clutches may be laid. D. A. Boag (pers. comm.) reported that a yearling female in captivity laid a clutch of seven eggs. Single clutches recorded by Dawson (1897) and Reed (1965) contained seven eggs. In this study 15 broods of six chicks each were sighted. Of these, two hens had a known clutch of six eggs and four broods were known to have chicks from other broods. For the remaining nine broods of six chicks each, there was no evidence that the chicks originated from other broods. In four of these broods the first count of chicks was made at an early age, thus the opportunity for mixing prior to the count was minimal and it was possible these hens had a clutch greater than six eggs. The truncation of clutch-size data in table 1 does indeed suggest that clutches of seven or more eggs are possible in the wild.

Data collected in this study provide the largest known sample for this subspecies of Spruce Grouse. Clutches presented here are similar to those reported earlier for this grouse: two clutches of seven eggs, one each in Washington (Dawson 1897) and British Columbia (Reed 1965); one clutch of six eggs from Montana (Bent 1932); and two clutches of three and five eggs from the same locality as the present study (McCourt et al. 1973). Unfortunately, in the first three citations above clutch size was merely mentioned in passing; and in all except the five-egg clutch there was no real indication that numbers of eggs recorded were full clutches.

Rand (1947) compiled a listing of 67 clutches, with 2-13 eggs each, from throughout the distribution range of *Canachites*. These data were taken from 19 different sources or locations and all collections but one (Tufts 1961) were of four clutches or less. Using the data provided by Tufts (N = 39), I calculated a mean clutch size of 5.8 (range of 4–10 although 38 clutches were between 4 and 7). Tufts' data for *C. c. canace* and those reported here (N = 21) for *C. c. franklinii* are significantly different (P < 0.01). The only other sizeable sample is for *C. c. osgoodi* by Ellison (1974) in Alaska; he gave a mean of 7.5 eggs (range 4–9) for 26 nests, significantly greater (P < 0.001) than the Alberta data.

In view of the most recent findings in Nova Scotia, Alaska, and Alberta, it is difficult to comprehend the clutches listed in Rand (1947) that were greater than

QUANTIFICATION OF NOCTURNAL PASSERINE MIGRATION WITH A PORTABLE CEILOMETER

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Students of nocturnal bird migration have long sought reliable methods of determining the magnitude of migration. Several techniques are now available. The oldest is the moon-watching method described by Lowery (1951). While accurate results can be obtained with this technique, its use is limited to a few nights each month and is highly weather-dependent. Migration volume can also be measured with long10 eggs. Rather large clutch sizes are often attributed to *Canachites* in the early regional listings of bird species, yet accurate, descriptive data were rarely provided. Further, some clutches listed by Rand were from captive birds, and some eggs were removed after being laid, and so direct comparisons are not really possible. Rand commented that there was little evidence for geographical variation in clutch size. The comparative data now available indicate otherwise, and results for Alaska and southwestern Alberta seem to be an example of increased reproductive potential with increasing latitude.

The help with field work by students in the Department of Zoology, University of Alberta, was greatly appreciated; in particular I acknowledge the keen interest shown by K. Smith and D. Thompson. I appreciate the assistance of D. A. Boag, University of Alberta, in reviewing an early manuscript. The Department of Zoology, University of Alberta, and D. A. B. provided all facilities at the R. B. Miller Biological Station and that assistance is gratefully acknowledged.

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range surveillance radars (Nisbet 1963a; Gauthreaux 1970) and low-power tracking units (Bruderer 1971), but such sophisticated equipment is available to only a small fraction of those who might wish to know something about the quantity of migration occurring at night.

Gauthreaux (1969) described an inexpensive portable ceilometer unit that can be used to observe the passage of low-altitude nocturnal migration. The narrow beam of light is directed vertically and observations are made with binoculars or a telescope pointed up the cone of light. The briefly illuminated birds can be counted as they pass through the field of observation and their flight directions noted.

Counts of birds during a known time interval can be converted to birds per hour or some other convenient *relative* measure of migration density (e.g., see the temporal patterns presented by Gauthreaux 1969). However, it is preferable to generate measures of migration volume in more absolute terms. Thus, we have worked out methods of quantifying nocturnal migration with the portable ceilometer which yield a measure of migration magnitude in units of birds per mile of front per hour, the same units obtained in moon-watching and some radar studies (Lowery 1951; Gauthreaux 1970).

METHODS

Observations were made during both spring and fall at two stations in the southeastern United States: spring, 1969 (Athens, Georgia; S.A.G.); fall, 1969 (Athens, Georgia; S.A.G.); fall, 1969 (Athens, Georgia; S.A.G., Lake Charles, Louisiana; K.P.A.); spring, 1970 (Athens, Georgia; S.A.G., K.P.A.); fall, 1970 (Athens, Georgia; K.P.A.). The ceilometers were 100-w units (General Electric 100-PAR64) as described by Gauthreaux (1969) and tests were made with one and two lights. Counts were made on clear nights for varying periods of time from 15–50 min/hr with either a 15 \times 60 or 20 \times 60 spotting scope or 20 \times 60 binoculars.

Ceilometer data can be collected throughout the night, but hourly samples can be compared only if the probability of detecting migrants aloft is the same for all samples. This is almost never the case because the altitudinal distribution of migrants follows a characteristic nightly pattern even when weather conditions remain constant (Able 1970). During the first 2 hr after dark, the exodus of nocturnal migrants occurs and most birds are flying at altitudes within the sampling area of the ceilometer. The mean altitude of the migrant population increases sharply to a peak (about 600 m) during the second hour after sunset and declines gradually thereafter. Thus, only samples taken at the same time of night (relative to sunset) can be compared directly. Because the number of birds aloft rises sharply toward its peak during the first 2 hr of darkness, and because birds are at low altitudes during most of this time, we have primarily used ceilometer counts made during this period (19:00-20:30). Only data collected under clear skies were used.

Immediately before and after each period of telescopic observation, migration traffic rates were determined with the Weather Surveillance Radar (WSR-57), using the methods described by Gauthreaux (1970). Radar traffic rates from the WSR-57 are based ultimately on moon-watching and have been shown repeatedly to be highly reliable indices of migration magnitude (Gauthreaux 1970, 1973, and unpubl. data).

RESULTS AND DISCUSSION

We have used two methods of deriving migration traffic rates from ceilometer counts. The first is based on the physical dimensions of the sampling space and the altitudinal distribution of passerine migrants; the second, on the relationship between ceilometer counts and simultaneous radar traffic rates. Both methods yielded similar results.

The data were examined for differences between observers (K.P.A. vs. S.A.G.), optical equipment used $(15 \times vs. 20 \times; \text{telescope vs. binoculars})$, and time of night (19:00 vs. 20:00). No significant differences were found and the data were lumped together for the subsequent analyses.

Direct computation of traffic rate. If one knows the area sampled by the portable ceilometer and the proportion of migrant numbers flying within this sampling area, it is possible to compute the migration traffic rate directly. The methods are analogous to those used in computing moon-watching traffic rates (Lowery 1951) except that the sampling space remains constant, thus simplifying calculations. The situation is complicated by two factors: the sampling space is conical, increasing in area with height, and the birds



FIGURE 1. Diagrammatic representation of the ceilometer beam showing the approximate dimensions of the sampling area and the frequency distribution of migrating passerines with altitude.

are not distributed uniformly through the altitudes sampled (fig. 1). Reasonable approximations of these factors are now possible.

Our observations have indicated that under good conditions, passerine birds are seen regularly to altitudes of 760 m with the portable ceilometer and 20×60 telescope. The Bausch and Lomb 20×60 spotting scope has a field diameter of 2.5°, or about 33 m at a range of 760 m. The altitudinal strata below 760 m contain about 75% of the passerine migrants aloft during the sampling period we have used (Able 1970), but birds are not distributed uniformly in this air space. Rather, the number of birds decreases with increasing altitude even below 760 m. On the other hand, the sampling space is conical, increasing in area with altitude up to the observation ceiling. Thus, the probability of intercepting migrants is greater at the altitudes where relatively fewer birds are flying.

TABLE 1. Ceilometer counts (birds/hr), simultaneous radar traffic rates, and their ratios. Observations during spring 1969 were made with $15 \times$ ocular; all others were made with $20 \times$.

Date/1	ocality	Birds/hr	Radar TR	(Birds/hr)/ Radar TR	Date/locality	Birds/hr	Radar TR	(Birds/hr)/ Radar TR
1969					3–4 October	170	7.400	43.5
Ath	ens. Ga.				4-5 October	22	1,900	86.4
11_12	Anril	18	1 500	83.3		28	3,000	107.1
16_{17}	April	77	3,000	30.0	10–11 October	38	1,900	50.0
20 - 21	April	26	1,200	46.2	11–12 October	90	4,700	52.2
21-22	April	20	1,200	95.0		108	3,000	27.8
25-26	Anril	56	3,500	62.5	13–14 October	812	18,500	22.8
2-3	May	18	1 400	77.8	14–15 October	130	4,700	36.2
4-5	May	48	1,900	38.6		60	3,000	50.0
6-7	May	39	1,000	30.8	21–22 October	44	4,700	106.8
19-20	May	18	2,400	133.3		60	4,700	78.3
21-22	August	30	2,400	80.0	23–24 October	28	3,000	107.1
23 - 24	August	101	5,500	54.5	1970			
		93	5.500	59.1	1970			
25 - 26	August	21	1.200	57.1	Athens, Ga.			
10-11	September	42	3,500	83.3	22–23 April	66	5,500	83.3
11-12	September	24	1.500	62.5	26–27 April	33	2,400	72.7
	*	30	1,500	50.0	27–28 April	123	3,000	24.4
12-13	September	45	1,400	31.1	28–29 April	116	2,800	24.1
	•	45	1,500	33.3		130	3,500	26.9
9-10	October	116	18,500	159.5	30–1 May	63	2,400	38.1
		88	18,500	210.2	15–16 August	16	2,400	150.0
14 - 15	October	221	34,000	153.8	25–26 August	268	8,000	29.9
		192	29,000	151.0	30–31 August	140	10,000	71.4
Tab	Charles Is				1–2 September	58	10,000	172.4
Lak	e Charles, La.				5–6 September	55	10,000	181.8
5-6	August	130	3,000	23.1	13–14 September	96	6,000	62.5
28-29	August	152	11,700	77.0	14–15 September	84	3,500	41.7
9–10	September	484	29,000	60.0	16–17 September	108	11,700	108.3
10 11	a . 1	328	46,000	140.2	22–23 September	28	3,500	125.0
10-11	September	792	29,000	36.6	24–25 September	80	3,500	43.8
	· ·	294	29,000	98.6	25–26 September	108	6,000	55.6
12 - 13	September	404	18,500	45.8	28–29 September	392	62,000	158.2
18-19	September	596	46,000	77.2		363	114,000	314.0
•••	a	616	46,000	74.7		503	106,000	210.7
20-21	September	260	11,700	45.0	30–1 October	314	10,000	31.8
	G . 1	194	29,000	149.5		234	10,000	42.7
22-23	September	328	29,000	88.4	12–13 October	48	1,900	39.6
30-1	Uctober	592	18,500	31.3	15–16 October	172	25,000	145.3
2-3	Uctober	111	11,700	105.4		108	25,000	231.5

Knowing the dimensions of the sampling space and employing Able's (1970) data on the height distribution of passerine migrants, we have estimated the effect of these factors. Approximately 50% fewer birds are seen than would be sampled if all birds below 760 m had an equal probability of passing through the field of observation.

To compute the total traffic rate, one first calculates the rate for the sampling area (i.e., up to 760 m).

$$\frac{1610 \text{ m/mi}}{33} = 48 \text{ scope fields/mi}$$

Correcting for the sampling bias and the fact that the altitudinal strata sampled include 75% of the total traffic rate (*TR*),

$$TR = 48(100/50)(100/75)B$$

= 115B,

where B is the number of birds observed per hour with the ceilometer. Given a count of birds passing through a ceilometer beam during a known time interval, a migration traffic rate can be computed easily by converting the count to birds/hour and using this multiplicative factor. Determination based on radar traffic rate. A number of the parameters used in the direct estimation of traffic rates with the ceilometer are not known very precisely (e.g., the upper limit of detectability, the effective radius of the visual cone, or the relative detectability of different bird species). Radar traffic rates, obtained from the WSR-57 as described by Gauthreaux (1970, 1973), provide an independent method of calibrating the ceilometer. The data are presented in table 1 and a regression of radar traffic rates on ceilometer counts is shown in figure 2. We have used a logarithmic transformation (ln) on both variables to linearize the relationship.

Counts of birds observed with the portable ceilometer (converted to birds/hr) were highly correlated with simultaneous radar traffic rates (r = 0.845; P < 0.001) and a significant regression equation ($F_{1, n} = 177.2$; P < 0.001) was obtained. The slope of this regression does not differ from unity and we can therefore use the simple ratio (birds/hr)/radar *TR* as a multiplicative factor. These ratios are shown in table 1; their mean is 83.6 ± 6.7 . By this method, then,

$$TR \equiv 84B.$$



FIGURE 2. Regression of radar traffic rate (TR) on the number of birds seen per hour with the portable ceilometer.

Figure 2 shows that there is considerable variability in the relationship between ceilometer counts and radar traffic rates. Errors of up to a factor of 3 are possible in estimating traffic rates by this method. This is small, however, compared to the several orders of magnitude by which migration volume may vary from night to night (Able 1973). WSR-57 traffic rates are very closely correlated with rates determined by moon-watching. Thus the scatter in points in figure 2 is probably due largely to errors inherent in the ceilometer data.

The multiplicative factors estimated by the direct and indirect methods are quite similar and there is no obvious reason to select one over the other. Therefore, we recommend using 100, the approximate average of the two estimates, as the multiplicative factor.

Use of the relationships we have derived is valid only when applied to data collected during the first 2 hr after dark. Theoretically, similar equations could be derived for other times of the night. This would be useful since it would allow comparison of migration density from hour to hour as in the studies of temporal pattern by Lowery (1951), Lowery and Newman (1955), Newman (1956), and Gauthreaux (1971). In practice, this has not been possible for several reasons.

In terms of obtaining accurate indices of the quantity of nocturnal migration, data collected with the portable ceilometer are subject to several sources of variation. Based on more than 500 hr of observation with ceilometers since Gauthreaux (1969) originally described the technique, we believe the most important influences are: systematic changes in the altitude of nocturnal migration, cloud cover, and atmospheric moisture.

The portable ceilometer is primarily an instrument for studying low-altitude migration. Even birds so low as to be out of focus with the optical equipment usually employed are readily detectable. After the exodus period early in the night, the mean altitude of migration increases to a peak between the second and third hours after sunset (Able 1970). At this time, many birds are above the sampling limits of the ceilometer and counts of birds characteristically drop off in spite of the fact that migration density normally peaks in the middle of the night (compare the temporal pattern curves of Lowery 1951 and Newman 1956 with the ceilometer counts published by Gauthreaux 1969). Furthermore, in spite of the fact that on a given night the altitudinal distribution and density of migrants tend to remain fairly constant for at least a couple of hours in the middle of the night, the mean altitude is quite variable from night to night (Able 1970). Mainly as a result of this altitudinal problem, there is little correlation between ceilometer counts and radar traffic rates during the middle of the night (e.g., at 24:00, r = 0.482; P < 0.05).

As the night progresses, the mean altitude of migrants decreases, thus bringing a greater proportion of the migrant population into the sampling area of the ceilometer. However, because birds begin landing during this period, the density of migrants aloft declines dramatically (see Lowery 1951; Lowery and Newman 1955; Newman 1956). Thus once the nightly migration has passed its peak, it is usually impossible to obtain adequate samples of birds.

Occasionally, several other factors influence one's ability to detect birds with the portable ceilometer and thus preclude use of the relationships derived here. The most important is the presence of cloud cover. On overcast nights we have noted that two 100-w ceilometers produce a visible spot of light on clouds with bases between 760 and 915 m. Even when cloud bases are somewhat higher, the background against which the illuminated birds are viewed is noticeably lighter than the almost black background when skies are clear. The resultant reduction in contrast between the birds and the background under cloudy conditions can drastically reduce the probability of detecting birds as they pass through the light beam. This becomes particularly obvious on nights of broken cloudiness when alternating patches of cloudy and clear sky pass through the field of observation. Birds are seen frequently during periods when the background is clear sky, very infrequently when clouds form the background. Often these conditions give the impression that the birds are flying above the clouds. While this may sometimes be the case, we have observed numerous occasions when the birds we saw were definitely flying below the cloud bases. Because of the great variability in the height and horizontal spacing of clouds, it has proven impossible to develop a reliable relationship between ceilometer counts and traffic rates under overcast skies.

When the lower atmosphere contains large amounts of moisture (haze), there may be considerable attenuation of the light beam. Fortunately, this problem is rarely serious during the early hours of darkness, but can hamper observations late in the night as relative humidity rises. Attenuation of the beam by haze influences sampling of birds in two ways: sufficient light to enable detection of birds does not penetrate as high into the air and higher birds are consequently missed; reflection of light from the moisture droplets causes the light beam to be far more conspicuous than normal and birds may be attracted to it. Both of these influences obviously preclude valid quantitative sampling. Fortunately, attraction of birds appears to be a decidedly rare occurrence, usually limited to nights when conditions are poor for ceilometer observations anyway (mist, fog, low overcast, etc.). Further, birds attracted to the light are usually obvious by their behavior, i.e., they frequently hover in the beam for several seconds.

A limitation of radar and ceilometer techniques of migration study is that finer categories of birds are not distinguishable. With the ceilometer, types of passerine birds (e.g., thrushes, warblers, etc.) can often be differentiated. Despite the apparent similarities in the patterns of altitudinal distribution of nocturnal passerine migrants in several areas of the world (Eastwood and Rider 1965; Nisbet 1963b; Able 1970; Bellrose 1971; Bruderer and Steidinger 1972), situations may be encountered in which birds migrate at considerably higher average altitude (e.g., during long water crossings). Different species groups may also behave differently with respect to altitude. Workers employing this technique in unfamiliar areas should be alert for these problems.

In sum, various factors may influence the reliability with which nocturnal migration may be sampled with the portable ceilometer. Use of the ceilometer to quantify nocturnal migration requires that these variables be held as constant as possible. For this reason, we have been able to work out a quantification technique based only on samples collected at the beginning of nocturnal migration. This precludes use of the technique to study temporal changes in the quantity of migration during single nights. However, the method can be used to study several aspects of nocturnal migration that are in need of further work: night-to-night variations in migration magnitude; seasonal and geographic patterns; and the relationships between migration and weather.

SUMMARY

Portable ceilometers may be used to study the orientation and magnitude of migration. We have used two independent methods to compute a migration traffic rate in units of birds per mile of front per hour from ceilometer counts made during the first 2 hr of nocturnal migration. One method is based on the physical dimensions of the space sampled by the ceilometer; the other, on a correlation between ceilometer counts and simultaneous radar traffic rates. Both methods yield similar results. The quantification method gives reliable results only when applied to data collected during the first 2 hr after dark and under clear skies. The technique provides a simple, inexpensive, highly portable means of obtaining measures of migration magnitude that can be used in studies of night-to-night, seasonal, geographic, or weather-dependent variations in nocturnal migration.

We gratefully acknowledge the assistance and hospitality of the personnel of the National Weather Service stations at Athens, Georgia, and Lake Charles, Louisiana. Without the virtually unlimited access to the radar facilities we enjoyed, this work would have been impossible. During part of these studies, we were supported by grants from the Air Force Office of Scientific Research to S.A.G. Ryland Loos prepared figure 1.

RANGE EXTENSIONS AND NEW RECORDS FOR BIRD SPECIES IN ECUADOR, PERÚ, AND BOLIVIA

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From July 1971 to November 1972, I conducted a field study to investigate aspects of bird community structure in Amazonian Ecuador, Perú, and Bolivia. In the process of gathering data for this study and traveling between sites, I encountered several species of birds that represented significant extensions of the known ranges or were previously unrecorded from one or

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more of these three countries. The purpose of this paper is to report these new records and range extensions.

The majority of the records are from the following localities (fig. 1) and indicated periods:

1. Limoncocha, Province of Napo, Ecuador $(0^{\circ} 24' S; 76^{\circ} 38' W)$, located in the northeastern part of the country near the Napo River (el. = 300 m) about 15 km S of the town of Coca (1 July 1971–19 April 1972).

2. Yarinacocha, Department of Loreto, Perú (8° 17'S; 74° 37'W), located in the east central part of the country near the Ucayali River (el. = 150 m) 15 km NW of Pucallpa (2 June-5 September 1972).

3. Tumi Chucua, Department of Beni, Bolivia (11° 8'S; 66° 10'W), located in the extreme northeastern part of the country near the Beni River (el. = 176 m)