

SPRING DRUMMING PATTERNS OF RUFFED GROUSE¹

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DURING the breeding season of 1970, I used automatic radio-tracking equipment (Cochran et al. 1965) to monitor the drumming and location of territorial male Ruffed Grouse (*Bonasa umbellus*). This paper reports on daily and seasonal distributions of drumming, individual drumming activity patterns, and communication between neighboring males.

Publications on drumming, which date back as far as 1755 (Allen *in* Bent 1932: 142), have been summarized by Bent (1932: 141-147) and Gullion (1967: 87). More recently Gullion (1966), Meslow (1966), Sumanik (1966), Boag and Sumanik (1969), Palmer (1969), McBurney (1970), Aubin (1970, 1972), Samuel (1974), Samuel et al. (1974), and Archibald (1974) have reported on various aspects of drumming behavior. Reviews of tetraonid reproductive behavior and social systems have been provided by Hjorth (1970) and Wiley (1974), respectively.

METHODS

This investigation was conducted at the Cedar Creek Natural History Area, about 48 km north of Minneapolis, Minnesota. The area has been described by Pierce (1954), Bray et al. (1959), and Archibald (1975). Meslow (1966) analyzed characteristics of drumming logs and surrounding vegetation on the study area.

Drumming was monitored with fixed directional antennae and modified automatic radio-tracking equipment (Appendix). Procedures for capture, examination, radio-marking, and release of study grouse have been described previously (Archibald 1975). The radio signal pattern of a drumming grouse, a series of pulses accelerating in both frequency and volume, is particularly obvious to the ear (Marshall 1965). The recording technique involved transduction of the radio signal pattern of a drum to a light pattern which was photographed to produce a recognizable image on 16 mm film (Fig. 1).

Drumming activity of individual grouse was read from a manual film viewer in one of two formats: (1) frequency of drumming in a 15-min period, or (2) starting time of each drum. For the first, signal quality during each 15-min period was judged either "receivable" (frequency obtained accurate) or "nonreceivable" (uncertain). For the second format, the starting time of each drum was determined to the nearest second (Appendix). Times at which signal quality became and ceased to be receivable were tabulated. For all 15-min periods with less than 2 minutes nonreceivable, starting time data were converted to frequency format.

Because no individual was receivable continuously, frequency data for all grouse monitored on each day were combined to provide a more complete record of drumming activity. Because highly significant ($P < 0.0005$) degrees of association

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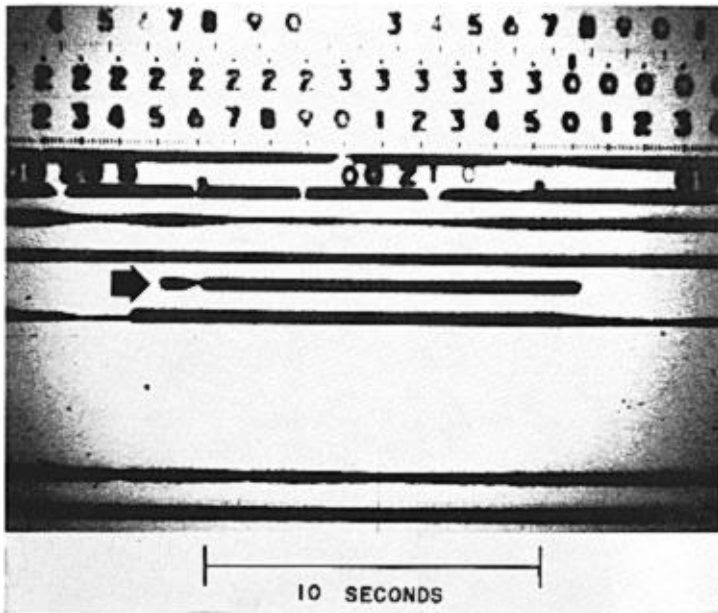


Fig. 1. Pattern of a drum recorded on 16 mm film. Arrow shows trace of visual indicator tube during drum. Start of drum (approximately 0020:59) represents the beginning of the first wingbeat performed. Recording system described in Appendix.

of drumming presence-absence were found in all 77 possible pairs of males (Table 1), I felt that combining data was justified.

The average of the drumming frequencies of all grouse receivable in a 15-min period provided the basis for defining 2 variables. First, drumming was arbitrarily defined as having "occurred" in a 15-min period if the mean frequency was ≥ 0.5 drums/receivable bird. Second, mean frequencies for each 15-min period in a day were summed to provide the "mean total number of drums" for the day. To compensate for poor signal reception, values were computed only for days that had at least one receivable grouse in 90% or more of the 96 possible periods.

The temporal distribution of drumming within weeks was examined in two ways. First, for each quarter-hour period of the day, the percentage of the total number of receivable 15-min periods in which individuals drummed one or more times provided "percent of periods drumming." Second, for each 15-min period in the day, the mean frequency/receivable drumming grouse was computed for each day in the week, and daily means were then averaged to provide "mean drumming frequency when drumming." To avoid extremely low sample sizes, values were based on a minimum of two daily means, each of which was based on at least two drumming grouse.

Weather data were recorded at the U.S. Weather Bureau Station at the Cedar Creek Natural History Area. Times of sunrise and sunset were obtained from U.S. Naval Observatory Chart No. 1155 for Minneapolis; lunar and twilight data were from the Nautical Almanac. All times are Central Standard Time.

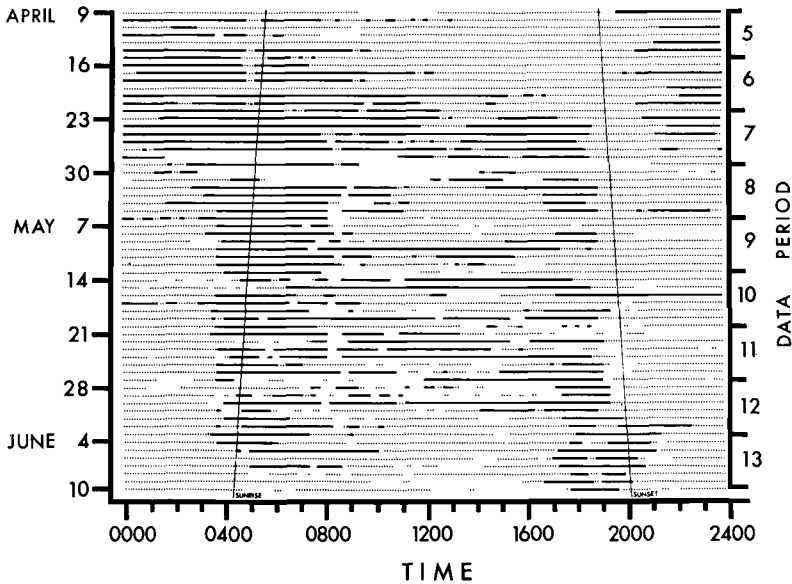


Fig. 2. Seasonal variation in the occurrence of drumming (mean drumming frequency ≥ 0.5 drums/receivable grouse in a 15-min period). Symbols are as follows: Solid line, drumming; dot, no drumming; blank, no data.

RESULTS

Drumming of 7 grouse was monitored from 7 to 56 days for a total of 269 bird-days and 21,363 drums. All study males were "active, site-associated" drummers (Gullion 1966) and appeared to drum normally in terms of both frequency of drumming and sound production.

Monitoring of drumming was initiated on 1 April 1970. Radio-marked males began drumming on 9 April and had greatly reduced drumming activity by 10 June (Fig. 2). Thirteen 7-day data periods, from 12 March through 10 June, were arbitrarily defined with 9 April as the first day of week 5. Results concerning space use and range overlap during the 13 weeks were reported elsewhere (Archibald 1975, 1976). Because of a decline in both drumming and number of birds monitored, data for the final week (4–10 June) were insufficient for analysis. For weeks 5–12, an average of 63.2% (range: 84.9% in week 6 to 45.7% in week 11) of 15-min periods was judged receivable. Reception declined as the study progressed, owing mainly to increasing incidence of electrical storms.

Grouse tended to drum or not drum at the same times of day (Table 1), probably in response to the same environmental variables. For weeks 5–12 (9 April–3 June), pairs of males were either both drumming or both

TABLE 1
ASSOCIATION OF DRUMMING PRESENCE-ABSENCE OF POSSIBLE PAIRS OF RUFFED GROUSE
IN MUTUALLY RECEIVABLE 15-MIN PERIODS

Week ¹	No. of birds	No. of possible pairs ²	Both birds		
			Drumming (%) ³	Not drumming (%) ³	Either drumming or not drumming (%) ³
5	6	15	15.54	72.74	88.28
6	5	10	30.89	50.74	81.63
7	5	10	38.88	31.40	70.28
8	5	10	22.95	57.89	80.84
9	5	10	20.95	65.23	86.18
10	5	10	39.63	49.22	88.85
11	4	6	54.18	37.62	91.80
12	4	6	17.73	63.13	80.86
Mean					83.59

¹ Week 5, 9-15 April; week 12, 29 May-3 June.

² Based on Chi-square tests (1 d.f.), association of drumming presence-absence was significant ($P < 0.0005$) in all 77 possible pairs.

³ Percent of total number of 15-min periods in which both grouse were receivable.

not drumming in an average of 83.6% of mutually receivable 15-min periods. Differences between weeks in the percent of periods in which both grouse were drumming (Table 1) reflect seasonal differences in the occurrence of drumming (Fig. 2).

TEMPORAL VARIATIONS IN DRUMMING ACTIVITY

During the first 2½ weeks of the drumming season, nocturnal drumming was recorded consistently for all radio-marked males except under windy or inclement weather conditions (Fig. 2). From 9-25 April, drumming was recorded from 2000 to 2400 on 11 of 17 nights. The average wind velocity on the 6 nondrumming nights was 15.6 km/h while that for the 11 drumming nights was only 4.9. Nights without drumming were characteristically overcast; cloud cover at 2100 exceeded 90% on 4 of the 6. Nevertheless relatively clear sky conditions were apparently not prerequisite to nocturnal drumming, for it was recorded on 3 nights with > 90% cloud cover. Two of these nights (19 and 20 April) immediately preceded the full moon (21 April).

In the span of about 5 days (26-30 April), the birds shifted to an almost exclusively diurnal drumming pattern (Fig. 2). During this transition the moon was setting in daylight hours and rising later each night. Moonrise was at 0114 on 27 April and had progressed to 0245 by 30 April. In addition, moonlight at last quarter (28 April) is only about 10% as bright as the full moon (Abell 1969). Perhaps the decline in nocturnal

drumming activity during this period could have been related to a progressive decrease in lunar stimulation. Nocturnal drumming was recorded only twice in May: on the 5–6th and the 16–17th (Fig. 2). Both of these nights were characterized by clear (cloud cover < 10%) and calm (wind < 1 km/h) conditions from 2000 to 2400.

Following the transition to a diurnal drumming pattern, early morning drumming generally began 1–2 hours before sunrise (Fig. 2). Early morning drumming was last recorded on 7 June. In contrast, late afternoon drumming, which began on 23 April, persisted in the case of two radio-marked males until at least 1 August.

Seasonal changes also were found in the extent and temporal distribution of drumming during the daylight hours (Fig. 3). Over the entire period (9 April–3 June) grouse drummed most consistently immediately before sunrise. In week 5 (9–15 April), relatively little drumming took place between 0800 and 1300, and none was recorded from 1300 to 1900. Week 6 (16–22 April) saw considerably more morning drumming, and some drumming occurred in the afternoon. In weeks 5 and 6, early morning drumming was interrupted by feeding from 0500 to 0515 (91 and 79% of 15-min periods active, respectively); this was not found in later weeks, but feeding occurred at sunset (\bar{x} = 92.5% of 15-min periods active) throughout weeks 5–12. Except during the sunset feeding period, grouse drummed throughout the daylight hours in week 7 (23–29 April). In contrast, the amount of drumming between 0900 and 1600 was substantially lower during weeks 8 and 9. Late afternoon drumming was not prominent in week 9. Weeks 10 and 11 (14–27 May) were characterized by relatively high drumming percentages throughout the day. The level of midday drumming was comparatively much lower in week 12.

The highest frequency noted for any individual was 13 drums/15 min, found twice for juvenile no. 1628: 2200–2215 on 19 April, and 0400–0415 on 12 May. Maximum recorded frequencies for the other 6 grouse ranged from 10 to 12 drums/15 min.

The highest individual drumming frequencies within a day tended to occur in two situations: (1) at the beginning of a drumming period, particularly after a long period of nondrumming, (2) shortly before sunrise, even if drumming had begun several hours before. The former, also noted by Petraborg et al. (1953), may be the result of a sudden release of “nervous energy” (Hjorth, pers. comm. cited in Sumanik 1966: 55) built up in the interim.

Following the start of a drumming period, there was a general tendency for linear increase of interval length with successive intervals (Fig. 4). This tendency was found to be most pronounced in late evening (2000–

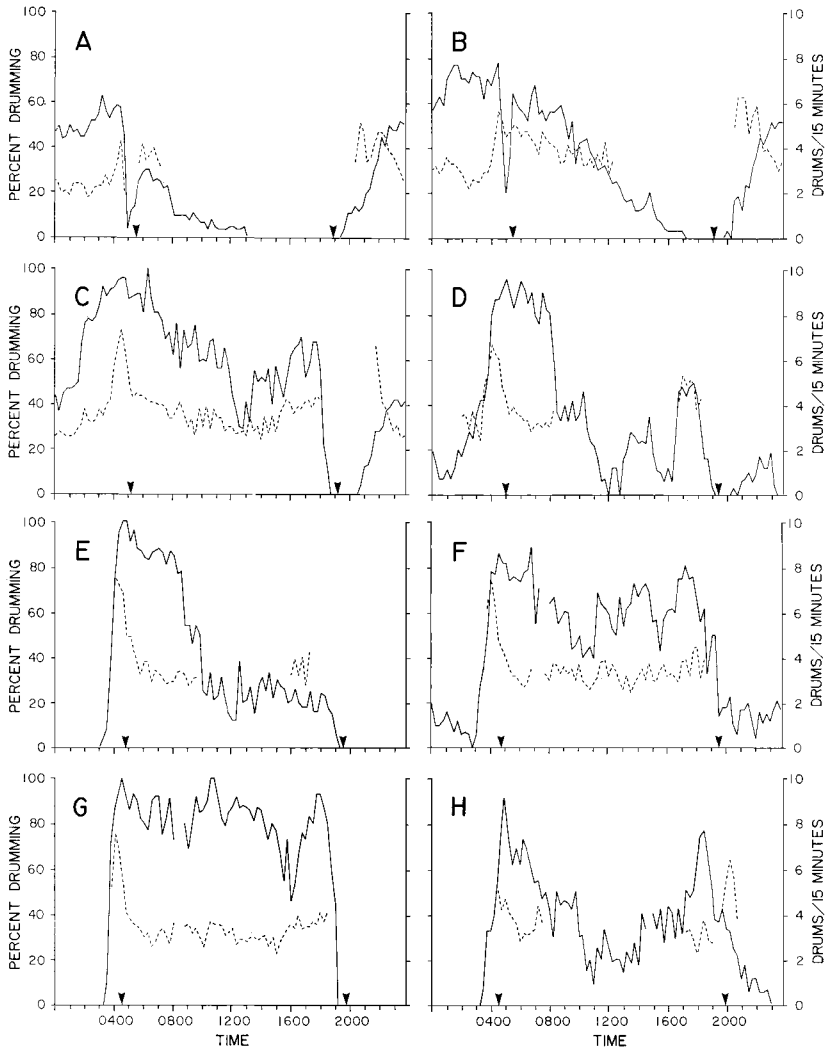


Fig. 3. Temporal distribution of percent of 15-min periods drumming (solid line) and mean drumming frequency when drumming (dashed line) in consecutive weeks: A, week 5, 9-15 April; B, week 6, 16-22 April; C, week 7, 23-29 April; D, week 8, 30 April-6 May; E, week 9, 7-13 May; F, week 10, 14-20 May; G, week 11, 21-27 May; H, week 12, 28 May-3 June. Arrows indicate times of sunrise and sunset.

2400) and least consistent during the daylight hours. When grouse had been drumming for several hours before sunrise, there often was a linear decrease in interval length with successive intervals up to the time of the maximum frequency period before sunrise.

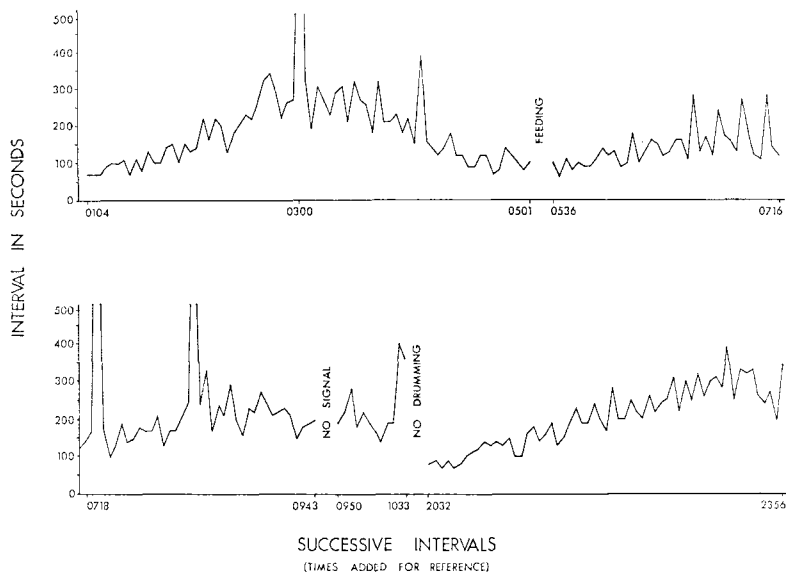


Fig. 4. Intervals between successive drums of juvenile no. 1628, 17 April. Interval length is plotted against interval number in the sequence. Prior to 0100, the bird had not been recorded drumming since the morning of the previous day.

In the early morning, the highest mean drumming frequency when drumming was recorded an average of 38.7 min before sunrise and 5.6 min before civil twilight was in weeks 5–11 (Table 2). Palmer (1969) reported that drumming intensity (frequency) appeared to peak about

TABLE 2
OCCURRENCE OF EARLY MORNING MAXIMA IN DRUMMING FREQUENCY OF
RUFFED GROUSE

Week ¹	Maximum mean drumming frequency when drumming (drums/15 min)	Time ²	Minutes before	
			Sunrise	Civil twilight
5	4.17	0437.5	56.5	26.5
6	5.60	0445	37	6
7	7.30	0430	41	9
8	6.68	0415	45	8
9	7.46	0415	36	3
10	7.55	0407.5	34.5	0.5
11	7.48	0415	21	-14
Mean			38.7	5.6

¹ Data for week 12 insufficient to determine maximum value. Week 5, 9–15 April; week 11, 21–27 May.

² Midpoint of 15-min period, or midpoint of two consecutive 15-min periods, if difference < 10% of larger frequency.

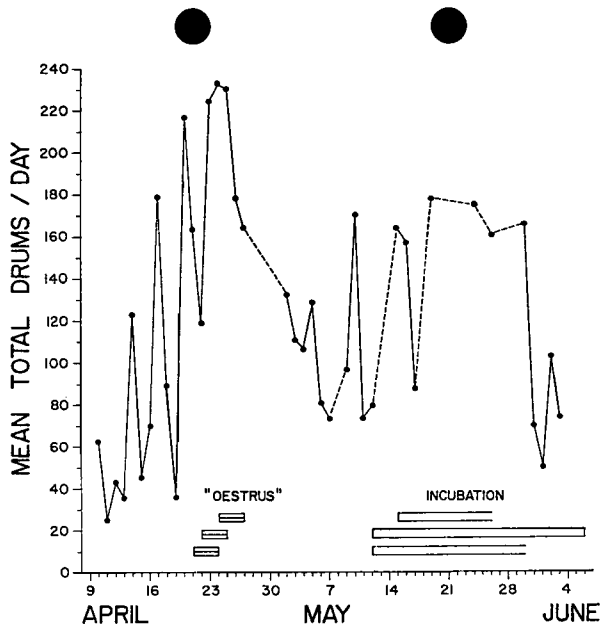


Fig. 5. Seasonal distribution of mean total drums/day in relation to full moons and nesting chronology. Dashed lines indicate days excluded due to poor radio reception; "oestrus" = estimated dates of copulation.

30 minutes before sunrise. The maximum drumming frequency occurred somewhat earlier in the first week (Table 2), when the morning feeding period coincided with civil twilight. In weeks 5 and 6 (9–22 April), the highest values of mean drumming frequency when drumming were recorded in late evening (2045) rather than in early morning (Fig. 3).

TABLE 3
CORRELATION OF MEAN TOTAL DRUMS/DAY WITH ABIOTIC FACTORS, 39 DAYS BETWEEN 9 APRIL AND 3 JUNE

Independent variable	First-order correlation coefficient	Partial correlation	
		Coefficient	Significance level ¹
Moon fullness index ²	0.48	0.71	0.0005
Wind (km/day)	-0.47	-0.61	0.0005
Min. temperature	0.00	-0.38	0.0125
Solar radiation ³	0.25	0.27	0.1
Max. temperature	0.20	0.22	0.1

¹ t test (32 d.f.).

² Range from 0 on day of new moon to 14 on day of full moon.

³ Data (langley/day) collected with an Eppley 50 junction pyrheliometer.

Notwithstanding violent day-to-day variations, two peak drumming periods were evident in the seasonal distribution of mean total drums/day (Fig. 5). The two peaks coincided with the full moons in April and May.

Five abiotic factors (Table 3) accounted for approximately 67% ($R = 0.82$, $F_{(5,33)} = 13.27$, $P < 0.001$) of the variation in mean total drums/day. Moon fullness and wind were by far the most significant of these factors. Moon fullness logically accounted for seasonal variability while wind accounted for day-to-day variation. Because electrical storms were responsible for the poor radio reception on many of the 17 days excluded, precipitation was not included in the multiple regression although it may have been important (Sumanik 1966, Gullion 1966). For example, the depression in mean total drums/day on 21–22 April (Fig. 5) may have been related to the 1.9 and 1.3 cm rainfalls on those days.

In view of the seasonal variation noted previously (Fig. 3), it is likely that the basic temporal pattern of drumming within a day is governed by a factor or factor complex other than weather. The high partial correlation coefficient for the moon fullness index (0.71) suggests that the moon may be involved. If so, precisely what the grouse respond to remains unknown; presumably it is moonlight intensity, but time and duration of night illumination might also be involved. Weather factors, particularly wind (Table 3) and extreme or prolonged precipitation, do modify the basic pattern and presumably are responsible for much of the day-to-day variation in both the amount and temporal distribution of drumming in a day. But a grouse's response to weather factors is variable, dependent on factors including day within the drumming season (moon phase?), time of day, and previous drumming activity ("nervous energy").

The correspondence between estimated dates of copulation (termed "oestrus" by Brander (1967) and others) and the April peak drumming period suggests that this peak was associated with mating (Fig. 5). Dates when females copulated were estimated from clutch size and date of incubation onset, assuming 2 eggs laid every 3 days and copulation occurring 3–7 days prior to the laying of the first egg (Bump et al. 1947). The second drumming peak may have been associated with remating of hens that had lost their initial clutch.

Since both the April drumming peak and copulation occurred at full moon, it is tempting to hypothesize a cause-and-effect relationship, but as my data represent only a single breeding season, this correspondence could have been fortuitous.

Grouse engaged in drumming activity slightly more than half of the time in the two peak weeks, 7 and 11 (Table 4). Although the percentages of periods in which drumming occurred were very similar in these weeks, the temporal distributions of drumming were quite different (Fig.

TABLE 4
PERCENT OF 15-MIN PERIODS DRUMMING AND WEEKLY AVERAGE OF
MEAN TOTAL DRUMS/DAY

Week ¹	% of 15-min periods drumming ²	Total no. of 15-min periods ³	Average of mean total no. of drums/day ⁴
5	20.80	3274	55.8 (6)
6	37.85	2853	125.1 (7)
7	53.06	2324	206.3 (5)
8	30.67	2116	111.8 (5)
9	27.63	1933	98.7 (5)
10	43.67	1557	146.7 (4)
11	51.99	1229	168.4 (2)
12	28.06	1379	92.6 (5)

¹ Week 5, 9-15 April; week 12, 28 May-3 June.

² Percent of total no. 15 min periods in which drumming occurred. Highly correlated with weekly average of mean total no. of drums/day, $r = 0.97$.

³ Decline in sample size caused by increased incidence of electrical storms and reduction in no. of birds monitored (Table 1) in later weeks.

⁴ No. of days in parentheses.

3). The highest weekly average of mean total drums/day was 206.3 in week 7 (23-29 April). Assuming that the weekly averages were reasonably representative, I estimate that the average "active, site-associated" (Gul-lion 1966) grouse drummed a total of 7038 times during 493 hours of drumming activity in the 8-week period (9 April-3 June). It would be interesting to know what this represents in terms of energy expenditure.

ONSET OF THE DRUMMING SEASON

All five males receivable at the time were first recorded drumming on the evening of 9 April, with onset times ranging from 1949 to 2108. Two intriguing questions were raised by this observation: (1) Why did each grouse begin drumming on 9 April? (2) Why did they begin from 58 to 137 minutes after sunset?

The first question probably can be partially explained on the basis of photoperiodically-controlled gonadal development. But year-to-year variation in dates of spring onset of drumming suggests that the exact date cannot be explained on the basis of photoperiodism alone. Disappearance of snow has been proposed as the main environmental stimulus for the start of spring drumming (Petra-borg et al. 1953). Rusch and Keith (1971) also reported an apparent relationship between initiation of drumming and spring thaw in Alberta.

Snow on the study area melted rapidly on 7 and 8 April, lending support to the "snow disappearance" hypothesis, but the reason for delay of the start of spring drumming until 9 April is not clear. Perhaps the snow surrounding drumming logs was not sufficiently melted until 9 April. Alternatively, the relatively strong winds and high temperatures

TABLE 5
SELECTED ENVIRONMENTAL DATA FOR THE EVENINGS OF 9 APRIL, WHEN SPRING
DRUMMING BEGAN, AND THREE PREVIOUS DAYS

	April ¹			
	6	7	8	9
Wind (km/h) (2000-2400)	1.2	14.5	15.3	2.8
Mean temp. (°C) (2000-2400)	-0.9	17.0	5.9	-0.8
% Cloud cover ² (2000-2100)	60-10	10	10	10
Time of moonset	1955	2113	2230	2341
Moon angle at naut. twilight ³	0.5°	19°	37°	54°

¹ No precipitation recorded during this period.

² Source: Surface weather observations, Crystal Airport, Minneapolis, Minnesota.

³ Approximate number of degrees above horizon at nautical twilight (14.5°/hour assumed).

(Gullion 1966) recorded between 2000 and 2400 on 7 and 8 April might explain the delay (Table 5).

The snow disappearance hypothesis provides no clue as to why spring drumming started shortly after dark, but some evidence suggests that the moon may have played a role in its stimulation. Four of the five grouse began spring drumming within 10 min of nautical twilight (i.e. 1958), when the crescent moon (age 3.7 days) was approximately 54° above the western horizon (Table 5). The moon began setting after nautical twilight on the evening of 6 April. But moonlight reaching ground level (tree-roosting is rare at this time of year) would be greatly reduced once the moon descended below the forest outline. Assuming that the outline of the leafless trees was about 35° above the horizon, the evening of 9 April was the first on which the moon was well above (19°) the forest outline at nautical twilight (Table 5).

DRUMMING ACTIVITY PATTERNS OF INDIVIDUAL MALES

While grouse generally drummed at the same times of day (Table 1), certain males drummed at shorter average intervals than others (Table 6). Differences among birds for the entire day (0000-2400) were significant ($P < 0.001$). With the exception of no. 1633 (nocturnal periods), the magnitudes of the mean intervals for all individuals were in the same relative order in each of the four time periods. Aubin (1972) also found that some territorial grouse drummed many more times than others. Within birds, mean intervals were greatest in the 0000-0400 period, least from 0400 to 0800, and more variable in the two nocturnal periods. While the sample is too small for any conclusion, my data suggest that territorial juveniles drum as or more often than adults. The three juveniles I studied

TABLE 6
MEAN AND SD OF INTERVAL BETWEEN SUCCESSIVE DRUMS, EXCLUSIVE OF LONG
INTERVALS, 9-26 APRIL

Bird no. ¹	Time period	Interval between drums			No. of long intervals ²
		No.	Mean (seconds)	SD	
1616	0000-2400	1190	231.9	99.25	23
	0000-0400	253	307.1	93.50	6
	0400-0800	437	197.8	89.87	9
	0800-1200	199	227.8	68.06	4
	2000-2400	233	219.7	102.10	4
1620	0000-2400	1147	265.2	116.00	65
	0000-0400	294	357.1	120.05	43
	0400-0800	264	207.0	88.36	6
	0800-1200	258	267.7	84.03	6
1624	2000-2400	250	224.9	108.84	7
	0000-2400	1824	196.9	82.04	17
	0000-0400	502	251.5	86.23	7
	0400-0800	547	165.5	64.71	6
1624	0800-1200	317	203.2	70.36	3
	2000-2400	345	169.6	70.62	0
	0000-2400	1666	208.1	93.33	40
	0000-0400	405	265.1	107.74	23
1628	0400-0800	532	165.9	62.27	12
	0800-1200	236	214.2	79.59	3
	2000-2400	357	205.4	99.44	1
	0000-2400	1440	236.1	115.28	52
1633	0000-0400	383	312.0	122.04	30
	0400-0800	463	191.6	79.52	11
	0800-1200	125	221.3	76.61	1
	2000-2400	353	236.1	123.44	10
Mean ³	0000-2400		227.6		
	0000-0400		298.6		
	0400-0800		185.5		
	0800-1200		226.8		
	2000-2400		211.1		

¹ Adults (22 or more months old): Nos. 1616 and 1620; juveniles (10-12 months old): Nos. 1624, 1628, and 1633.

² Intervals between 10 and 30 min; not included in computation of mean and SD.

³ Average of time period means for the five individuals.

were active drummers from the start of the spring drumming season (their status in the previous fall was unknown). Juveniles that do not become established on drumming logs until midway or later in the spring season probably drum far less intensively (Gullion pers. comm.).

The 227.6-sec average of the entire-day mean intervals for the 5 males (Table 6) is 12.4 sec less than the 4-min average reported by Petraborgh et al. (1953) and 15.4 sec less than that found by Palmer (1969). One factor that could affect comparability of interval means and variability is the maximum time between drums that is considered an interval. The number of "long" (i.e. 10-30 min) intervals gives some indication of the effect of the 10-min maximum I used (Table 6). Minimum recorded

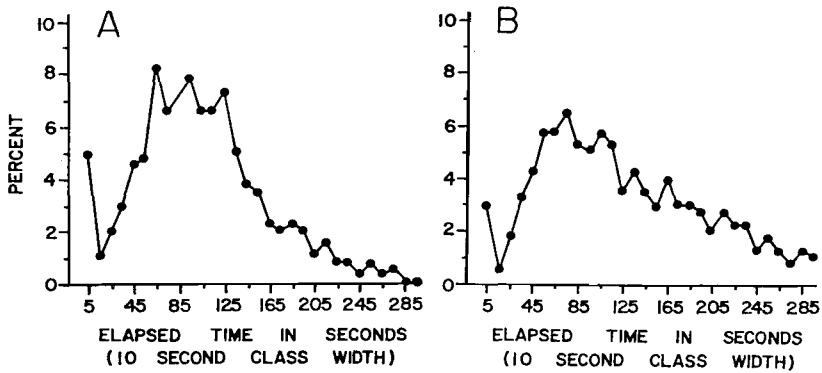


Fig. 6. Drumming stimulus-response functions for males 1620 and 1624, 9-26 April. Distance between drumming logs about 84 m. A: stimulus = no. 1620, 1087 responses by 1624; B: stimulus = no. 1624, 1350 responses by 1620.

intervals, an indication of the refractory period for drumming, ranged from 40 to 47 sec ($\bar{x} = 42.8$).

Significant serial correlation of interval length (Spearman coefficient of rank correlation with lag of 1, $\alpha = 0.05$) was found in 87 of 119 uninterrupted series of 30 or more drums (9-26 April). Thus, the length of an interval in a series of drums is often similar to the preceding one. Serial correlation of intervals was restricted to the hours of darkness and the immediately postsunrise period, apparently a reflection of the tendency for linear increase or decrease in interval length at these times of day (Fig. 4).

COMMUNICATION BETWEEN NEIGHBORING MALES

Stimulus-response functions (i.e. distributions of the time lapses between each drum of one grouse and the next drum of the other (Delius 1969)) for grouse 1620 and 1624 indicate that the drumming of each influenced the drumming pattern of its neighbor (Fig. 6). Both distributions show a tendency for the drums of the response bird to occur within 10 sec or between 50 and 130 sec following the stimulus. If the stimulus had no effect, the distribution theoretically should be relatively uniform, tailing off to the right from the lower incidence of longer intervals. Distributions for four pairs of males whose drumming logs were > 0.4 km apart were examined, and all were found to approximate the shape predicted assuming no effect. Unfortunately, data for the entire interval sampling period (9-26 April) were available for only this one pair of adjacent males.

The drumming sequences of 1620 and 1624 were scanned for further

No. 1620			No. 1624	
Start Time of Drum	Interval Between Drums (seconds)	Time Lapse Between Birds (seconds)	Interval Between Drums (seconds)	Start Time of Drum
0744:18		188	188	0742:20
		48		
0747:03	165 ←	117	166 →	0745:06
		155	272	0749:38
0751:15	252	97		
		54	151 →	0752:09
0753:06	111	57		
		113	170 →	0754:59
0755:37	151 ←	38		
		172	210	0758:29
0758:30	173 ←	1		
		190	191	0801:40
0802:19	229 ←	39		
0805:27	188	--		
		2	229 →	0805:29
0809:20	233 ←	231		
		3	234 →	0809:23
		--	197	0812:40
0813:19	239	39		
0816:27	188	--		
		4	231	0816:31
		--	253	0820:44
0822:51	384	127		
		109	236	0824:40
0825:42	171	62		
0828:42	180	--		
		2	244	0828:44
		--	189	0831:53
0832:39	237	46		
		179	225	0835:38
0836:40	241	62		
		172	234 →	0839:32
0840:16	216	44		
		161	205 →	0842:57
0844:11	235 ←	74		
		197	271	0847:28
0848:12	241	44		
		133	177	0850:25
0851:37	205 ←	72		

Fig. 7. Drumming sequences of males 1620 and 1624, 14 April. Prior to initial drums shown, no. 1624 had been drumming for 70 min but no. 1620 had not drummed for several hours. Location data indicated both grouse were on or near their only known drumming logs (ca. 84 m apart), excluding possibility of visual contact.

evidence of drumming interaction. Data for the morning of 14 April provide an example of the interactions identified (Fig. 7). Five time lapses were 4 sec or less in length. As the entire drumming performance lasts about 12 sec (Aubin 1972), this rapid response amounts to duetting with a phase difference. No time lapses were recorded in the 5–37 sec range. The reason for this hiatus, also evident in the stimulus-response functions (Fig. 6), is unclear. No. 1624 was the following bird in 4 of 5 rapid responses, and, in the last 3 (starting at 0809:23), it drummed twice consecutively before 1620 drummed again. In 3 instances 1620 drummed twice in a row at an interval of between 180 and 188 sec. Beginning at 0832:39, 1620's time lapses followed a regular pattern: 46, 62, 44, 74, 44, 72.

Another apparent drumming interaction, "interval copying," is indicated by arrows in Fig. 7. No. 1620's initial interval was within one second of the interval between the two previous drums of its neighbor. If one grouse's most recent interval is duplicated by its neighbor, this amounts to the neighbor's repetition of its own previous time lapse. In some instances the interval copied was not the most recent, but rather the first or second previous in time (Fig. 7).

No criteria were established to compare the recorded incidence of interval copying or rapid responses with chance expectations. Both phenomena were uncommon: 79 cases of interval duplication (± 3 sec) and 101 rapid responses (≤ 9 sec) were found in the 2437 intervals included in the stimulus-response functions for 1620 and 1624, but neither was randomly distributed in time. Fifty-four (68.3%) of the interval duplications fell in groups (i.e. each event < 20 min from another) of 2–8, and 59 (58.4%) rapid responses occurred in groups of 2–5. Single incidences probably resulted purely by chance and do not represent interaction. But where rapid responses and interval copying occurred in runs, interaction involving some sort of communication is suggested.

Six drumming periods were found in which several rapid responses and several interval duplications occurred concurrently: 14 April, 0742–0851 (Fig. 7); 16 April, 0058–0151; 17 April, 0853–0937, 2111–2229; 21 April, 2116–2222; 23 April, 2157–2238. Each took place at the beginning of a mutual drumming period and was preceded by 3–22 hours in which the birds had not been recorded drumming together. This temporal restriction suggests that the drumming interactions may represent an individual recognition process or even possibly a reaffirmation of a previously-existing dominance relationship.

In Chukar Partridges, Bobwhites, and California Quail, the second-ranking bird has been found to call the most (Williams and Stokes 1965). From range overlap data (Archibald 1976), it appeared that the dominant

bird was 1620, the adult. It is interesting to note that 1624, the juvenile, was found to drum considerably more often (Table 6).

DISCUSSION

As Allen (1934) suggested, drumming has both a territorial and a reproductive function. It serves to warn, threaten, and repel intruding males (Aubin 1970) and to attract females (Brander 1967). Thus, in the interpretation of drumming during the breeding season, possible effects on both hens and other males need to be considered. Gullion (1970) pointed out that "drumming serves the latter [mate attraction] function for perhaps a week or two out of the 7 or 8 months per year that male grouse are closely associated with drumming logs." If drumming also serves to stimulate female sexual development (Hjorth 1970, Aubin 1970), the reproductive function may encompass a somewhat longer timespan.

Several important questions about the drumming sound remain unanswered. First, both here and in the literature, the drums of an individual grouse tacitly have been assumed to represent a single "song" type. Could drumming instead consist of a repertoire of two or more drum types? Samuel et al. (1974) found significant ($\alpha = 0.05$) differences in the duration of the drums of 2 of 3 grouse among different days, and Aubin (1972) reported significant differences in both the duration and number of wingbeats ($P < 0.1$ for one bird) of drums of 3 birds in consecutive years. Second, significant differences in the sound pattern of drums among individuals have been demonstrated (Aubin 1972, Samuel et al. 1974), but the question of whether grouse can recognize the drums of their neighbors remains unanswered. In the Ovenbird (*Seiurus aurocapillus*), variation among individual songs has been shown to facilitate individual recognition (Weeden and Falls 1959). Third, the hen, attracted by drumming, is believed to seek out the territorial male at his drumming log (Brander 1967, Gladfelter and McBurney 1971). But whether variations in the sound pattern or time sequence of drums influence her selection of a mate is unknown.

Irregularity (e.g. several song types) in a communicative repertoire provides opportunity for exchange of information (Lemon 1968). If the assumption of a single drum type is valid and individual recognition is dismissed as unknown, uncertainty is limited to the timing of responses. The two kinds of drumming interactions found for grouse 1620 and 1624 (Fig. 7) may have involved an exchange of information. The rapid response (≤ 9 sec) seems analogous to duetting with phase-difference in the "yodelling" display of male Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) on adjacent territories (Hjorth 1970: 400). Interval copying, on the other hand, is something like matching of song types

(Lemon 1968), except that interval rather than type is matched. The hiatuses in the 10–40 second range of the stimulus-response functions were remarkably similar (Fig. 6). And the response hiatus and the refractory period for drumming ($\bar{x} = 42.8$ sec) were similar enough to arouse suspicion that the two may be related.

If the data for 1620 and 1624 are representative, two conclusions about drumming may be made: (1) the drumming of one grouse can affect the pattern of drumming of its neighbor, and some form of communication is involved; (2) males can “record” and duplicate intervals between both their own drums (serial correlation) and the drums of a neighbor (interval copying), an indication of a truly remarkable timing mechanism.

My results indicate that moonlight was the major external factor stimulating nocturnal drumming. The timing of the onset of the drumming season (Table 5), the April drumming peak (Fig. 5), and the end of the nocturnal drumming period all seemed to be related to moonlight.

Several authors have mentioned occasional nocturnal drumming (Fowle 1953, Allen in Bent 1932), but a consistent nocturnal pattern such as that found during the first several weeks of drumming in my study has not been reported. Petraborg et al. (1953) suggested that sporadic drumming throughout the night was associated with high population levels; the present study was conducted during a population “high.” However Gullion (pers. comm.) has recorded nocturnal drumming during population lows as well as highs. Scott (1942) noted that male Sage Grouse (*Centrocercus urophasianus*) may display sporadically throughout a bright moonlit night. Hjorth (1968) reported Black Grouse (*Lyrurus tetrix*) display activity throughout one cloudless, full-moon night. Nocturnal drumming also occurs in the fall, but its extent then is uncertain. During the equipment development phase of my study, no. 1616 drummed throughout the moonlit night of 27–28 October 1969, 3 days after the full moon.

It seems likely that nocturnal drumming would subject Ruffed Grouse to an increased risk of predation. One individual, adult 1622, was killed by an avian predator at night shortly after completing a drum, but male Ruffed Grouse are thought to be essentially invulnerable to predation while on their drumming logs (Meslow 1966, Gullion and Marshall 1968). Hjorth (1968) pointed out that, in the presence of snow, a displaying Black Grouse cock is extremely conspicuous, particularly from above. Delay of the initiation of spring drumming until the snow disappears may be a mechanism for decreasing the risk of predation. Part of the advantage of drumming at night may lie in greater audibility of the drumming sound. On the 11 drumming nights during the nocturnal period, wind velocity averaged 4.9 km/h between 2000 and 2400.

The literature provides little insight on the question of whether the timing of peak drumming periods is related to moon phase. In several previous studies (e.g. Gullion 1966), the peak of drumming activity was defined as the highest percentage of birds active during a single morning observation period. As the birds I studied were consistently active drummers, my criterion for the peak of drumming was the highest value of mean total drums/day, which was recorded on 24 April. Peaks determined by such different methods are not comparable. Gullion (1966) reported that the peak of drumming activity (i.e. maximum participation) fell within 3 days of 29 April during a 5-year period. Limited evidence from the same northern Minnesota study area suggests that the peak measured by the "standard" definition is not directly related to copulation. Assuming that copulation took place 3 days before the first egg was laid (Bump et al. 1947), hens probably copulated on 6, 8, and 10 May 1963 (Brander 1967) and 2, 10, and 13 May 1965 (Barrett 1970). The moon was full on 8 May 1963 and 15 May 1965.

The two peaks in mean total number of drums/day coincided with the full moons in April and May (Fig. 5). During the first peak, drumming activity occurred almost continuously except around sunset (Fig. 3). During the second peak drumming period, nocturnal drumming was recorded on only one occasion, but, once again, drumming activity occurred throughout the daytime (Fig. 3). In both cases, increased drumming during the day was correlated with moonlight at night. Hjorth (1968) reported that, in April and May, arrival of male Black Grouse at the arena took place much earlier on clear mornings during the week of the full moon. And, significantly, when the birds arrived early, the intensity of their ensuing morning display activity was greater. Thus, in both species the effect of moonlight apparently carries over well past sunrise.

The major factor influencing male Ruffed Grouse territorial behavior in both spring and fall is probably photoperiodically-controlled gonadal activity (Godfrey and Marshall 1969). Changes in hormone secretion in turn produce changes in threshold levels for environmental factors such as light. Hjorth (1968) found that the full moon had no effect on the morning arrival of male Black Grouse in March and the beginning of April and only a very limited effect by early June. At the beginning of June, arrival was affected only on the night of the full moon and the previous night. A similar change in threshold level may explain why a nocturnal drumming pattern like that recorded in April did not occur in May (Fig. 2). An environmental change also may have played a role. Alder (*Alnus rugosa*), an important component of the vegetation around and above the drumming logs of most study males, began to leaf

out about 28–30 April. Perhaps the similar pattern of nocturnal drumming, which should have begun about 8 May, did not materialize because insufficient moonlight reached the grouse through the shade of the newly formed deciduous leaves.

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SUMMARY

Drumming of 7 male Ruffed Grouse was monitored from 7 to 56 days with modified automatic radio-tracking equipment during spring 1970. Grouse generally drummed at the same times of day, but certain individuals drummed at shorter intervals than others consistently throughout the day. The highest drumming frequencies within a day tended to occur at the beginning of a drumming period and an average of 38.7 min before sunrise.

During the first 2½ weeks of the drumming season, nocturnal drumming was consistently recorded for all radio-marked males except under windy or inclement weather conditions. Then, within about 5 days, drumming became nearly exclusively diurnal and continued so thereafter.

Peak drumming periods coincided with the full moons in April and May. Estimated dates of copulation of three hens coincided with the drumming peak in April. The second peak may have been associated with remating of hens that had lost their initial clutch. Five abiotic factors accounted for approximately 67% of the variation in the seasonal distribution of the average daily total number of drums; the most important of these factors were moon fullness (seasonal variation) and km of wind/day (day-to-day variation).

Two possible forms of communication between adjacent males were identified: (1) drumming shortly after the start of a neighbor's drum, (2) duplication of the interval between successive drums of a neighbor. Stimulus-response functions for two neighboring grouse showed a tendency for the drums of one bird to occur either within 10 sec or between 50 and 130 sec after the drums of the other bird.

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APPENDIX

DESCRIPTION OF THE DRUMMING RECORDING SYSTEM

Near the laboratory, fixed yagi receiving antennae, 9 to 15 m in height, were placed within 0.8 km and pointed in the direction of the drumming log(s) of one or more Ruffed Grouse equipped with continuously broadcasting (53 mHz) radio transmitters (Cochran and Lord 1963) with 23 cm whip antennae. A small, battery operated preamplifier (Vanguard Electronics, Model 407) was located at the base of each yagi to provide signal amplification before transmission over coaxial cable to the laboratory. Coaxial cables from the antennae were connected at the laboratory.

In the laboratory, portions of the equipment used for radio-tracking (Cochran et al. 1965) were modified to record drumming. Following amplification, frequency conversion, and audio filtration, the signal was fed to radio receivers (U.S. Government surplus BS 453), one per individual. The output from each receiver was coupled to two pairs of visual indicator tubes (Mullard DM-70) wired in parallel. One pair was positioned near the receiver to facilitate tuning; a duplicate pair was located in a darkened camera room. One member of each pair of indicator tubes was set to respond to a lower input signal gain (volume) level than the other to provide recording capability over a greater range of gain levels. The base (bird inactive) gain level of the receiver output was adjusted so that the lower level indicator was barely to partially lit. Photographing with a slow-moving, shutterless 16 mm movie camera produced a thin trace on film. Increases in gain caused first the lower and then the higher level indicator tubes to become fully illuminated, which produced widening traces on the film in each case. Activity, manifested by variations in gain above the base level, thus produced a film pattern involving the lower level or both traces (Fig. 1).

In addition to indicator light traces and animal numbers, the film record included digital time and timing marks at 10-sec intervals. The starting time of a drum could be determined to the nearest second with a calibrated manual film viewer. Provision was made to monitor up to 12 individuals continuously and simultaneously as parallel pairs of traces along the same roll of film. This enabled precise reconstruction of time sequences of drumming of neighboring males.

Performance of the recording system was periodically checked by noting times of drums heard in the field and on radio receivers and comparing them with the film. This aided interpretation because drum patterns on film were found to be somewhat variable both among and within individuals, the latter dependent primarily on receiver tuning and gain level adjustment.

Although the system described here was used only to record drumming, the potential exists for monitoring other types of activity. One activity which was readily identifiable on film was "budding" (i.e. feeding in trees). Behavior patterns that involve unique, consistent, and vigorous sequences of motion are best suited for monitoring with this technique. A multichannel strip chart recorder could easily be used in place of the photographic recording method described here.