FACTORS AFFECTING THE INCIDENCE OF RALLY CALLING IN THE CHUKAR PARTRIDGE

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The purpose of this study was to investigate the factors which influenced the incidence of the rally call in a population of free-living Chukar Partridges (*Alectoris chukar*). We also made observations on captive chukars to measure the effects of sex and social organization on rally calling.

The rally call, a repeated *chukara-chukara-chukara* lasting one to 12 seconds, has been described in detail by Stokes (1961). The call is audible for 300 yards or more under good conditions and is given by both sexes through the year. In the breeding season, the call of the male is aggressive and serves to space individuals. Females call when separated from their mate. In the nonbreeding period, the call functions to regroup members of a dispersed flock and to space individual coveys. Our observations are limited to captive chukars and birds released in the wild prior to the study. Therefore, the following data may not be entirely typical of a natural wild population.

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METHODS

The Study Area

We observed rally calling by free-living chukars on Little Mountain, Box Elder County, in northern Utah. Little Mountain rises from Great Salt Lake Valley and is isolated from other mountains by flat desert, marsh, and croplands. The combination of steep slopes, rocky outcrops, sagebrush (*Artemisia tridentata*), and expanses of cheatgrass (*Bromus tectorum*) form ideal chukar habitat.

The northwest corner of the mountain is a three-sided basin 300 yards in diameter with slopes enclosing the south, west, and east sides. An elevated hillock in the center of the basin overlooks the entire area. From this point chukars using the basin could be seen throughout the day.

In early March of 1960, we released 100 pairs of adult chukars into the study basin. Of these, 100 were marked with a modification of the Nelson (1955) bicolored plastic tag. Within three weeks approximately three-quarters of this group had moved from the basin. The rest remained in the release area and paired. We observed no movement into or out of the basin following pair formation. In May we released five additional unmated, marked males on the same area. They left the vicinity within one day after having been chased by paired males. We made our observations only on those birds remaining in the basin, approximately 20 pairs.

Observational Details

Our primary concern during this study was to relate the number of rally calls heard during 15-minute periods to the physical and biotic factors existing at the time of calling. Many of the chukars were not visible while calling; therefore, data con-

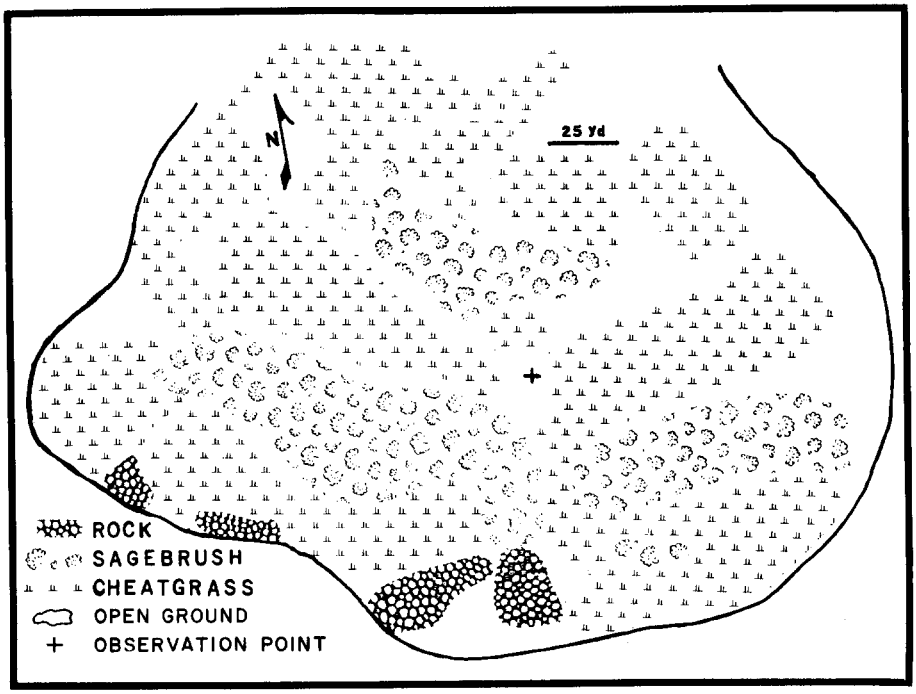

Fig. 1. Map of study area. The basin lies within the curved solid line.

cerning all of the behavioral situations in which the rally call was given were not known. A sampling unit consisted of a 15-minute period. Measurements of physical factors were taken at the beginning of each sampling unit. Light intensity was recorded with a light meter placed face down two feet above a standard-gray reflecting surface. We recorded temperatures with a thermometer placed in a shaded position four feet above the ground. We recorded rain as falling or absent for each period. Amount was not measured. Wind velocities were obtained with a hand-held anemometer.

We made our observations between one hour before sunrise and one hour after sunset (MST). Number of days and hours of sampling were: April, 7 days (66 hours); May, 8 days (55 hours); June, 6 days (67 hours); July, 6 days (50 hours). Initially an observation blind was used but this proved unnecessary.

RESULTS

Daily Activity Cycle

Birds in pairs.—The daily activities of chukar pairs followed a fairly predictable cycle through May. Birds roosted primarily on the rocky slopes of the basin's south side; normally they left the roost from 30 to 45 minutes before sunrise. Birds rarely rally called in the roost area. Calls at awakening seemed confined to *squee* (Stokes, 1961) and low contact calls. Following this activity, chukars flew as pairs to the open grass area in the bottom of the basin (fig. 1). This often occurred while it was still too dark to see the birds in flight. *Wheetu* (Stokes, *op. cit.*) calls were heard prior to and during flight.

Normally each pair moved about very little, presumably remaining within a limited area which included both grass and brush. Observations on marked pairs seen repeatedly in the vicinity of the observation point indicated a daily cruising area of approximately 450 square feet. However, for pairs occupying the periphery of the basin, movement to and from the roost exceeded 300 feet. The male defended his mate against approach by other birds, this being the occasion for bursts of rally calling. Feeding began almost immediately and continued for one to three hours. As midday approached, the chukars retired to brush cover adjacent to the grassy area and confined their activities to dusting, preening, and dozing.

The chukars left cover four to five hours before sunset to feed again in open grassy areas. While feeding, pairs occasionally moved into the vicinity of neighboring pairs. Walking to roost began just prior to sunset causing a rise in aggressive encounters between pairs as they came into close contact. Aggression stopped in the late evening as the chukars moved into the limited roosting area.

Birds in coveys.—As summer progressed, the hens did not nest, perhaps because they were unadjusted, newly released birds. In early June, the pairs broke up, and by June 15 all of the chukars within the basin area had congregated in two coveys. One of these normally occupied the west half of the basin and the other the east half. Precise boundaries did not exist, but there was no apparent mingling of the groups. The coveys did not come into the grass area as early in the day as pairs. They remained longer in the vicinity of the roost or in the higher brush. Although the coveys did not mingle, contact between birds of the two coveys released fighting, rally calling, and other signs of aggression. Errington (1933) described calling and fighting among two coveys of Bobwhites (*Colinus virginianus*) in a similar situation. Aggression and rally calling within the covey were also noted. This occurred more frequently immediately following covey formation and became less conspicuous in July, presumably after the intracovey social rank was established.

Rally calling in relation to activity.—A difference in the distribution of calling before and after formation of coveys occurred (fig. 2). When the birds were in pairs, calling peaks normally occurred early in the morning as the chukars apparently resumed defense of their mates upon flying down from the roost. Following formation of the coveys, birds left the roost somewhat later and did not characteristically fly down into the grassy area. Instead they were more apt to walk down. This delayed their arrival in the open grassy area with corresponding delay in peak of aggressive encounters and rally calling. A second or midmorning calling peak (see fig. 2) followed the feeding period. Some rally calling occurred as the majority of the birds were feeding, but the midmorning calling peak seemed to be associated with the cessation of the morning feeding. Calling was greatly reduced in both pairs and coveys during midday and rose to an evening maximum from 45 minutes before sunset to 15 minutes after sunset. Some rally calling occurred during aggressive encounters at midday but it was uncommon. Periods of maximum rally calling were most often associated with times of greatest activity. Thus movement to and from the roost area was always accompanied by high calling rates.

Influence of Physical Factors

We used a multiple regression analysis to determine the influence of physical factors on calling, as interactions and partial effects of the variables were evident (Elder, 1956). One assumption implicit in such an analysis is that the independent variables are fixed or measured without error. The measurements of physical variables

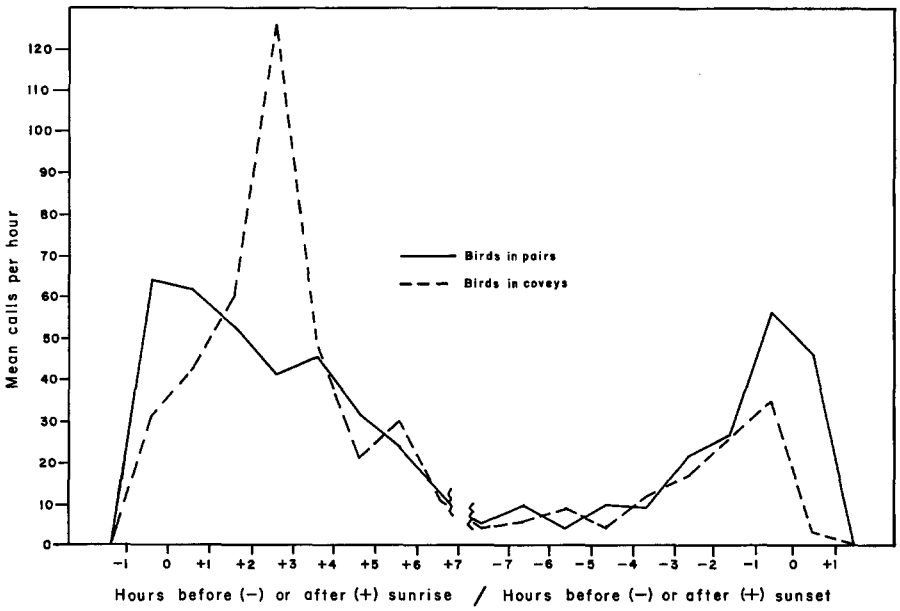

Fig. 2. Mean hourly rates of rally calling in Chukar Partridges while in pairs (April 1–June 11) and in coveys (June 15–July 31).

at the beginning of each sampling unit did not account for changes that occurred during the following 15 minutes. Hence there was probably some unmeasured effect on calling. Also variations in the biological or behavioral situations during sampling were not considered in the analysis. Computations were made on the IBM 1620 computer using a stepwise regression analysis program. Prohibitive costs of computer time required that we take two random 100-period subsamples from the total of morning and evening samples. The standard deviations of calls for these subsamples were in close agreement with the total deviations (a.m., total standard deviation, 13.9; sample, 13.8; p.m., total standard deviation, 8.5; sample, 8.7).

The coefficient of multiple regression, R, which measures the degree of association among the dependent and independent variables was 0.672 for the morning periods and 0.731 for the evening. The proportion of the sum of squares of the dependent variable which is associated with the multiple regression equations, R^2, was 0.452 for morning periods and 0.535 for evening periods. This means that 45 per cent of the variation in morning calling and 54 per cent of the variation in evening calling can be attributed to the effects of the physical variables analyzed here. The partial regression coefficients showing significance are listed in table 1. The mean number of calls per 15-minute interval in relation to wind, rain, light intensity, and temperature is given in table 2.

Calling rates varied most strongly with light intensity. The higher calling periods normally occurred at low light readings early and late in the day. However, low light intensities associated with cloudiness during the day did not always result in increased calling rates.

Wind velocities ranged from 0 to 45 miles per hour; however, there were only 47 sampling periods with velocities in excess of 10 miles per hour. At these times the

TABLE 1

PARTIAL REGRESSION COEFFICIENTS AND STANDARD PARTIAL REGRESSION COEFFICIENTS OBTAINED FOR THE MULTIPLE REGRESSION EQUATIONS

Variable	Partial regression coefficient	t test[1]	Standard partial regression coefficient
Morning			
Temperature	2.151	2.32*	2.105
Time × temperature	0.168	2.54*	8.332
Light × temperature	0.006	1.98*	4.801
Light[3] × temperature[3]	0.000	2.06*	1.276
Evening			
Time	7.637	2.96**	9.558
Light	0.357	2.74**	6.428
Time[2]	0.153	3.04**	7.901
Time × temperature	0.100	2.68**	11.006
Light × temperature	0.005	2.18*	7.733
Light[2] × wind[3]	0.000	2.63**	7.093
Light[2] × wind[3]	0.000	2.40*	0.762

* Significant at the 0.05 level.
** Significant at the 0.01 level.
[1] t test values are computed for the partial regression coefficients.

TABLE 2

MEAN NUMBER OF CALLS PER 15-MINUTE PERIOD IN RELATION TO LIGHT INTENSITY, TEMPERATURE, WIND VELOCITY, AND RAIN

Variable	Morning		Evening	
	Mean no. calls	No. periods	Mean no. calls	No. periods
Light intensity (ft.-c.)				
0–25	13	87	9	78
26–50	9	43	9	23
51–100	13	51	7	51
101–300	11	164	4	155
301–600	8	108	1	173
Temperature (°F.)				
30–49	13	88	13	19
50–65	11	186	4	76
66–79	11	120	4	136
80–96	5	59	4	249
Wind (mph)				
0–2	12	237	5	246
3–5	10	165	3	165
6–10	6	31	7	42
11–45	4	20	3	27
Rain				
Absent	11	422	4	471
Present	4	31	3	9

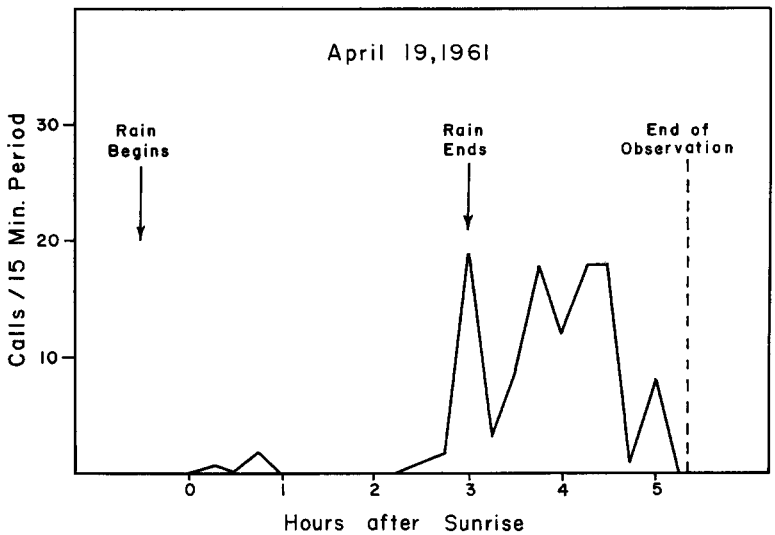

Fig. 3. The depressing effect of rain on rally calling.

chukars normally remained close to cover and did not call. The decrease in calling with increasing winds could be due to either the depressing effect of wind on the birds or the inability of a person to hear chukar calls above the noise of the wind. McClure (1939) observed that both of the above factors were operating in counts of Mourning Doves (*Zenaidura macroura*), but he felt that in pheasants (*Phasianus colchicus*) the chief cause for reduced call counts during windy weather was the hearing interference of the wind itself (McClure, 1944). In our study area we could see many of the chukars within the basin and often could detect the calling bird by its upright posture during calling. We never saw such calling birds in windy weather without also being able to hear the call. The duration of the call, as well as the bowl-shaped basin, enabled us to hear calls with winds in excess of 10 miles per hour. One morning we recorded 53 calls within a 15-minute period when it was raining and wind was in excess of 40 miles per hour. Hence, we believe the wind actually depressed the calling rate and had only a slight effect on our ability to hear the calls.

We recorded rain during 40 of 933 sampling periods, 29 of these occurring in the morning. Periods with rain are not included in the statistical treatment because of their limited number and unequal distribution in the mornings. Rainfall normally caused the chukars to move to cover and stop calling (fig. 3). The rain on April 19 began half an hour before sunrise and lasted until 8:45 a.m. It almost completely suppressed calling up to the time the rain stopped. Note the complete absence of the two peaks at sunrise and an hour later. Outside of the rainy periods, that day's calling was higher than normal for April.

When unusually motivated, chukars may continue to call despite wind and rain. On May 23 intense aggression between males resulted in 133 rally calls between 5:30 and 7:00 a.m. despite heavy rain and winds in excess of 30 miles per hour.

The changes in rates of calling throughout the day shown in figure 2 emphasize the relationship between calling and the periodic changes in the physical factors of light and temperature. However, the calling for an individual day (fig. 4) gives a

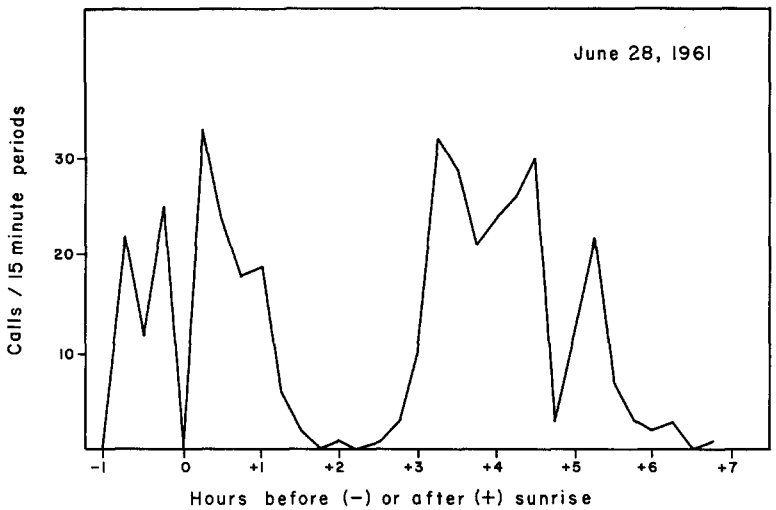

Fig. 4. A morning's variation in rally calls per 15-minute period when weather was favorable.

different picture. The oscillations in calling between successive 15-minute periods appear too great to be the response to changes in physical factors alone.

Influence of Biotic Factors

Interspecific relations.—Hawks and eagles affected rally calling. When a hawk flew over the study basin, the chukars normally remained silent even during hours when high calling rates normally occurred. On June 15 a Marsh Hawk (*Circus cyaneus*) circled over the basin from 7:15 p.m. until sunset at 7:57 p.m. During this time we recorded only 15 rally calls, but on June 17 when there was no hawk present we recorded 78 rally calls for the same period. Similar physical conditions existed on both days. We also observed increased calling after two Golden Eagles (*Aquila chrysaëtos*) flushed several pairs of chukars into another pair's grounds. After the eagles left, the resident male and the intruders called until the flushed pair returned to its own grounds. We noted a general reduction in calling on several other occasions when raptors were present. Hence, this is a strong influence on rates of calling, but it is a highly unpredictable one.

Intraspecific relations.—We observed that increased calling followed when two or more male chukars came into contact. Calling by several chukars also stimulated calling in nearby birds. The same is true in other species of birds. Borror (1961) demonstrated that the singing rate of a male Song Sparrow (*Melospiza melodia*) increased from 4 to 6 songs a minute to 8 to 10 songs when he played recorded song of the same or different individuals. The same is true for *bobwhite* calls in the Bobwhite (Stokes and Williams, MS). Peak calling periods in the morning and evening are always typified by several chukars calling simultaneously or alternately. The sharp fluctuations in calling between successive 15-minute periods, shown in figure 4, reflect the contagious nature of rally calling. These outbursts were typically followed by periods of relative silence, giving rise to the abrupt changes in rates of calling.

To study more closely the influence of sex and social rank on calling we observed

TABLE 3

RELATION OF RALLY CALLING, DISPLAY, AND COPULATION TO SOCIAL RANK IN CAPTIVE MALE AND FEMALE CHUKARS

Bird and social rank	Total no. calls (20 hrs. obs.)	Circling or waltzing by males	Copulation
Male 1	22	Infrequent	Infrequent
2	36	Common	Common
3	2	Never	Never
4	4	Never	Never
5	0	Never	Never
Female 1	26		Yes
2	40		Yes
3	27		Yes
4	30		No
5	32		No

chukars in captivity. We determined social rank of males by observing the incidence and outcome of aggression in the form of lateral stance, circling, and chasing (Stokes, 1963). As seen in table 3 the three lowest-ranking males showed little aggressive and sexual behavior and they rarely called. Among the less aggressive females there seemed to be no suppression of calling. It is characteristic of captive chukars and also of Bobwhites and California Quail (*Lophortyx californicus*) that the second-ranking individual of each sex calls the most and is generally the most active bird (Stokes and Williams, MS). These captive chukars were strongly stimulated to call by other captive chukars nearby but out of sight. Calling was oriented to this second group of chukars. The function of the rally calls by females in this situation seemed to represent that normally occurring outside the breeding season, that is, re-grouping a dispersed covey.

If we can apply the behavior of captive birds to those in the wild, there will be great differences in rates of calling between individual birds. Dominant males will call far more than subordinate birds, which may not call at all, as has been observed by Taber (1949) in the Ring-necked Pheasant.

The patterns of calling observed in this study were probably not entirely typical of the wild chukar. These birds were released into strange surroundings in March. Pairing and breeding activities at this latitude often begin at this time. A period of adjustment must normally follow when a bird is placed in new surroundings. The failure of birds in the basin to nest and the fact that coveys had formed by mid-June indicate an abnormal breeding phenology. In the Bobwhite, occurrence of coveys in the summer or compatibility of birds after initial covey break-up are signs of "recessed breeding" (Lehmann, 1953). Social contact in our chukar population, however atypical, did influence rally calling to a great extent.

FUNCTION OF THE RALLY CALL

The function of the song in many birds is twofold: (1) to attract a mate and (2) to repel rival males. The song of many birds falls off rapidly once a bird is mated. Stoddard (1931) reported this first for galliforms in the Bobwhite and we have also seen it in the California and Gambel (*Lophortyx gambelii*) quail. Only unmated males in these species call persistently. In contrast, the rally call persisted in mated chukars.

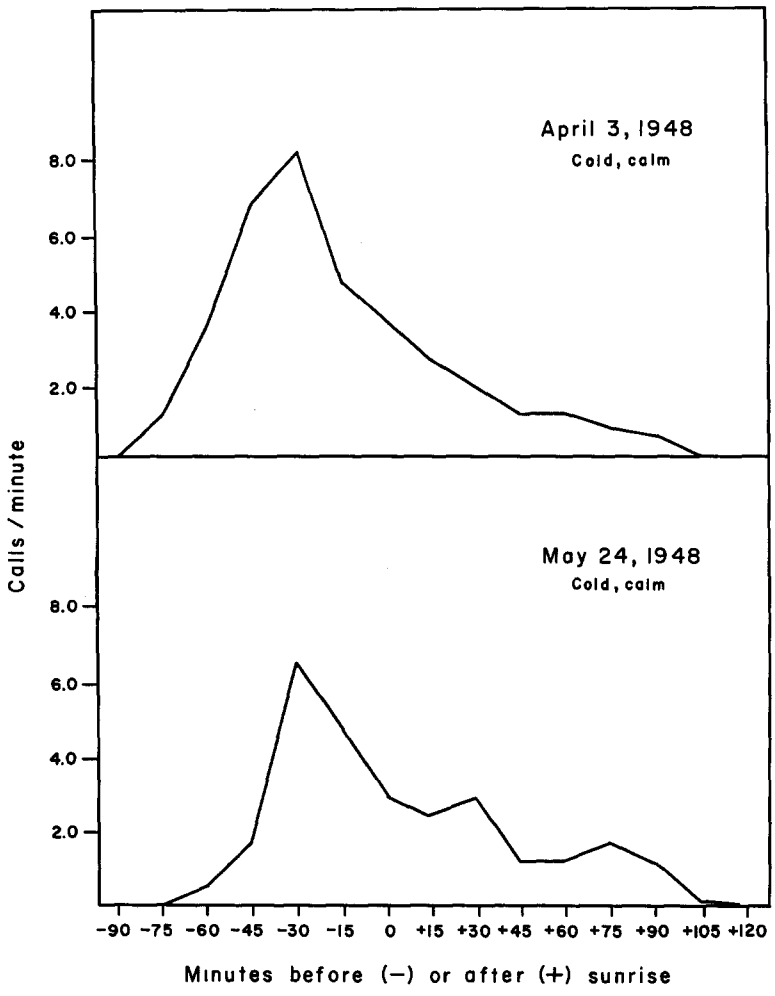

Fig. 5. Variation in rate of crowing in Ring-necked Pheasant per 15-minute period. Data collected from single point on all pheasants within hearing.

Unfortunately, we have no observations during the pair-formation period. The five unmated males were driven out of the study area soon after release, so all remaining birds were paired. But because of the persistence of calling by mated males, we felt the prime function of the rally call was to space the birds. At dawn and dusk the rally call serves as a generalized deterrent, perhaps with epideictic function (Wynne-Edwards, 1962:16), to regulate overall population density. Bursts of calling throughout the day more usually resulted from contact between two or more individual males and served to space adjacent pairs.

We may compare the pattern of calling in chukars with that recorded for the Ring-necked Pheasant by Taber (1949). The two curves in figure 5 show typical changes in calling in pheasants throughout two mornings, averaged by 15-minute periods as in our study. The changes in rate of calling in pheasants follow a far more uniform pat-

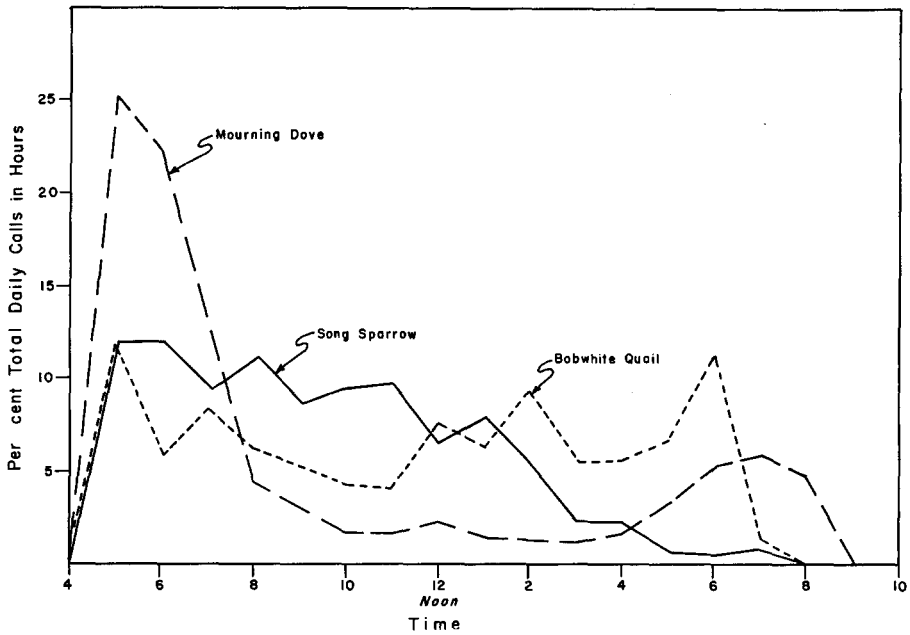

Fig. 6. The diurnal distribution of calling in three species of birds. The records for the Song Sparrow and Bobwhite Quail are for individual birds only.

tern than in chukars. The curves suggest that calling is under far greater influence of physical factors (as well as some internally controlled rhythm of calling) than in chukars. Our own observations indicate that calling in pheasants has little or no relation to aggressive encounters between pheasants either during or after fighting, as is true for chukars. Pheasant crowing may be essentially sexual in function, serving to attract and maintain a harem. Calling to repel other males may be a much less important function than in chukars, hence is little affected when there is aggressive contact between adjacent males.

Comparison of Diurnal Calling With Other Species

Considerable attention has been paid to the periods of onset and termination of bird song in the morning and evening (Leopold and Eynon, 1961). Most diurnal birds begin singing at dawn and gradually decrease their frequency around noon. Singing often increases again in the evening and continues until dark. But there are many exceptions to this pattern (Bourke, 1947; Davis, 1958; Rollin, 1958). In virtually all diurnal species, rate of calling rises to a sudden peak for the day in the first hour of calling. A prominent exception is the delay in calling by chukars when in coveys.

In a single day's record of one Song Sparrow made by Nice (1943:122), calling diminished gradually and steadily from its peak at dawn and showed no secondary peak at dusk (fig. 6). The Mourning Dove comes closest to the usual concept of bird song with great concentration of song at dawn, little calling during midday, and a smaller peak at dusk (McClure, 1939). Stoddard (1931:99) recorded total whistling of a single Bobwhite for one day and found peaks at both dawn and dusk but persist-

ent whistling throughout the day. He felt this sample of a single bird was typical for the species. Bennitt (1951) in Missouri observed the rate of whistling to drop to about half of the dawn peak in the three hours following sunrise. Kabat and Thompson (1963:115) reported whistling to fall to less than a fourth of the peak calling rate. It seems probable that the latter two studies are more representative of calling by Bobwhites in the wild than is Stoddard's. However, we lack records of calling at a single location throughout the day.

We have found no other complete records for other galliform birds. However, for pheasants, several observers have reported crowing to be at its peak at dawn with a steady decline thereafter (fig. 5).

The shift in distribution of calling that we have observed in chukars as the season advanced has also been observed in both Ring-necked Pheasants and Wild Turkeys (*Meleagris gallopavo*). Taber (1949) was able to observe the behavior of pheasants while at the same time recording crowing behavior. In late March and April, the cocks remained on their territories steadfastly. In May, however, they left their territories shortly after sunrise to feed on a common feeding ground at which time a second peak of calling occurred. A third but smaller peak came as the cocks left the feeding grounds (fig. 5). It seems likely that the second and third peaks occurred as cocks were crossing the territories of other males on the way to and from the feeding grounds. At the same time the peak of calling changed from about 40 minutes before sunrise in late March–April to only 10 minutes before sunrise in late May. A. S. Leopold observed a similar shift in the peak of gobbling by Wild Turkeys as the season advanced (Taber, *op. cit.*).

We had begun our study with the idea that we might use rates of rally calling as an accurate index of chukar numbers. If most daily variations could be attributed to changes in physical factors, it would be possible to apply correction factors and determine what calling would have been under optimum physical conditions. McClure (1939) attempted just such a correction for the Mourning Dove. However, our statistical analysis showed that variations in calling that resulted from temperature, light intensity, and wind accounted for only about half the variation in calling between days. It seems likely that interaction between birds accounts for most of the remaining variation. Since interactions between birds are not continuous variables such as light intensity, wind, and temperature, it is difficult to apply a correction factor for them. The rapid fluctuation of calling in successive 15-minute periods means that a brief count of calls at a particular place could be far from representative of the actual number of birds present. Additional variation due to suppression of calling by avian predators would be difficult to detect during the course of short-term census periods. Therefore, we conclude that yearly comparisons of density between areas must rely on repeated counts on the same areas to minimize these variations that cannot be corrected.

SUMMARY

Rally calling by the Chukar Partridge (*Alectoris chukar*) was studied from February through July, under both penned and natural conditions. The purpose was to measure the effects of physical and biotic factors on rates of rally calling. Calling was most frequent around sunrise and sunset with little calling in between. The morning peak of calling was delayed about two hours after the birds had formed into coveys in late May. Of the physical factors, light intensity and precipitation had the greatest effect on calling. The four factors of light intensity, temperature, wind, and rain ac-

counted for 45 per cent of the variation in morning calling and 54 per cent of the variation in evening calling. The presence of raptors strongly inhibited calling. Aggressive encounters beween males strongly stimulated calling and accounted for the great up-and-down fluctuations in calling during the day. In captivity females called more than males, but in the wild females seldom called when paired. Dominant males called more frequently than subordinate ones.

The function of the rally call was primarily to space males rather than to attract a mate, contributing to the much greater variability in calling rate of the chukar compared to that of the pheasant. Retardation of peak calling rates with advancing season occurs in chukars and other galliform birds. It reflects changes in time and degree of mobility.

Social interaction between males had a great influence on calling, yet was highly unpredictable. For this reason the use of the rally call as an index of chukar numbers is dependent on large samples.

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