The average rate of travel by migrating White-crowned Sparrows, *Zonotrichia leucophrys gambelii*, in spring

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The average rate of travel in overland migration has often been estimated from the earliest or average dates on which birds arrive at various localities or by the capture and recapture of banded migrants between two localities. The first method is hampered by the vagaries of observation and the second by the low recapture rate in most species of birds. A third method is implicit in the graphical model of migration developed by Preston (1966). In brief, Preston's method relies on systematic operation of traps or nets for an entire migration season at localities that are outside the breeding or wintering ranges but along the migration route of the species being studied. It requires fairly large samples and reasonably uniform distribution of effort to achieve reliable results. The number of birds captured during a migration season is compiled as a cumulative sum for successive days, and each day's sum is then converted to a percentage of the seasonal total. If the cumulative percentages form a reasonably straight line when plotted on a probability scale against the calendar date it shows that the temporal distribution of migrants conforms to a normal-frequency (or bell-shaped) distribution. If the plot is nonlinear, it means that the frequency distribution is non-normal (e.g., skewed or bimodal). The latter can provide information about the temporal dynamics of migration (Preston 1966) but is not useful for purposes discussed here.

If capture data are recorded at two or more localities similar in longitude but differing in latitude and yield straight, parallel lines when analyzed by Preston's method, then the time in days between the lines divided into the distance between latitudes is an estimate of the average velocity of migratory travel. We applied this method to data obtained during spring migration from captures of *Z. l. gambelii* at Blue Sky, Hart Mountain National Antelope Refuge, OR (42°21'N, 119°40'W) and Pullman, WA (46°N, 117°12'W). The sample from Pullman is an 11-year composite (1956-66), while that from Hart Mountain is confined to 1976. It is unfortunate that we do not have data for the same years in the two localities. However, the schedule of migration expressed in this way varies only slightly from year to

year at Pullman (a maximum of about ±2 days) and we assume a similar precision at Hart Mountain. Furthermore, the temporal distributions of migrants at Pullman and Hart Mountain are alike (i.e., the lines are essentially parallel in Fig. 1, indicating nearly identical standard deviations), which shows that we have sampled statistically similar populations.

The lines in Fig. 1 were fitted by the method of least squares using the cumulative percentages up to 90%. Above 90% the linearity (normality) of the relationship deteriorates, probably owing to stragglers apart from the main waves of migrants. The lines in Fig. 1 are nearly but not exactly parallel, being 7.5 days apart at
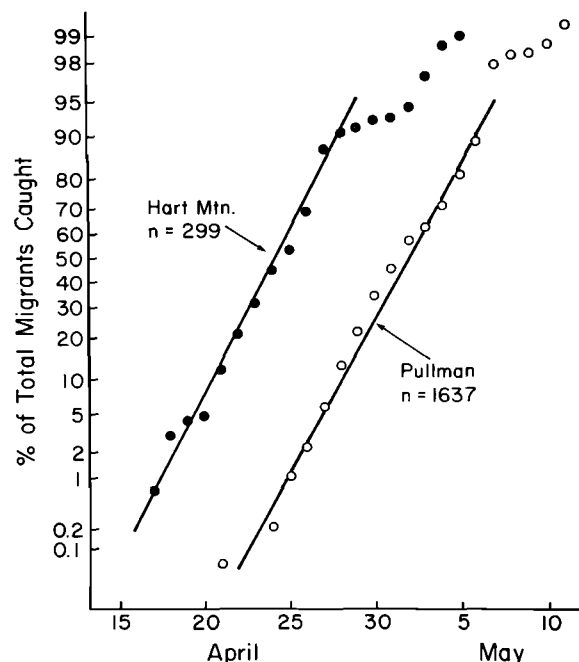

Fig. 1. Cumulative percentage of Z.l. gambelii caught in relation to date during spring migration at Hart Mountain, OR and Pullman, WA, plotted on a probability scale.

the beginning of passage and 8 days apart late in passage. This could result from mensural error and have no biological significance. The latitudinal difference between Hart Mountain and Pullman is 4°22′, which is equivalent to 484 km (List 1963). If we assume that the average velocity of travel is longitudinally invariant between the meridians of Hart Mountain and Pullman (2°28′ apart), then the average velocity of travel between these latitudes is 60-65 km/day, depending on whether passage requires 7.5 or 8 days.

Oakeson (1954) estimated that the average velocity of spring migration by Z. l. gambelii between Santa Barbara, CA, and Mountain Village, AK, is 124 km/day. This conforms reasonably well with the results of her later observations of flocks followed along a migration route in Canada and Alaska (50°N to 65°N), in which the average velocities of travel were in the range 108-121 km/day (DeWolfe et al. 1973). The data in Table 3 of that report, however, suggest a tendency for the velocity of travel to increase with latitude, in common with the schedules found in other species of overland migrants (Lincoln 1952). For instance, the estimated velocity of travel by Z. l. gambelii between 50°39′N and 52°08′N was 69 km/day while that between 60°01′N and 64°54′N was 183 km/day. Two records of Z. l. gambelii banded and recaptured during spring migration (Cortopassi and Mewaldt 1965) also suggest a greater average velocity of travel in the north (141 km/day, South Dakota to Manitoba, 995 km) than in the south (76 km/day, Arizona to Nevada, 842 km).

The average velocity of travel (AVT) between any two points by a nocturnal migrant such as Z. l. gambelii is determined by the distance (D) traveled per night of movement (= mean ground speed x hours of flight), the number (n) of nights of movement, and the mean duration of the stop-over periods (SOP) during which fat reserves are restored. If AVT is reckoned from dusk to dusk it can be estimated from

$$AVT = [n(D)]/[n(SOP)] \qquad (1)$$

which reduces to

$$AVT = D/SOP = km/day \qquad (1a)$$

It is thus apparent that the average velocity of travel is affected by the duration of stop-over periods as well as the velocity of migratory flight. We estimated the mean minimum stop-over period (Stack and Harned 1944, Borror 1948) at Hart Mountain from records of 85 recaptures of 299 Z. l. gambelii banded between 17 April and 9 May (Table 1). We cannot make a similar estimate at Pullman, as our operations there did not include recaptures. The average stop-over period at

Table 1. Repeat records for 299 Z. l. gambelii banded at Hart Mountain, 17 April — 9 May 1976

Stay in days	No. of repeats					Total	Total days
	1	2	3	4	5		
1	1	0	0	0	0	1	1
2	21	0	0	0	0	21	42
3	14	4	0	0	0	18	54
4	10	5	0	0	0	15	60
5	6	1	3	1	0	11	55
6	5	5	1	0	0	11	66
7	1	0	2	0	0	3	21
8	1	0	0	0	1	2	16
9	0	1	0	0	0	1	9
10	1	0	1	0	0	2	20

Total repeats 85
Total days (no. repeats x stay) 344
Mean minimum stay (days/repeats) 4.1

Table 2. Estimated average velocity of travel (AVT), stop-over period (SOP), distance (D) traveled per night of migration, and mean ground speed (V) during spring migration by Z. l. gambelii at two latitudes.

Locality	AVT km/day (1)	SOP days (2)	D km/night (3)	Mean night[1] hrs (4)	V km/hr (5)
Hart Mtn., 42° N	62	4.1	254	9.2	28
Watson L., 60° N	119[2]	2.5[2]	298	6.5	46

[1] Length of night is reckoned from the end of civil twilight at dusk to the beginning of civil twilight at dawn (List 1963). The range of values for the period of observation at 42° N is 8.8-9.7 hr, and at 60° N it is 5.4-7.5 hr.

[2] From DeWolfe et al. (1973)

Hart Mountain was 4.1 days. The frequency distribution of total days (last column in Table 1) differed significantly from normality (P < 0.2, Kolmogorov-Smirnov test: Sokal and Rohlf 1969), and so parametric expressions of variability (SE, SD) are meaningless. DeWolfe et al. (1973) estimated that the mean minimum stop-over period of Z. l. gambelii at about 60°N during 25 April — 17 May 1968 was 2.5 days (n = 51 recaptures). This is only marginally different (P = 0.1) from the mean SOP at Hart Mountain when tested by the non-parametric Mann-Whitney U statistic, but we will assume in the ensuing arguments that the difference in SOP between 42°N and 60°N is of the magnitude indicated by these estimates. We feel that the primitive state of the art in understanding the dynamics of migration sanctions this assumption for heuristic purposes at least.

A variable in addition to SOP that influences the average rate of travel is the distance flown per night. This can be roughly estimated (Table 2, column 3) by

Table 3. Seasonal variation of minimum stop-over period by migrating Z. l. gambelii at Hart Mountain in spring

Dates	Cohort[1]	No. of birds repeating	Min. stop-over days
17-22 Apr	1st	20	5.6
22-24 Apr	2nd	25	4.2
24-25 Apr	3rd	21	3.5
25-26 Apr	4th	9	2.9
26-27 Apr	5th	6	3.2
27 Apr-9 May	6th	4	2.5
Sum and Mean		85	4.1

[1] Fifty birds in each cohort except the 6th (49)

solving eq. 1a for D, given the estimated values of AVT and SOP (columns 1 and 2). From the relative values at 42°N (254 km/night) and 60°N (298 km/night) it is apparent that the northward increase of AVT in spring is the compound result of a decrease of SOP and increase of D. The latter is not necessarily expected, as the length of night after the vernal equinox is shorter in the north than in the south (Table 2, column 4). This suggests that Z. l. gambelii must either fly faster at northern latitudes or fly longer than the duration of the night if they are to perform as indicated in column 3. The estimated mean nocturnal ground speeds are given in column 5. These are within the range of air speeds predicted for a 31-g passerine by Greenewalt (1975: Table 22, 18-51 km/hr), and not far from the mean ground speeds against a 2.0 km/h headwind estimated by Gatter (1979) for Fringilla coelebs (37.1 km/h) and F. montifringilla (41.1 km/h). This concordance helps to verify that the other estimates are not grossly erroneous. The differences between 42°N and 60°N in estimated ground speed may or may not be real. Migrants may fly longer than the dusk-to-dawn span that we assumed, especially in the north where the nights are shorter. If so, this would decrease the estimated ground speed.

A final complication in the temporal dynamics of migration surfaces when we examine our sample of recaptures at Hart Mountain for variation in stop-over period by subdividing the sample into successive cohorts of 50 birds (or 49 in the last cohort) representing overlapping and successively later dates (Table 3). Except for a minor deviation in the 4th cohort, the data describe a curvilinear decrease of stop-over period from 5.6 to 2.5 days between the beginning and end of the migration period. This presumably results in an acceleration of the average rate of travel as the season progresses, but we have no data with which to test this hypothesis for a single locality.

Data of the kind that we have presented in this report can readily be obtained and analyzed by bird banders at localities along the migration routes of many species.

In fact, we suspect that many such data are already moldering in neglected record books. Obviously, students of migration can use such information to learn whether the analysis that we have sketched from fragmentary data can be generalized.
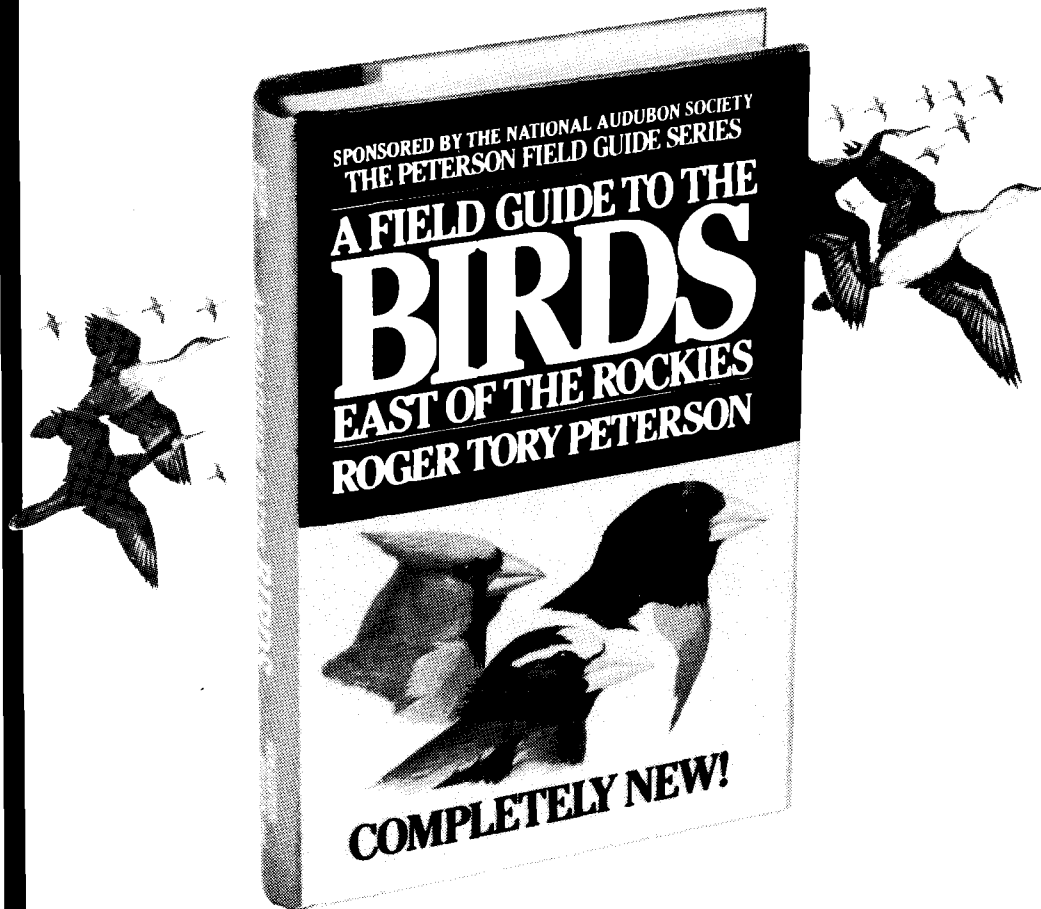
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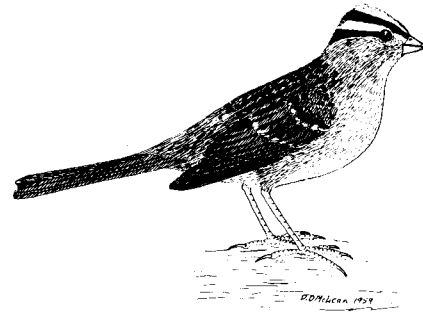
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