J. P. 1980. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Can. J. Zool. 59: 1527–1534.

OHMART, R. D., & B. W. ANDERSON. 1982. North American desert riparian ecosystems. Pp. 433–474 *in* Reference handbook on the deserts of North America (G. L. Bender, Ed.). Westport, Connecticut, Greenwood Press.

PEARSON, D. J., & G. C. BLACKHURST. 1976. The southward migration of palearctic birds over Nigulia, Kenya. Ibis 118: 78–105.

PERDECK, A. C. 1958. Two types of orientation in migrating Starlings *Sturnus vulgaris*, and Chaffinches *Fringilla coelebs,* as revealed by displacement experiments. Ardea 47: 1-37.

———. 1964. An experiment on the ending of autumn migration in Starlings. Ardea 52: 133-139.

———. 1967. Orientation of Starlings after displacement to Spain. Ardea 55: 194-202.

PULLIAM, H. R., & T. H. PARKER, III. 1979. Population regulation of sparrows. Fortsch. Zool. 25: 137-147.

RALPH, C. J., & L. R. MEWALDT. 1975. Timing of site fixation upon the wintering grounds in sparrows. Auk 92: 698-705.

RÜPPELL, W., & E. SCHÜZ. 1948. Ergebnis der verfrachtung von Nabelkrahen (*Corvus corone carnix*) während des Wegzuges. Vogelwarte 15: 30-36.

SCHÜZ, E. 1949. Die Spät-Auflassung ostpreussischer Jungströrche in West-Deutschland durch die Vogelwarte Rossitten 1933. Vogelwarte 15: 63-78.

SCHWARTZ, P. 1963. Orientation experiments with Northern Waterthrushes wintering in Venezuela. Proc. 13th Intern. Ornithol. Congr.: 481-484.

SHUFORD, D., & D. F. DESANTE. 1979. The changing seasons. Amer. Birds 33: 255-262.

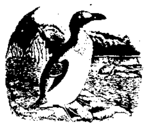
TUCKER, V. A. 1971. Flight energetics in birds. Amer. Zool. 11: 115-124.

WOLFSON, A. 1945. The role of the pituitary fat deposition and body weight in bird migration. Condor 47: 95-127.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall.

---

100 Years Ago in The Auk



From "Bird nomenclature of the Chippewa Indians," by W. W. Cooke (1884 Auk 1: 242-250):

"During a three years' residence among the Chippewas at White Earth, Minn., I had many opportunities of learning the names which they give to birds, and some of their ideas regarding them. These Indians claim to have a name for each and every kind of bird inhabiting their country; as a fact, they have no specific name for fully one-half of those which yearly nest before their eyes, or pass by in migration. We may say in general that they give names to all winter residents, since at that time bird life is so scarce that each one is accurately noticed, while summer birds of much greater dissimilarity receive but one name.

Among summer residents, nearly all those that are hunted for food are named and described. Indeed, few white hunters, or ornithologists, can recognize the different species of Ducks as quickly or at as great a distance as many of these Indians. Of the other summer birds, most of the large species have names, but some of these, as, for example, those of the Hawks and Owls, are very loosely applied. They all seem to be familiar with the names, but not with the particular bird to which each belongs. This may be accounted for by the large number of stories about these birds which are told to the children, teaching them the names, but not the appearance of the birds. The small birds of summer seem to the Indian beneath his notice, and when asked the name, the answer not uncommonly is, "Why do you want to know its name? It isn't good to eat." They consider that when to a small winged animal they have given the name 'bird,' they have done their whole duty."

[Cooke then provides over 100 examples, among which are the following:]

"Shrike . . . **Kitch'-i-win'-di-go-bi-ne'-sji**, big cannibal-bird."

"Song Sparrow . . . **Kos-kos-ko-ni'-chi**, making a scraping or whispering noise. This name is also indiscriminately applied to any small dull-colored bird, which is seen in the grass or on low shrubs. Probably thirty or more species would be included under this name."

"Bobolink . . . **Shi-ka'-go-bi-ne'-shi**. Chicago bird, that is, skunk bird, from the white stripe down the middle of the back."

"Yellow-headed Blackbird . . . **Bwan-ence'-as-sig'-gi-nak**, little Souix blackbird; because its home is in the west in the land of the Souix."

"Yellow-shafted Flicker . . . **Mo-ning'-gua-ne**,' bird with dirty colored wings."

"Bald Eagle . . . **Mi'-gi-zi** . . . . When young, or gray, it is called *Ini'-ni'-zi*, man Eagle; when old and white, *Wa'-bi-jush-kwe*,' white woman."

"Loon . . . **Mang**, brave. This is almost the only word of one syllable in the Chippewa language. In English, to call a person a loon is not very complimentary, but the Indians use loon-hearted just as we do lion-hearted, to denote extreme bravery. In the fall, when the colors get dull, the name **A'-shi-mang** is given, meaning false Loon."